



Biophysical Habitat Features Explain Colonization and Size Distribution of Introduced Trochus (Gastropoda)

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The tegulid gastropod, *Rochia nilotica* is harvested in small-scale fisheries throughout Southeast Asia and the Pacific Islands, many of which were created from inter-country translocations. This species is found on structurally complex shallow reefs, but its specific habitat requirements have not yet been quantified in order to maximize the success of future translocations and help future-proof the fishery in changing ocean conditions. At 28 sites around Samoa, where the species was introduced in the early 2000s, we measured a suite of habitat variables along transects in which *R. nilotica* were counted and the shell sizes measured in a parallel study. Boosted regression tree analyses revealed that *R. nilotica* were most abundant at reef locations that were shallow, with fairly consistent depth, had high coverage of branching coral, low cover of erect macroalgae, low wave exposure and high surface complexity. Smaller individuals were associated with wide reef flats and high cover of branching coral, whereas larger animals occurred in deeper water with high surface complexity. Multivariate analyses showed this species to be a habitat generalist, sharing much of its niche with an endemic herbivorous gastropod, *Tectus pyramis*. Future stocking programs should focus on sites with habitats optimal for both adults and juveniles. *R. nilotica* populations are likely to be especially affected by broadscale stressors that result in declines in live coral cover and substratum complexity and increasing coverage of macroalgae on coral reefs.

Keywords: habitat association, invertebrate, fishery, climate change, coral reef, species translocation, *Rochia nilotica*

INTRODUCTION

Coral reefs are naturally highly complex and provide habitat for a diverse suite of marine species (Spalding et al., 2001; Hoegh-Guldberg et al., 2007). Important habitat characteristics may include: substratum type, cover of benthic biota, reef surface complexity, wave exposure, and depth (McCormick, 1994; Graham and Nash, 2013; Komyakova et al., 2013). These habitat features are likely to influence key ecological processes such as recruitment, competition, foraging and predation (Luckhurst and Luckhurst, 1978; McCormick, 1994; Graham and Nash, 2013). In order to understand population patterns, we therefore require a clear understanding of the habitat requirements of animals in relation to potential biophysical factors. Such knowledge can reveal habitat traits driving distributional patterns of marine invertebrates and, importantly, enhance the success of stock restoration projects by identifying optimal deployment locations (Bell et al., 2005).

Coral reefs are increasingly under threat from global climate change through rises in sea temperature, ocean acidification, coral bleaching, and an increased frequency and severity of storm events (Hoegh-Guldberg et al., 2007; Ham, 2018; Hughes et al., 2018). These stressors and other disturbances such as coral-eating starfish, fishing pressure, and pollution threaten coral reefs through the reduction in reef surface complexity, loss of live coral cover, and phase-shifts to macroalgal dominated systems (Hoegh-Guldberg et al., 2007; Fabricius et al., 2013; Hughes et al., 2018). Changes in coral-reef habitats can have serious consequences for substrate-dependent species, including altering distribution patterns and species interactions, often leading to reductions in population abundance (Przeslawski et al., 2008; Bozec et al., 2015; Hughes et al., 2018).

Subsistence and commercial fisheries often form the primary basis for economic development, food security, and coastal livelihoods in Pacific Islands (Wright and Hill, 1993; Bell et al., 2013; Gillett and Tauati, 2018). The most socio-economically important invertebrate resources are sea cucumbers, giant clams, lobsters, octopus, and gastropods (Gillett and Tauati, 2018). In efforts to maintain or enhance stocks, certain invertebrates have been translocated to reefs throughout the Pacific Islands (Bell et al., 2005). Broodstock of two marine snails, *Rochia nilotica* (trochus) and *Turbo marmoratus* (green snail) have been translocated on numerous occasions to localities beyond their natural distributions, with the intention of creating new populations of self-replenishing stocks (Purcell and Cheng, 2010; Gillett and Tauati, 2018). Considerable research effort is usually required to maximize the success and cost-effectiveness of such programs, often necessitating lengthy studies of optimal conditions (Bell et al., 2005). However, for many fisheries, including for *R. nilotica*, these conditions are often poorly defined.

The herbivorous gastropod, *R. nilotica* (formerly *Trochus niloticus*, then *Tectus niloticus*) (WoRMS, 2020) is one of the largest members of the order Trochida, with a basal shell width (BSW) of up to 150 mm (Smith, 1987; Nash, 1993; **Figure 1**). *R. nilotica* grows at an estimate of 25 mm per year in the first 3 years and 15 mm per year thereafter (Heslinga, 1981; Smith, 1987). *R. nilotica* reach sexual maturity between 50 and 90 mm BSW and can live up to 10–15 years (Nash, 1993).

R. nilotica is found on coral reefs with suitable habitat for all life-history stages (Pakoa et al., 2010; Dumas et al., 2017). The larval phase is characteristically short (3–7 days) and larvae are believed to settle close to natal sites (Smith, 1987; Lee et al., 2001). The juveniles tend to be found mostly on intertidal reef flats with high cover of consolidated coral rubble and turfing algae and high reef surface complexity (Castell, 1997; Colquhoun, 2001; Crowe et al., 2002). Adults tend to inhabit consolidated, rocky forereef zones (Long et al., 1993; Purcell et al., 2009; Dumas et al., 2013), typically in depths shallower than 10 m (Nash, 1993; Rees et al., 2003). Optimal habitat features for adults are believed to be a high percentage of coral cover, low sand cover, abundant turfing algae, and a complex reef surface, although habitat associations are spatially variable (Colquhoun, 2001; Purcell et al., 2009; Ceccarelli et al., 2011).

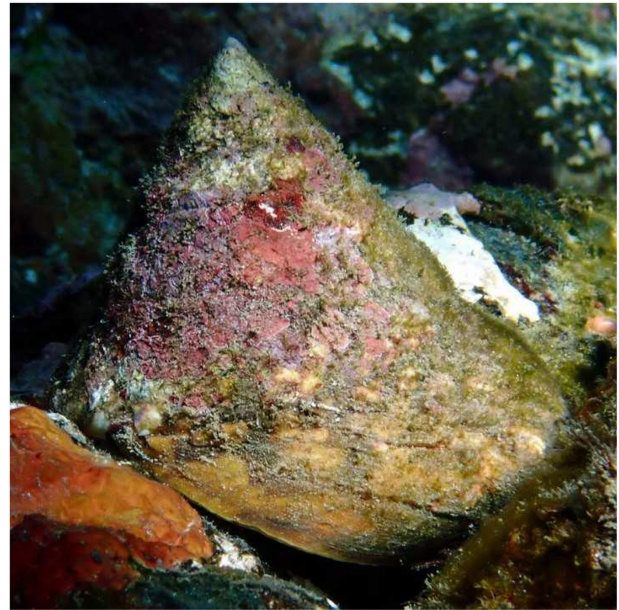


FIGURE 1 | *Rochia nilotica* on the reef in Samoa (illustrated specimen ~90 mm BSW) (Photo: Steven Purcell).

Rochia nilotica is a non-selective herbivore, feeding on turfing, and encrusting algae (Nash, 1993). Potential competitors for food resources could include *Trochus maculatus*, *Tectus pyramis*, *Turbo chrysostomus*, and *Turbo argyrostomus* (Gosliner et al., 1996; Tiitii and Aiafi, 2016). The native *T. pyramis* is harvested by subsistence fishers in Samoa and fishing pressure has previously led to diminished stocks (Taule'alo, 1993).

With an aim to enhance resources for subsistence fishers, *R. nilotica* was first introduced to a far-eastern site in Samoa in 1990 (Gillett, 1993; Lober et al., 2003). A total 118 individuals were translocated to Samoa from Fiji and an unknown number translocated from Tonga, however, F₁ populations were not established (Gillett, 1993; Tiitii and Aiafi, 2016). Broodstock were further introduced from Vanuatu and Fiji in 2003 and 2004, where ~360 individuals were distributed at three sites across two operations (Lober et al., 2003; Tiitii and Aiafi, 2016). In 2004, 500 locally cultured juveniles were stocked at additional sites (Lober et al., 2003; Tiitii and Aiafi, 2016). These stocking events led to populations being established around both of the main islands, Upolu and Savai'i (Tiitii and Aiafi, 2016). Socioeconomic surveys of fishers in 2018 suggested that the populations became well established only in the past 4–10 years, depending on the location (Purcell et al., unpublished data).

The primary aim of this study was to determine the associations of *R. nilotica* densities and shell sizes with a range of biophysical habitat features. To ensure our surveys found *R. nilotica* within ample abundances for future analysis, we aimed to assess the most suitable habitat reported in the primary literature. Such data can inform decisions about the best sites for future stocking in the Indo-Pacific and aid in forecasting future shifts in fisheries productivity and ecosystem services of

this important species in rapidly changing oceans. A previous study by Dumas et al. (2013) investigated “the influence of small-scale (10^1 m) habitat structure” and the related distribution of *R. nilotica* and examined sediment type and substratum coverage. Dumas et al. (2017) similarly examined associations of *R. nilotica* with sediment type and substratum coverage. We make significant advances on that approach by examining larger-scale habitat variables and incorporating physical variables (wave exposure, reef width from shore, reef topography, substratum complexity), leading to a more comprehensive evaluation of habitat associations to guide future stocking of this key species. Our broad sampling scale (28 sites across 350 km of coastline in Samoa) permits inferences to a broad range of reef types and conditions which, together with our modeling approach using boosted regression trees (BRTs), offers a template for future research on habitat associations of other marine taxa.

Our secondary objective was to provide insights into the partial niche breadth of *R. nilotica* and identify potential niche overlap with other common, herbivorous gastropods. Such information forms a basis for debate about the potential ecological consequences of translocations. Reefs on the northern coast of Upolu island in Samoa have also been partly degraded by pollution, sedimentation and nutrient inputs (Ziegler et al., 2018). Across many reef sites in Samoa, the coverage of live coral has declined recently, attributed to coral bleaching events associated with thermal stress from climate change, crown-of-thorns starfish, and cyclones (Samuelu and Sapatu, 2009; Ziegler et al., 2018). We discuss our findings about habitat relationships of *R. nilotica* in the context of impacts of such major stressors on reef habitats. The approach we use to examine habitat associations to infer about vulnerability of this species to changing habitats is widely used throughout other studies. This study has broad significance, not just for *R. nilotica* as an important resource in Samoa and throughout the Pacific, but also as it may provide insights into considerations about habitats for stock restoration and enhancement of other marine invertebrates.

MATERIALS AND METHODS

Study Site

Samoa is an island country in the central Pacific, between latitudes 13°S and 14°S and longitudes 171°W and 173°W (BOM and CSIRO, 2011). Samoa's volcanic geology provides coastlines of old lava flows which support $>10,000\text{ km}^2$ of narrow fringing coral reef (Taule'alo, 1993; MNRE, 2013). The reefs are mostly characterized by shallow lagoon and patch reef extending out to the high energy reef crest and steep reef slope (MAF, 1997; Spalding et al., 2001), however, specific geospatial data on reef types across the Samoan coastline were unavailable.

Coral bleaching, tropical storms, cyclones, and flooding have led to recent loss of live coral across reefs in Samoa (MNRE, 2010, 2013; Ziegler et al., 2018). Indeed, many reefs are currently dominated by algal-covered dead coral, indicating relatively recent coral mortality, some of which may be related to mass bleaching events between 2014 and 2017 (Berthe et al., 2016; Ziegler et al., 2018). While coral cover in Samoa was moderately

high in the early 2000s (Samuelu and Sapatu, 2009; MNRE, 2010) cover has now declined to $<1\%$ on some reefs (Berthe et al., 2016; Ziegler et al., 2018).

Study Design

Habitat assessments were conducted concurrently with a broader population assessment (Purcell and Ceccarelli, unpublished data). Underwater visual censuses and habitat surveys were conducted at 28 coral reef sites surrounding the two main islands (Upolu and Savai'i, **Figure 2**) from January to March 2018. The sites were chosen on the boat, before entering the water to conduct surveys, in a haphazard fashion in order to avoid surveyor bias and to enable a broad range of reef sites to be surveyed. Each site extended 200–300 m across the reef front with sites spaced at least 5 km apart. Habitat assessments were conducted on independent (>10 m apart), replicated ($n = 4-8$), 50×2 m transects, positioned haphazardly on the reef crest and reef slope at depths between 1 and 10 m. A total of 155 transects across 28 sites were surveyed, with 81 transects on Upolu and 74 on Savai'i. Transects shallower than 5 m were surveyed on snorkel and deeper transects were surveyed using SCUBA. Apart from the site of Lano on Savai'i, which was on the reef flat behind the crest due to reasons of field safety, the other sites were situated on the reef crest and upper reef slope habitats. This habitat has been shown to be the most important, by far, for populations of *R. nilotica* in Samoa and elsewhere in the Pacific (Purcell et al., 2009; Tiitii and Aiafi, 2016), and so was the focus of the population assessment. This strategy to focus on reef fronts maximized the chance of finding *R. nilotica* at sites, if they existed there. The reef sites covered a wide range of conditions, including orientation to predominant winds, varying extent of wave exposure, and distance from shore. Our data collected along transects also show that the sites covered a broad spectrum of habitat conditions including depth, coral cover, substratum complexity, and transect-scale topography. Hence, while being focused on reef front habitats, the array of site features and habitat conditions offers a broad capacity for extrapolating the results beyond these sites.

Population Assessments

All *R. nilotica* found during our field searches were counted; this involved carefully inspecting under ledges, in holes and crevices. The maximum BSW of the first 16 individuals was measured to the nearest mm *in situ*, which provided ample replication for calculating average shell sizes and satisfied time constraints. To assess the potential niche overlap with other common gastropods, the number of *T. maculatus*, *T. pyramis*, *T. chrysostomus*, and *T. argyrostomus* were also counted on each transect. The latter two were pooled due to low replication and to overcome difficulty in identification in the field.

Habitat Assessments

Habitat assessments involved measuring reef surface complexity, benthic cover, depth, topographic complexity, densities of *Echinostrephus* sp. (a small boring sea urchin), reef distance from shore, and site exposure. Reef surface complexity was measured using the “chain and tape” method at three predetermined

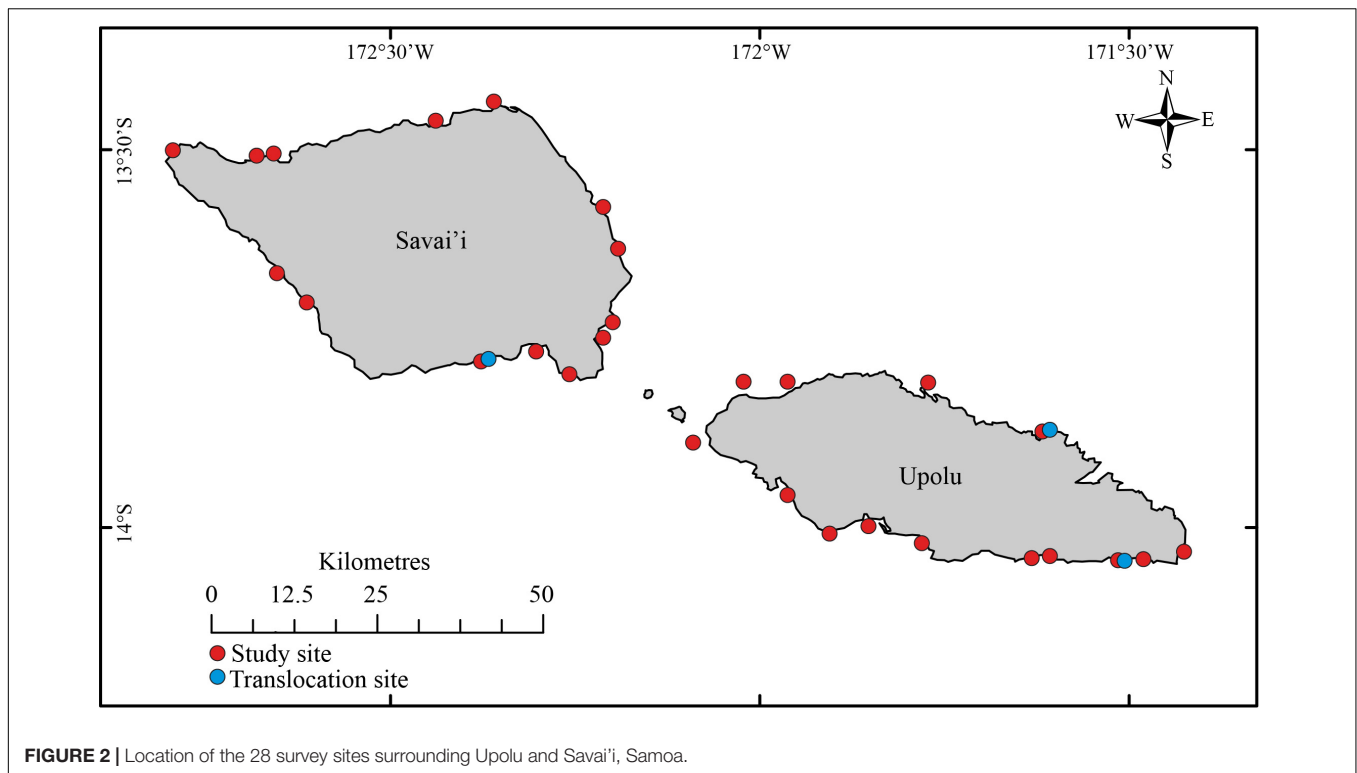


FIGURE 2 | Location of the 28 survey sites surrounding Upolu and Savai'i, Samoa.

random points on each transect and averaged to provide an index of rugosity (Luckhurst and Luckhurst, 1978).

$$\text{Rugosity} = \frac{\text{Surface contour distance}}{\text{linear distance}}$$

Coral Point Count with Excel extensions (CPCe) (Kohler and Gill, 2006) software was used to quantify the cover of benthic organisms and substratum types from eight randomly allocated replicate photographs taken at a fixed distance from the substrate (0.7 m) with a 0.57-m² (92 cm × 62 cm) field-of-view. A total of 1240 photos was imported into CPCe and the software overlaid each photo with 20 randomly distributed points. Habitat underlying each point was allocated to one of the following categories: turf algae, crustose coralline algae, unconsolidated benthos, consolidated benthos, macroalgae, invertebrates, dead coral, other coral, encrusting coral, branching coral, and plate coral (Table 1). The number of *Echinostrephus* sp. on each photo was counted and averaged to provide a density across each transect.

Depth was measured using a digital depth gauge at eight predetermined random points and at the start and end of each transect. Tidal records were obtained using *WS Tides* software and depth measurements were corrected to zero tidal datum. Topographic complexity was obtained by calculating the standard deviation of the depth measurements on each transect as a summary metric of reef topography at the transect scale. The distance from the shore to the reef crest (reef distance) was determined as the average of measurements from three points on each transect using Google Earth. Exposure to high energy over the reef crest was assessed at each site using a rank system defined

by the sites' physical surrounding, wave exposure, surge potential, and orientation to dominant winds and currents (Table 2). Five Samoan fishery officers independently scored each site, assigning an exposure rank between 1 and 5, and an average rank score was calculated across officers for each site.

Statistical Analyses

The strength of the association between each environmental variable and the density and size of *R. nilotica* was estimated via boosted regression tree (BRT) analyses (De'ath, 2007; Elith et al., 2008; Ridgeway, 2018). Analyses of size relationships used the average size of *R. nilotica* on each transect and excluded transects lacking *R. nilotica*. Each BRT was run against a Gaussian distribution and included 1000 trees with an interaction depth of 4, bag ratio of 0.5 and shrinkage of 0.01. Overfitting was controlled with the use of three cross-validation folds (Ridgeway, 2018). The relative influence of each covariate was estimated as the proportion of all tree splits involving the focal covariate. The relative influence associated with a covariate was considered substantial if it exceeded 100/*p* where *p* is the number of covariates. Partial dependency plots, in which predictions were plotted against single covariates, were used to explore the nature of associations. All partial dependencies were considered non-monotonic and there were no correlations between predictor variables. Ninety-five percent confidence intervals on partial effects and relative influences were provided by bootstrapping the BRTs 100 times (each with a random subset of the original data). All BRTs were performed using the gbr package in R (Ridgeway, 2018).

TABLE 1 | Benthic classification categories for photo analysis.

Category	Sub-category	Description
Consolidated benthos	Sand	Fine grain substrate, granules <2 mm
	Gravel	Grainy substrate, granules 2–10 mm
	Cobble	Small to medium rocks, 10–255 mm diameter
Unconsolidated benthos	Rubble	Unconsolidated coral, no corallite structures, <10 cm
	Rock	Consolidated bedrock
Turf Algae	Boulder	Large rocks, >255 mm
	–	Fine algal turf, growth in patches on hard substrata
Crustose coralline algae	–	Pink, purple, maroon or red. Brittle, flattened crust
Macroalgae	Erect	Vertical growth, canopy forming or sheet like
	Calcareous	Jointed or segmented calcifying algae
	Laminate	Low profile, lobed or plate like
Invertebrates	Zoanthid	Colonial anemones, form a basal mat, often cylindrical
	Sponge	Erect, massive and cup-like forms
	Ascidian	Colonial and solitary forms
	Anemone	Fleshy base, ring of tentacles around a central mouth
Dead coral	Echinoderm	Astroidea, Echinoidea and Holothuroidea
	–	Dead colony, recognizable corallite structures
Other coral	Soft coral	Low tabular mounds, digitate or ridged surfaces
	Massive	Ball or boulder shaped, fairly symmetrical
	Sub-massive	Massive forms with protrusions, knobs or wedges
	Staghorn	Cylindrical branches up to 2 m long
	Solitary	Free living, disc-like shape
Encrusting coral	–	Flat, thin, horizontal growth adhering to substrate
Branching coral	Branching	Secondary projections on branches
	Digitate	Small branches without secondary projections
Plate coral	Tabulate	Flat, table structures of fused branches
	Foliose	Broad, flattened growth, smooth plate or whorls

To compare partial niches among the target species, differences in their associations with habitat and environmental variables were explored using analysis of similarity (ANOSIM) and similarity percentage (SIMPER) routines in PRIMER v7 using the density of each species (Clarke and Gorley, 2015). Square-root and log transformations of the environmental variables were conducted to improve normality where appropriate. The transformed dataset was standardized, and a resemblance matrix was formulated based on Bray–Curtis similarities. ANOSIM was performed using a one-way unordered design and Spearman rank correlation. SIMPER was performed on the Bray–Curtis resemblance matrix

TABLE 2 | Site exposure rank system.

Rank	Exposure	Description
1	Sheltered	Leeward orientation
		Sea state is mostly calm
		Site may be in a semi enclosed bay
2	Mostly sheltered	Rarely (1–4 times a month) experiences large waves on the reef crest
		Leeward orientation
		Sea state is mostly smooth with small ripples and small waves
3	Semi sheltered	Swell is mostly small (less than 1 m)
		Seldom (1–2 days a week) experiences large waves on the reef crest
		Sea state is mostly rippling with small waves
4	Mostly exposed	Protected features in the reef may provide bays or channels
		Swell is mostly moderate (1–2 m)
		Sometimes (3–4 days a week) experiences large waves on the reef crest
5	Exposed	Windward orientation
		Sea state is often choppy with moderate waves
		Swell is often high (2–3 m)
5	Exposed	Relatively often (5–6 days a week) experiences large waves on the reef crest
		Windward orientation
		Sea state is mostly choppy, often with whitecaps and large waves
5	Exposed	Site may be with little protection, on a point or isolated from landmass
		Often, almost always experiences large waves on the reef crest

of predictor variables using a one-way design and 50% similarity cut-off.

RESULTS

Habitat Characteristics

Habitat variables differed considerably among sites, allowing for relationships with *R. nilotica* to be examined over a broad spectrum of conditions (**Supplementary Table 1**). The average depth of the reef across our sites was 3.3 ± 2.2 m, within a range of 0.3–11.4 m. The topographic complexity (i.e., the variability of depth at the transect scale) ranged from 0.1 to 2.6 m and was on average 0.6 ± 0.3 m. The variability in topographic complexity reflects some reefs with prominent spur and groove formations, however, we found that most of the reefs had fairly consistent depths across the reef front. Reefs were comprised of consolidated dead coral and rocky pavement forming a matrix of holes, crevasses, and ledges, the reef surfaces were typically complex with an average rugosity of 1.5 ± 0.8 . The reef distance, a measure of the lagoon and reef flat between the shore and reef crest was highly variable, ranging from 0.1 to 2.2 km. Reef crests were considerably exposed with an average rank of 3 across all sites. Site exposure ranged from sheltered sites in a bay to fully exposed sites such as those across steep rocky

shores exposed to dominant winds and swells. Turfing algae and crustose coralline algae dominated benthic cover with average values of $29 \pm 12\%$ and $39 \pm 16\%$, respectively. The cover of algae was highly variable, ranging from 6–60% for turf algae and 0–80% for crustose coralline algae. The cover of live coral was generally low ranging from 0–46% and averaging $11 \pm 10\%$, with only 5 out of 28 sites having average live coral cover over 20%. The dominant growth forms of live coral were encrusting and branching coral.

***R. nilotica* Density**

In the transects examined in this study, a total of 433 *R. nilotica* were found on 64 out of the 155 transects at 18 of the 28 sites. The BRT modeling found that the best predictors for high densities of *R. nilotica* were shallow depths (0–1.5 m), high coverage of branching coral (>10%), low transect-scale topographic complexity (standard deviation in depth along transects <0.3), low site exposure, high reef surface complexity (surface contour distance > 1.5 times greater than linear distance) and low cover of erect macroalgae (<3%) (Figure 3).

***R. nilotica* Size Distributions**

Shell diameter of the 295 *R. nilotica* found along transects averaged 87 ± 19 mm; range: 35–136 mm. The BRT model suggests that *R. nilotica* shells were larger in places with greater depth (>2.5 m) and where the coverage of other sessile invertebrates was high (>4%) and, to a lesser extent, where the reef surface was reasonably complex (Figure 4). The modeling also indicates that smaller *R. nilotica* were found at shallow depths (0–2.5 m), and where the reef flat was wider than ~1 km between shore and the reef crest, where there was at least ~8% coverage of branching coral and reasonable (>1.5) surface complexity (Figure 4).

Niche Breadth and Overlap

We found a total of 69 *T. maculatus* on 42 transects, 25 *T. pyramis* on 20 transects and 16 *T. chrysostomus*/*T. argyrostomus* on 14 transects. There was a significant segregation in habitat niche among the studied species (ANOSIM: $R = 0.03$, $p = 0.003$). ANOSIM revealed that *R. nilotica* share some of the same habitat as the native *T. pyramis* but occupy different habitat to *T. maculatus* and *T. chrysostomus*/*T. argyrostomus* (Table 3).

Each gastropod species had a wide niche, displaying generalist habitat requirements (Table 4). The SIMPER routine found that site exposure was a key variable affecting the density of all studied species and depth was important for three species (including *R. nilotica*) (Table 4). The topshell gastropods (Trochida) were strongly associated with reef areas that had a high degree of rugosity (fine-scale substratum complexity), but not the *Turbo* species, whilst larger-scale topographic complexity (at the transect scale) was important for all species other than *R. nilotica*. Densities of *R. nilotica* were greatest at sites where the reef crest was far from shore, allowing for an extensive reef flat habitat, but this habitat feature did not appear to be associated closely with any other studied species.

DISCUSSION

The present study provides a comprehensive approach to examining the relationships between benthic reef invertebrates and a range of biophysical habitat features. This study revealed the strong influence of physical habitat variables not assessed in previous studies, such as depth, site exposure, reef distance, and substratum complexity. We also demonstrate that physical habitat variables need to be measured and analyzed alongside traditional measures of substratum coverage of benthic biota in order to provide a complete evaluation of habitat associations relevant to site selection for future stocking programs. While previous studies have provided assessments of densities and sizes of *R. nilotica* across different reef types, they have not directly linked populations with specific habitat features (Smith, 1987; Dolorosa et al., 2010; Pakoa et al., 2010). Other studies have assessed *R. nilotica* habitats using multivariate analyses of sediment type and substratum coverage variables (Dumas et al., 2013, 2017). We demonstrate the advantage of a multivariate approach to view multiple possible predictor variables within the analysis. These analyses provide a sophisticated approach to visualize the relative influence of each predictor variable, whilst holding all other variables constant in their influence. Our framework of measuring both biological and physical features of sites and analysis with BRTs offers a useful template for future studies of habitat associations of other marine taxa.

The most influential habitat features in this study pertained to reef configuration, physical forces, and fine-scale substratum structure at the site. *R. nilotica* displayed characteristics of a generalist species, it is therefore not surprising that there has been so much success in translocating *R. nilotica* throughout the Pacific despite reef habitat features varying from one country to another. The clear associations among biophysical variables and the densities and sizes of *R. nilotica* provides further insight into the reasons for the relative success of introductions and guidelines for stock-enhancement programs. Nevertheless, we found that *R. nilotica* lives most abundantly at reef sites with features predicted to be strongly modified by climate change and other stressors. Our study identifies key habitat features for future stocking programs yet paints an uncertain future for productive *R. nilotica* fisheries due to declines of reef-building corals on tropical reefs.

Habitat Associations

Among the focal species (*R. nilotica*) and the other three recorded species, the prevalent association of depth, surface complexity, site exposure, and coral cover indicates that these can be influential characteristics driving the distributions of herbivorous gastropods on coral reefs. Highest densities of *R. nilotica* should be expected on shallow reefs with a relatively consistent depth across the reef front and complex surface habitat, corroborating earlier speculation in the literature (Smith, 1987; Rees et al., 2003; Purcell et al., 2009; Dolorosa et al., 2010). *R. nilotica* have previously been found to inhabit the higher-energy reef crest in their highest abundance with declining numbers onto the outer reef slope into deeper waters (Ceccarelli et al., 2011). The present study found an apparent gradation in the

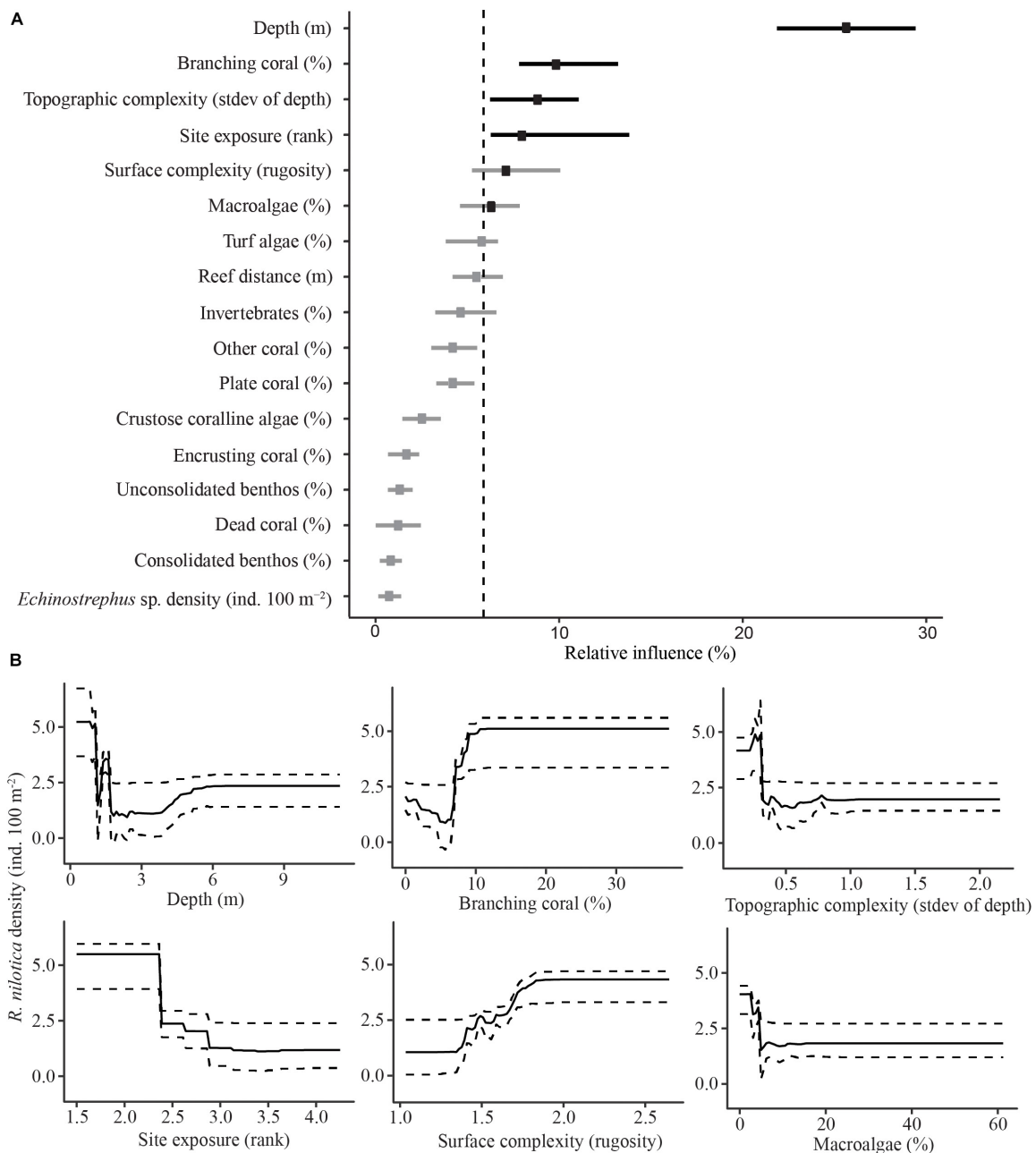


FIGURE 3 | Boosted Regression Tree relative influence plot for predictor variables of *R. nilotica* density **(A)**. Dots represent means for each predictor variable and bars represent upper and lower 95% quantiles. The vertical dashed line represents the significance threshold (100/17), variables exceeding the threshold are in black and those that do not are gray. Partial effects for significant predictor variables against *R. nilotica* density **(B)**. Solid lines represent means for each predictor variable and dashed lines represent upper and lower 95% quantiles.

distribution of different-sized individuals, with smaller animals having higher abundance in shallow depths, especially on the reef crest. Larger individuals were more commonly found in deeper waters on the outer reef slope, which supports the long-held hypothesis of ontogenetic migration to deeper waters (Nash, 1993; Castell, 1997).

The topshells were positively associated with reef surface complexity and this may be owing to their cryptic nature of

requiring physical refugia (Gosliner et al., 1996; Dolorosa et al., 2010; Soekendarsi, 2018). The surface structural complexity of the reef is considered as an important factor dictating the distribution of marine invertebrates including *R. nilotica* (Ceccarelli et al., 2011; Dumas et al., 2013; Fabricius et al., 2013). The most suitable habitat for promoting high densities of *R. nilotica* are those with a high degree of structural complexity. High structural complexity provides holes and crevices within the reef in which individuals

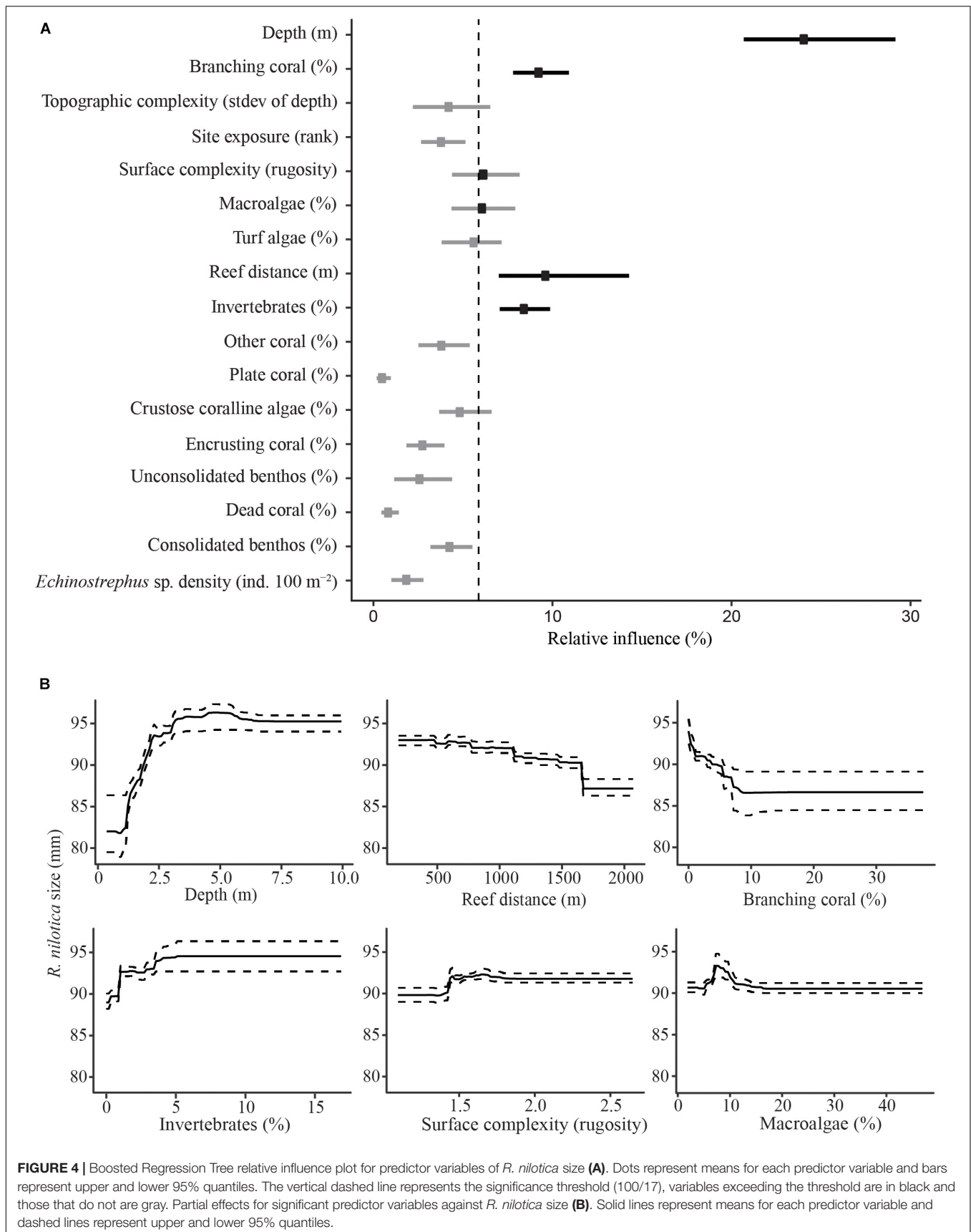


TABLE 3 | Analysis of Similarity test (ANOSIM), pairwise *R* values and statistical significance levels for habitat variables relating to the density of different gastropod species.

	<i>T. maculatus</i>	<i>T. pyramis</i>	<i>T. chrysostomus/T. argyrostomus</i>
<i>R. nilotica</i>	0.038*	−0.001 ^{ns}	0.083**
<i>T. maculatus</i>	–	0.037 ^{ns}	−0.046 ^{ns}
<i>T. pyramis</i>	–	–	0.113*

ns, not significant; **P* < 0.05; ***P* < 0.01.

TABLE 4 | Similarity percentage routine (SIMPER) on the habitat variables relating to the density of each gastropod species, displaying the key habitat variables that altogether contributed at least 50% to habitat similarity among replicates within each species.

Species	Group similarity (%)	Key variable	Similarity contribution (%)
<i>R. nilotica</i>	61	Surface complexity	9.1
		Site exposure	8.7
		Reef distance	8.7
		Crustose coralline algae	8.6
		Macroalgae	7.8
		Depth	7.7
<i>T. maculatus</i>	61	Site exposure	9.5
		Invertebrates	8.3
		Topographic complexity	8.2
		Macroalgae	8.2
		Surface complexity	8.2
		Encrusting coral	8.1
<i>T. pyramis</i>	65	Unconsolidated benthos	10.4
		Depth	9.4
		Turf algae	9.0
		Topographic complexity	8.4
		Surface complexity	8.3
		Site exposure	8.2
<i>T. chrysostomus / T. argyrostomus</i>	64	Invertebrates	10.8
		Topographic complexity	9.1
		<i>Echinostrephus</i> sp. density	9.0
		Site exposure	8.7
		Depth	7.5
		Crustose coralline algae	7.3

can seek refuge from predation (Komyakova et al., 2013; Bozec et al., 2015; Dumas et al., 2017).

We posit that the narrow fringing reef sites in Samoa might have sparse densities of *R. nilotica* because they have high wave exposure and lack an extensive reef flat

habitat (MAF, 1997; Spalding et al., 2001). In this study, *R. nilotica* were typically found at sites with moderate-low wave exposure, however, this notion is contested throughout the literature, with dense populations found at wave-exposed sites in some cases (Rees et al., 2003; Pakoa et al., 2010) but not others (Smith, 1987). Our study suggests that the optimal habitat for *R. nilotica* are those with a moderate degree of wave exposure. The incongruence with our findings might be attributable to different measures of exposure among studies, leading to differing interpretation of results.

The present analyses predict that *R. nilotica* populations establish better on reefs at greater distance from shore (~1 km between shore and reef crest). We found that juvenile *R. nilotica* associated with extensive reef flats and the requirement of the reef flat as a nursery habitat is well documented (Nash, 1993; Castell, 1997; Purcell and Cheng, 2010). Certain sites might possess suitable reef crest and fore-reef slope habitats but lack a wide reef flat needed for settlement and development of juveniles (Nash, 1993; Castell, 1997), such as across the south-eastern coastline of Savai'i in Samoa. The most suitable reefs for *R. nilotica* populations to establish are those which possess the reef types that are optimal for both the juvenile and adult, within close proximity. This may help to explain why *R. nilotica* were sparse or absent at certain sites that otherwise have reef crests and fore-reef slopes that appear to be excellent habitat for adult populations.

Our findings are congruent with previous studies indicating that a moderate cover of live coral is influential in typifying higher densities of marine invertebrates (Pakoa et al., 2010; Dumas et al., 2013, 2017). Apparently *R. nilotica* settle and establish on healthy coral reefs, therefore the conservation values of these healthy reefs are important for the ongoing success of the fishery. This study further supports previous studies that *R. nilotica* are mostly found on coral reefs and do not favor areas with an abundance of erect macroalgae (Long et al., 1993). The cover of branching coral appears to play an important role for the size distribution of *R. nilotica*, whereby smaller individuals associated with higher cover of branching coral. Thus, we should expect to find higher abundance of smaller *R. nilotica* on reefs that have >10% cover of live branching coral. In previous studies, juvenile *R. nilotica* have been associated with rocky substrata and lagoon reefs with ample coral rubble, however, the cover of live coral in these studies was often quite low and patchy (Castell, 1997; Colquhoun, 2001; Pakoa et al., 2010). Extensive cover of branching coral may be favorable as settlement sites for protection; however, these relationships have not been widely explored for marine gastropods.

Future Invertebrate Translocations in the Indo-Pacific

There have been limited negative environmental or ecological consequences reported from previous *R. nilotica* introductions (Fao, 1992; Bell et al., 2005). Coral reefs throughout the Pacific have supported exotic invertebrate introductions and

are believed to have capacity to support a wide range of herbivorous grazers (Fao, 1992; Bell et al., 2005; Vunisea et al., 2008). Our results suggest that all four gastropod species are generalists and can occupy a wide range of habitat conditions. Within the forereef habitat zones studied here, *R. nilotica* shared similar niche requirements with *T. pyramis* and it is likely that this is due to their taxonomic and biological similarities. Dumas et al. (2013) also examined habitats of *T. pyramis* and concluded that it and *R. nilotica* “share very similar ecological niches,” although their study did not show differences in habitat occupancy of the two species. We are cautious in our interpretation of niche of the other gastropod species due to their low replication in this instance. In this study we were unable to study all potential habitats, therefore limiting our interpretations of niche breadth. Our data types and multivariate analyses have been used to examine niche breadth in a wide range of other marine species, so this is not a novel approach (Dumas et al., 2013; Purcell et al., 2014; Jankowski et al., 2015; Bennice et al., 2018), such information forms a basis for debate about the potential ecological consequences of translocations. We are also cautious about inferring any competition based on overlap in habitat associations, since it may be that food and refugia might not be limiting in many cases. Whilst *T. pyramis* numbers in this study were fairly low, previous surveys indicated that *T. pyramis* populations were fairly patchy and moderately abundant prior to *R. nilotica* introductions (Vunisea et al., 2008).

Future studies for marine invertebrate habitat should consider a multivariate approach, including a range of biophysical characteristics such as depth, availability of juvenile habitat, reef exposure, substratum complexity and substratum cover of benthic biota. Our findings offer additional guidance for future stocking efforts of *R. nilotica*, by identifying areas where translocations might be sub-optimal. Sites should have a moderate cover of live coral (>10%) and a good cover of turfing algae (>40%) to provide food supply for grazing invertebrates. The reef flat should be extensive and highly structurally complex to provide holes and crevices for gastropods to seek refuge (Colquhoun, 2001; Fabricius et al., 2013; Dumas et al., 2017). Our results strongly suggest that the failure of initial translocation at some sites is most likely related to their high wave exposure, relatively low coral cover, and low surface complexity. Two of the three initial seeding sites (to which *R. nilotica* adults were first transplanted) appear to have habitats unsuitable for fostering abundant populations of *R. nilotica* in the long term. While these sites have evidently provided suitable conditions for adults to survive and spawn, they are likely to have been sub-optimal for substantive colonization by their progeny. For fisheries, these findings infer that higher productivity can be expected where both juvenile and adult habitats are present (Smith, 1987).

Reef Degradation and Invertebrate Fisheries Productivity

At many sites around both Upolu and Savai'i islands, dead coral skeletons dominated the seascape. Few sites appear to have been spared by recent impacts of broadscale stressors and retained

a moderate cover of live hard coral (5 of 28 sites had greater than 20% live hard coral cover; **Supplementary Table 1**). The turfing and fleshy encrusting algae covering the coral skeletons has offered an abundant food supply to herbivores such as *R. nilotica*. The proliferation of this introduced topshell might be helping to maintaining top-down control over these smaller algal types, thus contributing to coral recovery (Francis et al., 2019). However, the indirect effects of coral loss on this gastropod species should be considered.

The predicted indirect impacts of climate change and other broadscale stressors on reef fishes are well reported (Roessig et al., 2004; Munday et al., 2008; Pratchett et al., 2008) but few reports provide evidence for susceptibility of reef invertebrates, many of which are vital for coastal livelihoods and food security (Przeslawski et al., 2008). The degree of climate change stressors as well as other anthropogenic threats could impact corals and, in turn, affect the habitats to which *R. nilotica* closely associate. Hard corals, especially branching and plate growth types, enhance the surface complexity of reef substrata (Alvarez-Filip et al., 2009; Graham and Nash, 2013), but with the decline of these reef builders the complexity of coral reefs is also predicted to decline (Graham et al., 2006; Fabricius et al., 2013; Bozec et al., 2015). Our results indicate that *R. nilotica* need high surface complexity to enable dense populations, implying that fisheries of this topshell are likely to be strongly affected by broadscale stressors that threaten reef-building corals.

The impacts of declining coverage of hard corals can shift benthic community dominance towards fleshy macroalgae on Indo-Pacific reefs (Diaz-Pulido et al., 2009; Graham et al., 2015), although effects might not be universal across algal types (Anthony et al., 2011; Bender-Champ et al., 2017). Our analyses illustrate that the highest densities of *R. nilotica* occurred where macroalgae cover was particularly low (<5% cover). These findings suggest that a growing prevalence of fleshy macroalgae on reefs through impacts of climate change and other broadscale stressors (Hughes et al., 2018), or coastal eutrophication, will further disfavor *R. nilotica* populations and fishery productivity.

Through the habitat associations of *R. nilotica*, this study furnishes evidence to link expected impacts of coral degradation to the productivity of invertebrate fisheries. *R. nilotica* have shown to closely associate with habitat characteristics that may be predicted to change such as, high structural complexity, live coral cover and algal phase shifts, this can be used to infer their vulnerability to broad-scale change to reef habitats that can occur from climate change. The *R. nilotica* fishery in Samoa has been praised as a success story of Australian foreign aid and coastal communities are gaining a livelihood benefit from the fishery. Paradoxically, our findings highlight the precarious future of this fishery because the habitat features favored by *R. nilotica* are threatened by climate change and other broadscale stressors.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

KS and SP conceived the research and conducted the fieldwork. All authors analyzed the data and wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00223/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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