Shellfish have been introduced to countries beyond their native distributions in order to develop new fisheries, but the success of such translocations has been variable. In 2003 and 2006, adult trochus (*Rochia nilotica*), a herbivorous coral reef gastropod, were translocated from Fiji and Vanuatu to Samoa. This translocation extended their natural range and created a new fishery in Samoa. In 2018, we had the opportunity to assess the population structure of trochus stocks at 28 sites around Samoa’s two main islands using underwater visual censuses along transects. This assessment revealed that the distribution of populations showed no correspondence with initial translocation sites. Densities of trochus were spatially variable, and very high (>500 individuals/ha) at some sites. Size-frequency distributions also varied among sites, yet all populations contained some large individuals. There was no evidence of competitive dominance of trochus over native gastropods or negative impacts to coral communities. This study shows that stocked shellfish such as trochus can develop to exploitable population levels within 15 years. Translocations of marine organisms must be considered with great caution. Our study indicates that livelihood benefits of introducing alien shellfish species are likely to be spatially variable. Translocations of the right species could support food webs and provide further food security and livelihood options to coastal fishing communities.

**Key words:** alien species introductions, gastropod, invertebrate fishery, shellfish, stock enhancement, trochus

### Implications for Practice

- Trochus, a herbivorous coral reef gastropod, does not have strong harmful effects on native biota and can assist with controlling algae on coral reefs following coral bleaching events.
- Geographic colonization of introduced shellfish can be highly variable.
- Colonization might not occur at the initial translocation sites, due to unpredictable dispersal or unsuitability of the sites for all life-history stages.
- Abundant trochus stocks in Samoa were established at many sites within 15 years of their introduction.

### Introduction

#### Stock Enhancement of Shellfish Fisheries

The UN’s sustainable development goals (SDGs) advocate actions to improve responsible food production and contribute to poverty reduction (http://sustainabledevelopment.un.org/). Similarly, the Blue Economy agenda promotes new food and revenue opportunities from oceans while safeguarding environmental interests (Cohen et al. 2019). Sadly, stocks of many species of shellfish have become globally overfished (Ward 2006; Anderson et al. 2011). The largest shellfish fisheries worldwide are scallops, abalone, queen conch, clams (including giant clams), pearl oysters, edible oysters, and topshell snails (Bell et al. 2005). Aside from overfishing, shellfish populations are threatened by the projected impacts of climate change, habitat degradation, and the globalization of markets (Ortega et al. 2012). Many of these fisheries are also data-poor, making it difficult to track their status, assess drivers of abundance, and set management restrictions on catches (McClanahan et al. 2009).

Consequent to the declines in fishery stocks, one pathway to address the SDGs in capture fisheries is through the restocking or enhancement of wild stocks (Bell et al. 2008; Cao et al. 2017; González Laxe et al. 2018). Shellfish have been stocked into the wild in order to reestablish severely depleted fisheries (i.e. restocking), for the augmentation of an existing fishery (i.e. stock enhancement), or for creating new fisheries...
(i.e. stock translocation) (Eldredge 1994; Bell et al. 2005). Increasing seafood production through stocking, however, requires prudent choice of species that are productive but also nonthreatening to native communities as well as appropriate research to validate the effectiveness of the stocking programs (Bell et al. 2006). The time frames and patterns of restocking of new populations can be hugely variable, so empirical examples from broad-scale population surveys offer valuable insights for future stocking programs.

Shellfish successfully used in restocking programs include scallops (Uki 2006), giant clams (Gomez & Mingoa-Licuanan 2006), abalone (Hasman 2006; Arnold 2008; Hamasaki & Kitada 2008), mussels (Calvo-Ugarteburu et al. 2017), and queen conch (Stoner & Davis 1994; Stoner 2019). Restocking success can be variable spatially and temporally (Bell et al. 2006; Gomez & Mingoa-Licuanan 2006). Common reasons for the failure of restocking programs include high cost involved in translocations, bio-security concerns, the high mortality of released individuals, lack of community support, and inadequate monitoring (Teitelbaum & Friedman 2008).

Species Translocations and Introductions

The introduction of new species outside their natural geographic distribution raises bio-security issues, including the introduction of foreign parasites and diseases, and the potential invasiveness of the introduced species (Briggs 2007; Ricciardi & Simberloff 2009). Indeed, introduced or alien species (e.g. from ballast water) are considered a key anthropogenic threat to global biodiversity, including in marine ecosystems (Bax et al. 2003; Sorte et al. 2010). “Invasive” is a term often applied when the alien species shows tolerance to a wide range of environmental conditions, attains numerical dominance over native species, and colonizes a wide geographical area (Ruiz et al. 1997; Sakai et al. 2001; Hutchings et al. 2002).

A primary concern is that the introduced species might out-compete native species when the two occupy a similar niche (Ward 2006). In the early 2000s, a staggering 287 alien marine and brackish-water invertebrates were reported in Hawai‘i (Ward 2006). In the early 2000s, a staggering 287 alien marine species compete native species when the two occupy a similar niche (et al. 2001; Hutchings et al. 2002).

Shellfish species that have been introduced beyond their range for fisheries purposes include shrimp (Wang et al. 2006), green snails (Turbo marmoratus) (Andréfouët et al. 2014), pearl oysters (Bell & Gervis 1999), Pacific oysters (Troost 2010), giant clams (Friedman & Teitelbaum 2008), and a range of other clam species (Jensen et al. 2004; Strasser & Barber 2009). The giant clam translocation programs have encountered high mortality of released juveniles, high hatchery-related costs, and variable compliance with stock protection measures (Teitelbaum & Friedman 2008). In French Polynesia, after 45 years since their introduction, green snails have successfully spread across some islands, but not others (Andréfouët et al. 2014).

Rochia nilotica; formerly Trochus niloticus and Tectus niloticus; Williams 2012) is a large herbivorous topshell snail found on coral reefs of southeast Asia and the central-western Pacific (Nash 1993). Its natural (“original”) distribution extends from southeast Asia to the central-western Pacific Ocean, as far east as Fiji (Bour 1990), with extensive introductions outside its natural range (Eldredge 1994). It has been heavily exploited could be seen as lowering their extinction risk (Thomas 2011). The introduction of some alien marine species has occasionally resulted in a net gain in local and regional biodiversity, complementarity with native species, or improved ecosystem functioning (Occhipinti-Ambrogi 2007).

Alien marine species can also sometimes have positive impacts on humans, which are part of broader social-ecological systems, through the creation of new economic opportunities. For example, Manila clams (Venerupis philippinarum) introduced to the western United States created lucrative fisheries with minimal negative impacts on native species (Talley et al. 2015). Pacific oyster was introduced to Fiji in the 1970s and is now an important income source for rural women, who favored them over native oysters (Kinch et al. 2019). Green snail (Turbo marmoratus) has been translocated to island groups in the Pacific (e.g., French Polynesia) to create new fisheries, and its ecological impacts are reported to be benign (Andréfouët et al. 2014). In lieu of manipulative experiments, mensurative indicators of deleterious impacts of alien species introductions could be inverse relationships between the abundance of the alien species and the abundances of native competitor species or habitat-forming biota (Sakai et al. 2001).

Positive benefits to livelihoods need to be weighed against potential deleterious effects on ecosystems (Bax et al. 2003). Societal benefits of species introductions might outweigh potential risks in low-income countries or communities because introduced species are often incorporated into local livelihoods (Pejchar & Mooney 2009). Translocations of certain marine species might also enhance resilience of social-ecological systems in the Anthropocene (Dulvy & Kneesevater 2017; Hughes et al. 2017). This is pertinent in an era when other marine resources are becoming limiting and key ecosystem processes need repair (Bell et al. 2009; Hughes et al. 2012).

Marine invertebrates that have been introduced beyond their range for fisheries purposes include shrimp (Wang et al. 2006), green snails (Turbo marmoratus) (Andréfouët et al. 2014), pearl oysters (Bell & Gervis 1999), Pacific oysters (Troost 2010), giant clams (Friedman & Teitelbaum 2008), and a range of other clam species (Jensen et al. 2004; Strasser & Barber 2009). The success has been variable. In various countries throughout the Indo-Pacific region, giant clam translocation programs have encountered high mortality of released juveniles, high hatchery-related costs, and variable compliance with stock protection measures (Teitelbaum & Friedman 2008). In French Polynesia, after 45 years since their introduction, green snails have successfully spread across some islands, but not others (Andréfouët et al. 2014).

Trochus as a Fishery Resource

Trochus (Rochia nilotica; formerly Trochus niloticus and Tectus niloticus; Williams 2012) is a large herbivorous topshell snail found on coral reefs of southeast Asia and the central-western Pacific (Nash 1993). Its natural (“original”) distribution extends from southeast Asia to the central-western Pacific Ocean, as far east as Fiji (Bour 1990), with extensive introductions outside its natural range (Eldredge 1994). It has been heavily exploited...
Throughout this geographic range for its flesh and the nacre of its shell, which is used to make buttons and handicrafts (Nash 1993; Bell et al. 2005; Gillett et al. 2020). Among Pacific Islands, trochus has contributed to fishery exports in Cook Islands, Fiji Islands, Federated States of Micronesia (FSM), New Caledonia, Papua New Guinea (PNG), French Polynesia, Solomon Islands, Vanuatu, and Wallis and Futuna (Pinca et al. 2010; Gillett 2016; Gillett et al. 2020). The shallow and predictable habitat preference of trochus makes the species easy to collect, and the shells can be stockpiled to await sale or optimize sales. These qualities also make it vulnerable to high rates of exploitation, but the fisheries are often relatively robust because the animal is highly fecund, fast growing, and short lived, and juveniles are highly cryptic (Nash 1993; Bell et al. 2005). This assertion is further supported by archeological evidence showing long-term population resilience to episodic harvesting (Ulm et al. 2019). An important life-history trait is the unusually short larval duration of 3–7 days (Nash 1993; Lee & Lynch 1997). This has meant that trochus do not disperse far from natal sites and explains why the original distribution was geographically limited.

In some countries, trochus flesh constitutes an important resource for household subsistence consumption (Lasi 2010; Gillett & Tauati 2018). The shells are either transported domestically to factories that can cut out the button blanks, or exported to countries that have these factories (Gillett et al. 2020). Prices for trochus shell were relatively high through the 1990s, at around US$6–8/kg, but dropped since 2000 due to the replacement of trochus shell buttons with plastic imitations (Lasi 2010). Prices paid to fishers in the Pacific Islands region between 2010 and 2014 ranged from US$2.20 to US$4.00 per kg of shell, depending on shell grade (Tiitii & Aiafi 2016).

**Trochus Introductions in the Pacific Islands**

Adult trochus (i.e. “broodstock”) have been translocated to at least 60 places throughout the central-western Pacific Islands over the past 80 years (Gillett 1993; Eldredge 1994; Bell et al. 2005). Successful fisheries have developed as a result of these introductions in some areas, such as the Cook Islands and French Polynesia (Gillett 1993; Nash et al. 1995). Most of the successful restocking and stock translocation programs of trochus have involved either the release of cultured juveniles or the translocation of adults (Bell et al. 2005). Translocation of adults is most effective when attempting to create a new fishery. For greater success, introduction of adults should be accompanied by an initial fishing ban to allow a self-sustaining population to develop (Purcell 2004).

Introduced trochus are believed to have limited negative ecological impacts. The animal feeds on encrusting and turfing algae and does not appear to competitively exclude other gastropods (Gillett 1993). There are few, if any, reports of deleterious ecological impacts across its numerous introductions (Bell et al. 2005; Pakoa et al. 2010). In fact, grazing by trochus can help to maintain algal biomass at a low level that prevents overgrowth of corals, and the animals further contribute to food webs as prey for benthic invertivores as well as providing food and livelihood alternatives for coastal fishing communities.

**Aims and Objectives of This Study**

This primary aim of this study was to determine the extent of population colonization of trochus introduced on reefs around the two main islands of Samoa. We compare morphometric relationships of trochus shells in Samoa with those published from data on shells in other countries to explore potential geographic variation. We examined the patterns of abundance and sizes of trochus among reefs in relation to the original sites where broodstock were first translocated to draw more generalizable lessons about the dispersal and development of new fishery populations. This case study also offers insights into potential time frames and lessons for restoration of severely depleted populations of reef gastropods through captive-release programs. Relationships between the abundance of trochus and that of endemic gastropods and coral communities allow some critique of potential ecological impacts. Comparison of population densities within and among sites offers regionally relevant insights into spatial variability in trochus densities and the differential impacts of translocation programs for coastal fishing communities.

**Translocations of Trochus to Samoa**

**Early Introduction in 1990.** Historically, trochus did not occur in Samoa. Trochus was first introduced to Samoa in 1990 from Fiji, with a total of 112 live trochus released at Namu’a Island at the southeastern end of Upolu island (Fig. 1) (Eldredge 1994; Satoa & Sapatu 2010). Despite reported sightings in 1998, trochus populations were not believed to have become established from that translocation, as fishers did not report seeing it on their reefs and it was not observed in local market surveys by the Ministry of Agriculture and Fisheries (MAF) until the mid-2000s (Tiitii & Aiafi 2016).

**Introductions in 2003–2006.** In 2003, MAF, with assistance from the Australian Centre for International Agricultural Research (ACIAR), introduced trochus again under the assumption that no trochus were present on the recipient reefs from previous introductions (ACIAR 2004). The translocation of trochus stock to Samoa followed established guidelines by Munro and Bell (1997) and Humphries (1995), and in accordance with the International Council for the Exploration of the Sea (ICES) Code of Practice on the Introductions and Transfers of Marine Organisms (ICES 1995). Trochus broodstock introduced from Fiji in 2003 were released on reefs at Saleapaga on Upolu island (n = 360) and in 2005, trochus broodstock from Vanuatu were released at Saoluafata at Upolu island and at Papa Puleia at Savai’i island (n = 360 per site, Fig. 1). A fourth introduction from Vanuatu in 2006 resulted in another 400 adult trochus broodstock being distributed among the same three release sites (Fig. 1). Hatchery rearing of trochus in Samoa in 2004 provided for a further 500 juveniles that were released at additional sites on both Upolu and Savai’i (Satoa & Sapatu 2010) (Fig. 1). In
total, 1,480 adult broodstock and 500 juveniles were released in Samoa between 2003 and 2006.

Stock Management. At the time of the study, trochus in Samoa were managed by a minimum legal-size limit of 90 mm basal shell width (BSW). However, few fishers were apparently aware of this regulation, resulting in many undersized trochus shells in catches (Purcell et al. 2020). Fishing of trochus occurs on all of the islands of Samoa where it is now found (Purcell et al. 2020). Exports of trochus from Samoa are currently not permitted because MAF has wanted to firstly allow stocks to become abundant.

Methods

Study Sites

This study was conducted from January to March 2018 on Samoa’s two main islands: Upolu and Savai’i. Samoa’s volcanic geology has formed coastlines of old lava flows and >10,000 km² of narrow fringing coral reef (Taule’alo 1993). Along the coastlines of Upolu and Savai’i, there are fringing reefs close to shore with little or no reef flat habitat, and reefs further from shore that provide for a narrow shallow lagoon with reef flat habitat and patch reefs (Tiitii & Aiafi 2016).

Underwater visual censuses of trochus were conducted on the reef crest and seaward reef slope at 28 coral reef sites surrounding Upolu (n = 14) and Savai’i (n = 14) islands. Sites were selected on the basis of habitats characteristically preferred by trochus, as well as ensuring a spread of sites across the two islands (at least 5 km apart). Sites were also determined by accessibility and prevailing sea conditions. Each site covered about 2–3 ha of reef area, and was surveyed using independent, replicated 50- m × 2-m belt transects (n; range = 8–16; median: 11). The transects were deployed haphazardly on the reef crest and reef slope at depths of between 1 m and 10 m, approximately 10 m apart. For each transect, either a measuring tape or a measured rope of 50 m length was laid on the reef along a relatively consistent depth profile. A total of 322 transects were surveyed across the 28 sites, with 167 transects on Upolu and 155 on Savai’i. Transects shallower than 4 m were
surveyed using breath-hold diving and deeper transects were surveyed using scuba.

**Data Collection**

Along each transect, all trochus were counted within 1 m either side of the transect line, which was measured by the arm span of the observer plus a determined distance from their fingertips to equal 2 m. Within each transect, the substrate and reef structure was searched carefully, including inside crevices and ledges (Fig. 2A). Only the shells of live trochus were used for analyses. Three native and potentially competitive gastropod species (*Tectus pyramis*, *Trochus maculatus*, *Turbo chrysostomus/T. argyrosomus*) were also enumerated on transects. *Turbo chrysostomus* and *T. argyrosomus* were combined due to their similar morphology, which was difficult to distinguish in the field.

The maximum BSW of the first 16 individuals of trochus found along each transect was measured to the nearest mm in situ using rulers (Fig. 2B). This protocol provided ample replication for calculating average shell sizes, and satisfied time constraints when more than 16 individuals were found along a transect. Divers were trained prior to field surveys by deploying empty shells of varying sizes along underwater transects. Since we only measured the first 16 individuals on each transect, we used percentages to express size frequency for ease of viewing the bars on the size frequency charts (see Table 1 for the number of trochus recorded and measured on each transect). Depth was measured using a digital depth gauge at the start and end of each transect, and the average of the two was used as the transect depth.

**Statistical Analysis**

All trochus counts from transects were converted to density (individuals/ha), and an average density and standard error were calculated across all transects at each site. Size-frequency distributions were calculated from the BSWs. The relationship between size and density was tested with a Pearson’s linear correlation analysis using SPSS version 25, and the relationship between BSW and weight was determined with a regression analysis of the standard growth function \( y = ax^b \) and compared to published growth functions of trochus measured from other countries (Nash et al. 1995; Foale & Day 1997; Dolorosa et al. 2010; Murphy et al. 2010). Relationships between the site-scale density of trochus and the density of the three endemic gastropods were also examined using Pearson’s linear correlation analysis in SPSS version 25. Potential significant negative relationships between densities of trochus and the endemic species could be considered as preliminary evidence for potential exclusion by introduced trochus, while positive correlations could infer that both species favored similar habitats, which could indicate a potential for competition. Therefore, testing for such relationships could furnish results to underpin further study (including manipulative experiments) to account for confounding factors such as harvest rates.

**Results**

**Patterns of Abundance**

Trochus densities at many sites were indicative of an established population at both Upolu and Savai’i despite high variability between sites (Table 1). On Savai’i, trochus were only found on the northern and eastern coasts, while on Upolu they were distributed around most of the island (Fig. 3).

Very high variability in densities was apparent on Savai’i, where the standard deviation among sites averaged 294 individuals/ha. The sites of Salelavalu and Fagamalo had extraordinarily high densities over 1,000 individuals/ha. Other sites on Savai’i held 0–300 individuals/ha. Densities of trochus around Upolu were less widely variable, with standard deviation among sites averaging 187 individuals/ha. Around Upolu island, trochus were denser at southern sites, with several sites holding more than 200 individuals/ha.

Densities of the three endemic gastropods were roughly an order of magnitude lower than the densities of trochus. Of the three species, *T. maculatus* was the most abundant, and *T. chrysostomus/T. argyrosomus* the least abundant (Fig. 4).
Both *T. maculatus* and *T. pyramis* tended to occur in higher densities at Upolu. The relationships between average trochus densities at sites and the corresponding average densities of the three endemic gastropod species were all largely nonsignificant (*p* values = 0.81–0.97). That is, the abundances of trochus bore no relationship with the abundances of endemic gastropods at reef sites (Fig. S1).

**Table 1.** Summary of sites surveyed, replication, average depth of the transects, the total number of trochus recorded and measured, and numbers of each of the native gastropods: *Tectus pyramis*, *Trochus maculatus*, and *Turbo chrysostomus/argyrostomus*.

| Island | Site Name            | No. of Transects | Average Depth (m) | No. of Trochus Found | No. of Trochus Measured |
|--------|----------------------|------------------|-------------------|----------------------|-------------------------|
| Savai’i| Cape Falealupo       | 11               | 2.95              | 0                    | 0                       |
|        | Faga                 | 11               | 4.85              | 2                    | 3                       |
|        | Fagamalo             | 12               | 3.12              | 170                  | 1                       |
|        | Fagasala             | 13               | 4.20              | 3                    | 3                       |
|        | Fatuvalu             | 11               | 3.16              | 33                   | 1                       |
|        | Foaimalo             | 11               | 3.90              | 0                    | 0                       |
|        | Lano                 | 9                | 1.65              | 9                    | 2                       |
|        | Papa Puleia          | 11               | 6.45              | 0                    | 0                       |
|        | Salelavalu           | 12               | 5.28              | 229                  | 1                       |
|        | Saleoloaga           | 8                | 3.39              | 6                    | 0                       |
|        | Satuiatua            | 11               | 4.18              | 0                    | 0                       |
|        | Tafua                | 12               | 3.13              | 0                    | 0                       |
|        | Vailoa Palauli       | 12               | 3.60              | 0                    | 0                       |
|        | Vaisala              | 11               | 4.55              | 15                   | 0                       |
| Upolu  | Lepa                 | 11               | 3.50              | 1                    | 2                       |
|        | Malemalu             | 12               | 3.31              | 63                   | 5                       |
|        | Manono               | 11               | 1.95              | 1                    | 1                       |
|        | Mulifanua            | 15               | 2.13              | 22                   | 6                       |
|        | Mulimu’u             | 11               | 5.23              | 19                   | 1                       |
|        | Nofoali’i            | 10               | 2.13              | 5                    | 2                       |
|        | Saanapu              | 11               | 2.27              | 14                   | 3                       |
|        | Safata               | 14               | 3.19              | 54                   | 1                       |
|        | Salani               | 9                | 5.27              | 4                    | 0                       |
|        | Saleapaga            | 11               | 4.18              | 0                    | 0                       |
|        | Saolafata            | 16               | 2.64              | 2                    | 0                       |
|        | Savaia               | 10               | 2.81              | 29                   | 1                       |
|        | Siumu                | 11               | 4.26              | 29                   | 1                       |
|        | Vailoa Aleipata      | 15               | 4.13              | 17                   | 1                       |

Both *T. maculatus* and *T. pyramis* tended to occur in higher densities at Upolu. The relationships between average trochus densities at sites and the corresponding average densities of the three endemic gastropod species were all largely nonsignificant (*p* values = 0.81–0.97). That is, the abundances of trochus bore no relationship with the abundances of endemic gastropods at reef sites (Fig. S1).

**Size-Frequency Distribution**

Size-frequency distributions of trochus around both Upolu and Savai’i show a relatively high frequency of large adult individuals (i.e. 70 mm BSW and above; Fig. 5). At a few sites, all individuals encountered were in the same size category. Smaller individuals likely to be immature (i.e. <60 mm) (Nash 1993) were found at 28% of sites on Savai’i and 43% of sites on Upolu. There was no significant relationship between population density and mean BSW per site (*r* = –0.015, *p* = 0.949). The largest individual had a BSW of 136 mm, while the smallest measured 13 mm.

Of the 572 trochus measured across all transects, 57% measured at least 90 mm BSW, which is the minimum size limit for the fishery. Legal-sized trochus made up a considerable proportion of the shells of live animals measured at most of the sites, and no marked pattern of the distribution of legal-sized trochus between islands or between Upolu and Savai’i islands was evident (Fig. 5).

The morphometrics of trochus shells surveyed in Samoa closely follow the relationship reported from trochus in the Cook Islands (Fig. 6). Trochus shells in Samoa, however, gained weight more rapidly with increasing shell width than in the Solomon Islands, but more slowly when compared with trochus shells in the Philippines and northern Australia.

**Discussion**

**Colonization of Trochus**

Our study shows that trochus populations have successfully colonized coral reefs around most of Samoa. Compared with densities in other countries where the species is exploited (Pinca et al. 2010), the stocks in Samoa represent a viable new fishery since population density at many sites was above 100 individuals/ha—a density (from randomly allocated reef front and reef flat surveys) above that advocated as a minimum to allow harvests (50 individuals/ha; Purcell 2004). The fishery is currently small-scale and operated by approximately 1,000 coastal community fishers generally using paddle canoes or swimming and wading from shore (Purcell et al. 2020).
The patchy abundance and size distributions of trochus in Samoa could be attributed partly to the effects of variable fishing pressure on trochus population demography, but also to ocean currents and dispersal patterns (Cohen & Alexander 2013). Nevertheless, adult individuals were found at most sites and average densities (155 individuals/ha at Upolu and 300 at Savai’i) were intermediate or high when compared with field data from other Pacific Island countries (Pinca et al. 2010). A review of densities collected during surveys by the Pacific Community (SPC) reported densities of 300–800 individuals/ha in Palau, the Cook Islands, and French Polynesia, and lower densities (below 100 individuals/ha) in Fiji, PNG, the Solomon Islands, and the FSM (Tardy et al. 2008a; Tardy et al. 2008b; Lasi 2010). Spatial distribution patterns of marine organisms provide important information for management, such as dispersal and colonization potential and population history (Ward 2006). Understanding these patterns is also helpful for the optimization of release programs and harvesting regimes (Lorenzen 2006).

A parallel socioeconomic study found that fishers from villages close to nearly all of our study reefs reported harvesting trochus, so trochus populations at sites we surveyed were generally subject to some fishing pressure (Purcell et al. 2020). In the present study, no trochus were found on the southern and western coasts of Savai’i. However, interviews with fishers in the parallel socioeconomic study demonstrate that trochus have been establishing near those sites since 2009, but are still in low densities (Purcell et al. 2020). Our site locations were randomly selected taking into consideration appropriate habitat conditions for trochus. These sites, however, may not be sites where trochus have colonized well. The findings highlight the benefit of
conditions are suitable for successful recruitment to neighboring sites. We found no trochus at two of the three sites where the species had been translocated in 2003 and 2006 (i.e. Saleapaga and Papa Puleia). Fishing for trochus occurred near some of these sites but there was no evidence that they were particularly targeted by artisanal fishers to infer that their absence from those sites was mainly due to fishing (Purcell et al. 2020). Those sites might have been suitable for adults to survive and breed, yet unsuitable for settlement of larvae and/or recruitment of juveniles. Ideally, sites for stocking benthic invertebrates should be chosen on the basis of optimal habitats for both juveniles and adults (Munro & Bell 1997; Ceccarelli et al. 2018).

This study shows that populations of reef invertebrates such as trochus can take up to 15 years to become established. We further surmise that the time frames for population establishment could be even higher for longer-lived species such as sea cucumbers and giant clams (see Bell et al. 2005). For at least some sites, low densities and smaller sizes of trochus appear to reflect an early stage of population colonization. This inference is corroborated by local fishers near those sites claiming that they only first began seeing and collecting trochus in these areas within the past decade (Purcell et al. 2020). Therefore, translocation and restocking programs for marine invertebrates may need to anticipate decadal timescales to achieve success.

Translocations need to be considered cautiously and are not recommended with species that already exist in the receiving country, or with species known to harm native species or ecosystems. With the data at hand, we found no evidence of deleterious ecological impacts on benthic communities. Trochus were abundant where live coral cover was high and were also found in abundance at some sites where coral cover was low (cf. supplementary information in Seinor et al. 2020). These latter areas were apparently the result of recent coral bleaching events and cyclones (Ziegler et al. 2018). A separate study, which modeled the relationships between densities of trochus and habitat features, found that trochus tended to be more abundant where coral cover was high (Seinor et al. 2020). Hence, both pieces of evidence suggest that trochus do not seem to limit or affect the growth and persistence of hard corals. This inference is further corroborated by aquaria experiments showing that trochus actually enhances the survivorship of corals presumably by its grazing on algae that can otherwise overgrow young corals (Villanueva et al. 2013).

Further, trochus did not appear to affect densities of endemic competitor species, since their abundances were unrelated. Indeed, Bell et al. (2005) noted few, if any, reported negative environmental or ecological impacts from the numerous introductions of trochus across the Pacific Islands region. In hatcheries, the effects of trochus on the giant clam Tridacna derasa reared in the same tanks were reported to be either negligible or, at high trochus densities, even positive by grazing algae in grow-out tanks (Clarke et al. 2003). Previous underwater surveys in Samoa, prior to trochus colonizing the reefs, concluded low abundance of endemic gastropod species (ACIAR 2005). Naturally or historically low densities of Tectus pyramis have also been reported from other localities (Dolorosa et al. 2010).

Clearly, careful consideration must be given to deliberate species translocations in order to enhance food systems and fishery-dependent (e.g. socioeconomic) surveys to complement the data and inferences about stocks based on underwater visual censuses.

Fishery Outlook
Trochus populations at many sites appear viable to sustain fishing intended for shell exports, although abundances at some sites were still relatively low. This could reflect habitat quality at the sites, since not all sites within a fishery will be optimal for the species (Purcell, Gossuin, & Agudo 2009). Alternatively, trochus might still be in a phase of establishment in some areas. The management decision in Samoa to not allow the exports of trochus shell has likely limited the incentives of fishers to harvest intensely, although 7 million trochus are estimated to be harvested annually for food (Purcell et al. 2020). Prohibiting exports for the time being serves to promote abundant colonization of populations that can support heavier fishing pressure later.

The morphometrics of shells from the new fishery in Samoa closely follow the relationship of trochus introduced to the Cook Islands. Cook Islands first received introduced trochus in 1957 (Gillett 1993; Eldredge 1994). The comparable morphometrics of Samoan trochus shells augur well for potential exports in the future.

Lessons for Stocking Programs of Benthic Invertebrates
Optimal colonization for the purposes of creating new stocks or stock restoration will rely on the choice of release sites. Our findings indicate that populations might establish nonetheless as long as the translocated adults can breed and that hydrodynamic conditions are suitable for successful recruitment to neighboring sites. We found no trochus at two of the three sites where the species had been translocated in 2003 and 2006 (i.e. Saleapaga and Papa Puleia). Fishing for trochus occurred near some of these sites but there was no evidence that they were particularly targeted by artisanal fishers to infer that their absence from those sites was mainly due to fishing (Purcell et al. 2020). Those sites might have been suitable for adults to survive and breed, yet unsuitable for settlement of larvae and/or recruitment of juveniles. Ideally, sites for stocking benthic invertebrates should be chosen on the basis of optimal habitats for both juveniles and adults (Munro & Bell 1997; Ceccarelli et al. 2018).

This study shows that populations of reef invertebrates such as trochus can take up to 15 years to become established. We further surmise that the time frames for population establishment could be even higher for longer-lived species such as sea cucumbers and giant clams (see Bell et al. 2005). For at least some sites, low densities and smaller sizes of trochus appear to reflect an early stage of population colonization. This inference is corroborated by local fishers near those sites claiming that they only first began seeing and collecting trochus in these areas within the past decade (Purcell et al. 2020). Therefore, translocation and restocking programs for marine invertebrates may need to anticipate decadal timescales to achieve success.

Translocations need to be considered cautiously and are not recommended with species that already exist in the receiving country, or with species known to harm native species or ecosystems. With the data at hand, we found no evidence of deleterious ecological impacts on benthic communities. Trochus were abundant where live coral cover was high and were also found in abundance at some sites where coral cover was low (cf. supplementary information in Seinor et al. 2020). These latter areas were apparently the result of recent coral bleaching events and cyclones (Ziegler et al. 2018). A separate study, which modeled the relationships between densities of trochus and habitat features, found that trochus tended to be more abundant where coral cover was high (Seinor et al. 2020). Hence, both pieces of evidence suggest that trochus do not seem to limit or affect the growth and persistence of hard corals. This inference is further corroborated by aquaria experiments showing that trochus actually enhances the survivorship of corals presumably by its grazing on algae that can otherwise overgrow young corals (Villanueva et al. 2013).

Further, trochus did not appear to affect densities of endemic competitor species, since their abundances were unrelated. Indeed, Bell et al. (2005) noted few, if any, reported negative environmental or ecological impacts from the numerous introductions of trochus across the Pacific Islands region. In hatcheries, the effects of trochus on the giant clam Tridacna derasa reared in the same tanks were reported to be either negligible or, at high trochus densities, even positive by grazing algae in grow-out tanks (Clarke et al. 2003). Previous underwater surveys in Samoa, prior to trochus colonizing the reefs, concluded low abundance of endemic gastropod species (ACIAR 2005). Naturally or historically low densities of Tectus pyramis have also been reported from other localities (Dolorosa et al. 2010).

Clearly, careful consideration must be given to deliberate species translocations in order to enhance food systems and
livelihood alternatives responsibly (Bell et al. 2006). Filter-feeding, deposit-feeding, and herbivorous animals that are nonpredatory pose less risk to habitat structure. They are also known to have limited competitive effects on native species. This study offers promising findings that trochus is a suitable candidate for diversifying food production and livelihood alternatives in an era demanding innovative solutions to meet global Sustainable Development Goals. Our primary aim was not to test ecological impacts of the trochus introductions, but rather to report on the distribution and abundance of introduced trochus. Although we did not find evidence for deleterious impacts on native gastropods, further experimental studies are needed to directly test for potential exclusion and competition.

Lastly, we contend that introductions of trochus might improve the resilience of reef ecosystems from the projected impacts of climate change and other environmental stressors (e.g. cyclones and crown-of-thorns sea stars). Trochus are prey to a wide range of reef predators, including wrasses, pufferfish and triggerfish, loggerhead turtles, octopus, mantis shrimp, and a variety of predatory gastropods and crabs (Vermeij 1976; Castell & Sweatman 1997; Dobson 2000). Hence, introduced trochus populations should also bolster coral reef associated food chains. Moreover, since trochus can become much more abundant than endemic gastropods and are large herbivores, they could serve to control excessive growth of reef algae. Trochus graze on fleshy encrusting algae and turfing algae that cover dead coral and other reef surfaces (Nash 1993; Lee & Lynch 1997). Their grazing might pose a problem in localities where algal resources are limiting. Overall, however, introduced trochus could help to control algal overgrowth and promote the
settlement of new coral, thereby improving resilience of the reef system and coastal community fishers that are dependent on coral reefs for food and their livelihoods.

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Supporting Information
The following information may be found in the online version of this article:

Figure S1. Relationships between the density of Rochia nilotica (individuals/ha) and densities of the three native species of gastropod: Tectus pyramis, Trochus maculatus and T. chrysostomus/argyrostomus.

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