

# Experimental removal of the invasive peacock hind (roi) *Cephalopholis argus*, in Puakō, Hawai'i: methods for assessing and managing marine invasive species

Jonatha Giddens<sup>1,\*</sup>, Alan M. Friedlander<sup>1</sup>, Eric Conklin<sup>2</sup>, Chad Wiggins<sup>2</sup>,  
Kostantinos Stamoulis<sup>1</sup>, Mary K. Donovan<sup>1</sup>

<sup>1</sup>Fisheries Ecology Research Lab, Department of Biology, University of Hawai'i at Manoa, 2538 McCarthy Mall, Edmonson Hall 216, Honolulu, Hawai'i 96822, USA

<sup>2</sup>The Nature Conservancy of Hawai'i, 23 Nu'uuanu Avenue, Honolulu, Hawai'i 96817, USA

**ABSTRACT:** Invasive species are a growing concern for marine biodiversity, particularly in Hawai'i with its large proportion of endemic species. This research focused on the feasibility of removing the introduced predatory peacock grouper *Cephalopholis argus*, locally known as roi, as a management tool for Hawaiian coral reef ecosystem restoration. The objectives of this study were to investigate the dynamics of *C. argus* on 1.3 hectares (ha) of coral reef at Puakō, Hawai'i, and to (1) compare population density estimate methods in order to accurately evaluate abundance, (2) estimate population mortality and catchability rates, and (3) quantify the re-colonization rates by mapping distribution and movements in response to a depletion experiment. The number of individuals removed during a fish-down experiment provided a direct measure of initial population abundance (20.2 roi ha<sup>-1</sup>). A Leslie depletion model yielded the most accurate assessment of initial density (−15.8% error) compared to belt transects (+75.7% error) and tow-board census (−70.2% error). Estimates of total mortality were low (0.12 to 0.14), and fishing mortality ranged from negligible to 8.0% yr<sup>-1</sup> in west Hawai'i. Roi movement was monitored through a mark and re-capture program. Tagged individuals traveled 50 to 150 m from the periphery toward the center of the removal area (1 roi every 1 to 2 mo). This study engaged the local Hawaiian fishing community in assessing and managing marine invasive fish species, quantified the feasibility of roi removal as an ecosystem management tool, and provides evidence for effective roi population control through spear-fishing methods at the local (1.3 ha) patch-reef scale.

**KEY WORDS:** Invasive species · *Cephalopholis argus* · Hawaii · Mortality rate · Leslie depletion · Predator removal · Marine introduction · Grouper · Ecosystem restoration

— Resale or republication not permitted without written consent of the publisher —

## INTRODUCTION

Introduced species are a major anthropogenic stressor that weaken coral reef ecosystem resilience and undermine ecosystem services (Ruiz et al. 1997). Introduced predators can lead to reductions in biodiversity and abundance via predation or competition with native species for resources (Balon & Bruten 1986, Molnar et al. 2008). Although less pervasive

than terrestrial introductions, marine introductions have dramatically altered a number of ecosystems around the world. In the Caribbean, the invasive lionfish *Pterois volitans* has had devastating effects on the recruitment and abundance of native fishes, which in turn has led to decreased coral reef ecosystem resilience and function (Albins & Hixon 2013). Because introduced species exacerbate modifications to systems already undergoing multiple environmental and

anthropogenic stressors (Hughes et al. 2003, Mora 2008), biological invasions have been identified as one of the largest single threats to the diversity of the world's coastal waters (Lowe et al. 2000).

The Hawaiian Islands are the most isolated archipelago in the world and host one of the highest marine fish endemism rates in the Pacific (Randall 1987, DeMartini & Friedlander 2004, P. Mundy & J. Randall unpubl.). Hawaii's shallow-water reef fish assemblages evolved with a low diversity of benthic predators compared with the rest of the Indo-Pacific region (Hourigan & Reese 1987, Briggs 1999). Assessments of the composition of Hawai'i's fish assemblages in the 1950s determined that important shallow-water game fish had declined and families such as snappers and groupers were missing in the Hawaiian fauna. It was thought that the introduction of several mid-size predatory fishes into Hawaiian waters to fill this 'empty niche' would enhance catches in lieu of fisheries regulations (Division of Fish and Game 1956). Because Hawai'i had few near-shore groupers (epinepheline, serranid), the peacock hind *Cephalopholis argus* or roi (as it is locally referred to by its Tahitian name) and several other species were selected for introduction based on their ecological characteristics and potential popularity as food fishes in their native ranges.

The Hawai'i Division of Aquatic Resources (HDAR) made 3 introductions of roi between 1956 and 1961 from their native range in French Polynesia, with a total of 2385 roi released (Randall 1987). After a 4 decade lag, this species increased in abundance during the 1990s and became the dominant predator on many near-shore reefs throughout the main Hawaiian Islands (Friedlander et al. 2007, Dierking et al. 2009). Due to high rates of ciguatera poisoning (Dierking & Campora 2009, Bienfang et al. 2011), many local fishers do not recognize roi as a target species. In the absence of sustained fishing pressure, populations of roi continued to rise another 22% from 1999 through 2005 (HDAR unpubl. data), spreading 21 km yr<sup>-1</sup> throughout the Main Hawaiian Islands and as far northwest as French Frigate Shoals in the Northwestern Hawaiian Islands (NWHI; Friedlander et al. 2009). Roi populations peaked in 2004 and have declined by 38% since the start of the HDAR fish monitoring program in 1999 (Walsh et al. 2013).

In their native range of French Polynesia, roi compete with 13 other species in the same family (Meyer 2008). In their native habitat, they grow at a slower rate (J. H. Choat pers. comm.), have decreased longevity (10 to 15 yr in Moorea vs. 25 to 26 yr in Hawai'i) (Donovan et al. 2013), and display reduced

body condition compared to conspecifics in Hawai'i, suggesting competitive release in the introduced range (Vignon et al. 2009, Meyer & Dierking 2011). In Hawai'i, roi diets are composed almost exclusively of small fishes (97% diet, mean total length [TL] = 7 cm), with an annual consumption estimate of 8.2 million reef fish yr<sup>-1</sup> based on data from captive individuals (Dierking 2007). The same authors subsequently noted that Hawaiian roi caught in the wild had a stomach vacuity rate of almost 50% (Dierking & Meyer 2009), a finding that is consistent with thousands of roi caught at tournaments annually (C. Wiggins pers. obs.). The published diet study did not account for intra-annual variations in prey availability, and therefore, the prey consumed in the wild is probably less than what the laboratory feeding study would predict. Nevertheless, the large-scale consumption potential and high relative abundance indicate that roi may play a major role in shaping native reef fish assemblages in Hawai'i (Dierking et al. 2009).

A fishery is not feasible for roi in Hawai'i due to their association with ciguatera fish poisoning (Dierking 2007), although limited commercial harvest takes place. Local fishers attribute the decline in valued food fishes to predation or competition by roi (D. Tanaka pers. comm.). This in turn has led to grass-roots efforts to remove roi from reefs throughout Hawai'i. Multiple roi removal initiatives have been organized at the community level since 2008 by fishers to combat the threat they perceive as decimating Hawai'i's native reef fish populations. 'Roi Roundup' fishing tournaments are intended to be an environmental conservation movement with the aim of restoring Hawai'i's native reef fish populations by removing invasive fish, especially roi. While research has verified that the predation potential of roi can be substantial (Dierking 2007), it is unclear to what degree predation by roi (or competition by roi with other predators for prey) has detrimental effects and if roi removal is feasible as a management tool for restoring native reef fish assemblages.

To address these concerns, this study focused on experimental *in situ* roi removal to assess its feasibility as a management tool and effectiveness as a restoration action. The specific goals were to (1) compare roi population density estimation methods in order to accurately evaluate fish abundance, (2) estimate roi population mortality and catchability to inform population models, and (3) quantify the recolonization rates of roi by mapping their distribution and movements in response to the depletion experiment.

## MATERIALS AND METHODS

### Site description

Two geographic areas were selected for this study. The depth range for both of these areas was between 12 and 18 m.

**Puakō.** The coral reef of Puakō, West Hawai'i, is dominated by 3000 to 5000 yr old lava flows and carbonate substrate (Hayes et al. 1982). Established in 1985, The Puakō Fisheries Management Area (FMA) extends seaward 250 m, or to the edge of the fringing reef, and restricts gill net fishing (HDAR 2011), reducing confounding factors. The treatment site (1.3 ha) is comprised of relatively discrete patch reefs

dominated by the reef-building finger coral, *Porites compressa*, and is bounded on all sides by sand channels (Fig. 1).

**Ka'ūpūlehu.** Ka'ūpūlehu (~25 km south of Puakō) is a fringing reef with similar habitat complexity, also dominated by finger coral *P. compressa*. Like Puakō, this reef drops steeply from 3 to 12 m before sloping rapidly to >30 m; however, the extent of the reef flat at Ka'ūpūlehu is much greater than that at Puakō. Aquarium fish collecting and gill net use were prohibited in Ka'ūpūlehu in 2000 (HDAR 2011). This reef is contiguous over 3.2 km of coastline, and a 2 ha section of this large fringing reef was demarcated as a removal reef for this study.

### Roi removal

Local fishers were contracted to assist with roi removal over 11 d during April and May of 2011 at Puakō and over 4 d during August 2011 at Ka'ūpūlehu. To the extent possible, fishing effort was kept consistent at each site. SCUBA spear fishers removed roi from both treatment sites, recording the number of fishers, hours fished, roi total length to the nearest 1 mm, weight to the nearest gram, and location of each fish caught. Dive times ranged from 37 to 56 min, with 1 to 3 dives per day. The effort of roi removal was assessed by calculating catch per unit effort (CPUE) of roi removal at the treatment sites:

$$CPUE = \frac{C}{h} \quad (1)$$

where  $C$  is the catch,  $h$  is the number of hours, and total effort was averaged across all divers and dives for each day.

The actual number of roi removed during the fish-down experiment at the Puakō study site provided a direct measure of the initial population abundance. Because of the high visibility to divers of this large-bodied predator and the high site fidelity within fixed ranges (Meyer 2008), there is high confidence that all roi were seen and that >90% of the population was re-

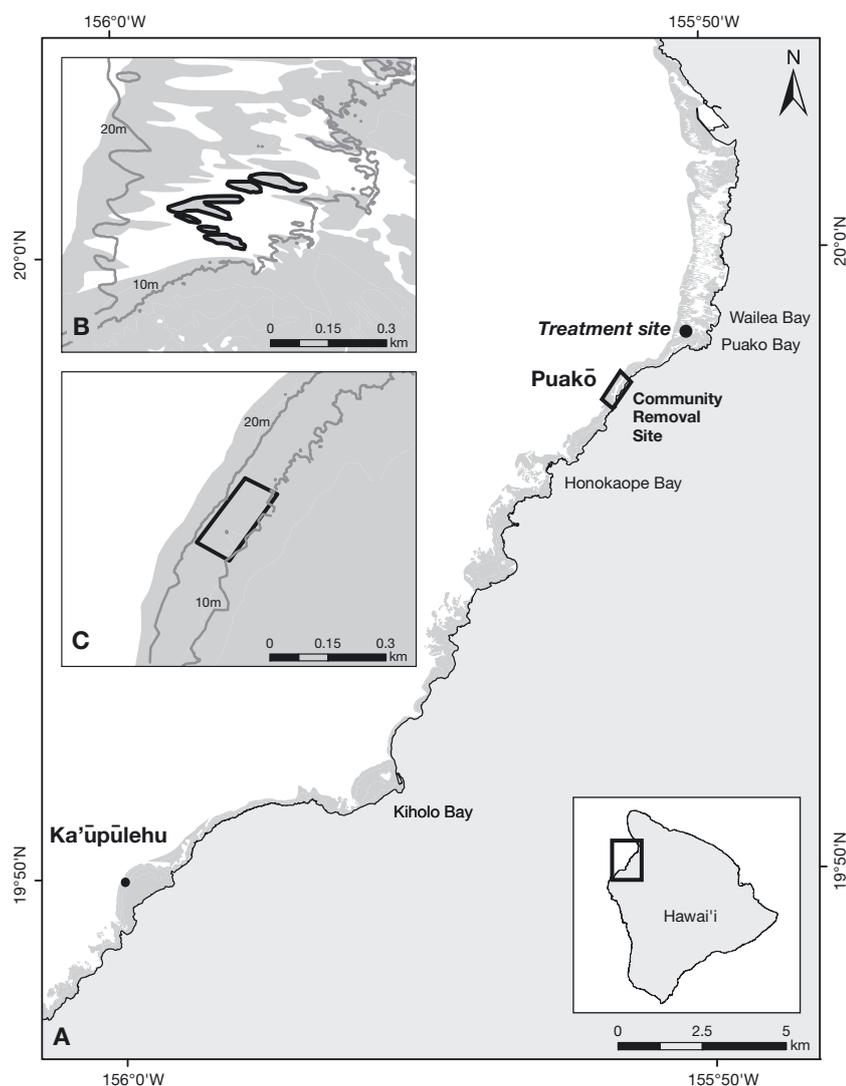


Fig. 1. (A) West Hawai'i, showing study sites and the community removal site (outlined in bold), with details of the (B) Puakō and (C) Ka'ūpūlehu experimental roi removal areas. Hard bottom reef habitat (dark grey) and depth contours from 0 to 30 m are shown

moved. Regular site monitoring and spear-fishing occurred (1 dive-day per month) in order to maintain depleted roi populations at the treatment reef.

**Population estimates: Leslie depletion model.** In a closed population with a constant catch rate, estimates of the initial population size may be obtained by monitoring how the relative abundance decreases with increasing catch. The roi population may be considered closed and with a constant catch rate for this analysis based on the low ingress of fish from the adjacent area during the fishing activity (1 roi every 1 to 2 mo; this study). Only the first 6 d of the 11 d fish-down were used in this analysis, to account for the learned avoidance behavior of groupers to spearfishers, which might impact catchability rates over time (Côté et al. 2014, present study). Following this approach to estimating local abundance, we constructed a Leslie depletion model (Leslie & Davis 1939). The application of this model assumes that fishing effort in a small area over a number of days would reduce the local population size and that this reduction would be indicated by a significant decline in abundance with accumulated catch. Initial population is estimated by regressing the catch per fisher hour against the cumulative catch:

$$N_t = N_{t-1} - K_t \quad (2)$$

where  $N_t$  is the population at time  $t$ ,  $N_{t-1}$  is the initial population, and  $K_t$  is the cumulative catch. CPUE is related to  $K_t$  by the slope  $q$ , where  $CPUE = qN_{t-1} - qK_t$  (Leslie & Davis 1939). A regression of the cumulative catch  $C_{cum}$  against  $\log(CPUE)$  is used to estimate  $q$  and the initial population size, where the intercept is  $N_{t-1}$  (Parkes et al. 1996). To assess catchability, or the gear efficiency for catching roi, we conducted a fish-down experiment in 2 locations and compared the rate of the declining catch per unit effort.

SCUBA divers spent 19:26 h spear-fishing at the removal site over 11 d and observed a change in roi behavior concurrent with targeted fishing effort. Whereas roi were initially relatively easy to approach and dispatch, over time, the dwindling number of individuals became very wary of divers and would flee immediately on sight. By changing approach tactics, some of these individuals were dispatched with great effort (1 roi per 3 dives). Others were struck but not landed, and 2 of these fish exhibited an aversion to divers sufficient to make them essentially uncatchable. Although we experimented with time of day, traps, and freediving to dispatch these individuals, none of the alternate methods were successful. This did allow us to differentiate between resident and re-colonizing roi, as the new arrivals were easily approached.

## Underwater visual survey

**Belt-transect survey.** Nineteen permanent transects were established at the Puakō patch reef treatment site, fixed with GPS location and marked for underwater recognition. Visual fish surveys were conducted along  $5 \times 25$  m belt transects (Friedlander et al. 2007), whereby 2 SCUBA divers swam a fixed bearing in tandem along parallel (~5 m apart) 25 m fixed replicate transects at a constant speed (~15 min per transect). All fishes observed within the transect were identified to the lowest possible taxon, and TL was visually estimated with size bins (0.0 to 4.9 cm TL, 5.0 to 9.9 cm TL, 10.0 to 14.9 cm TL, etc.). Divers were previously trained in visual underwater size- and distance-estimation techniques (Kulbicki et al. 2010, Bozec et al. 2011). Each pair of diver observations was averaged to obtain the value of fish abundance for each transect. Live wet mass,  $W$ , of all fishes recorded during surveys was calculated from the visually estimated TL using the length–weight relationship  $W = aTL^b$ , where  $a$  is the allometric growth parameter and  $b$  is a scaling constant. Species-specific length–weight parameters were obtained from published and unpublished sources (Donovan et al. 2013, M. Donovan et al. unpubl.).

Fish transect surveys were conducted at Puakō during March/April 2011 before any roi were removed in order to establish baseline conditions at the treatment site. Follow-up surveys were conducted semi-annually during winter and spring following roi removal. At Ka'ūpūlehu, surveys ( $n = 24$ ) occurred over the course of 17 d during October 2012.

**Tow-board survey.** To assess roi population distributions throughout the wider area, fish censuses focusing solely on roi were conducted semi-annually in removal and control areas. This census was conducted using tow-boards following the National Oceanic and Atmospheric Administration Coral Reef Ecosystem Division protocols, and followed isobaths from 10 to 30 m, covering a total area of 0.4 km<sup>2</sup> (Holzwarth et al. 2003). These census rounds took place in April, June, and November 2011 and in June and October 2012. Paired divers were towed from a 50 m tow line, each with a planing board equipped with datasheet, timers, depth gauge, and signaling device for communication with the boat. Divers were towed along a pre-determined course designed to completely cover the area of interest at a constant speed. Maintaining depth ~3 m from the bottom, divers visually estimated and recorded the TL, time, and depth of each roi sighting within 5 m of either

side of the straight line trajectory. Communication was maintained between diver pairs both above water and during the survey to ensure that roi were not double counted.

### Mortality estimate model

The equilibrium length of a population is inversely related to the mortality rate experienced by that population (Ricker 1975); therefore, the mean length of a fish population can be used to estimate the mortality rate from basic growth parameters.

**Beverton and Holt.** Instantaneous total mortality rate  $Z$  was derived using the length-based Beverton and Holt model (Beverton & Holt 1956):

$$Z = K \times \frac{L_{\infty} - L}{L - L'} \quad (3)$$

where  $L_{\infty}$  is mean asymptotic length,  $K$  is the rate of decline in growth rate with increasing size,  $\bar{L}$  is the mean length of the sample, and  $L'$  is the lower limit of the smallest length class included in the computation.

This method assumes equilibrium conditions, an infinite exploitable life-span, and that the dynamics of the population are adequately described by the von Bertalanffy and exponential-mortality models (Beverton & Holt 1956). A range of estimates for  $Z$  were calculated by the same equation, based on adding and subtracting 1 standard error for each von Bertalanffy growth parameter from Donovan et al. (2013) (Table 1 in the present study).

**Ault and Ehrhardt.** The Ault & Ehrhardt (1991) method for estimating instantaneous mortality was developed from a truncated equation for average length to more accurately represent the heterogeneous patterns observed in tropical artisanal fisheries. This method considers the length at first capture as well as the maximum retainable length in the catch and is sensitive to variations in these parameters:

$$\left( \frac{L_{\infty} - L_{t_{\infty}}}{L_{\infty} - L_c} \right)^{Z/K} = \frac{Z(L_c - \bar{L}) + K(L_{\infty} - \bar{L})}{Z(L_{\infty} - \bar{L}) + K(L_{\infty} - \bar{L})} \quad (4)$$

where  $L_{\infty}$  is asymptotic length,  $L_{t_{\infty}}$  is length at maximum age,  $Z$  is total mortality,  $K$  is the rate of decline in growth rate with increasing size,  $\bar{L}$  is mean length in the sample, and  $L_c$  is length at first capture (Ault & Ehrhardt 1991).

Minimum and maximum estimates were calculated by the same equation, based on adding and subtracting 1 standard error for each von Bertalanffy growth parameter from Donovan et al. (2013) (Table 1 in the present study).

Table 1. North Kona roi life-history parameters adapted from Donovan et al. (2013), where  $L_{\infty}$  is the mean asymptotic length,  $K$  is the rate of decline in growth rate with increasing size,  $t_0$  is the theoretical age at which length is 0 cm,  $L_c$  is the minimum size of individuals fully recruited to the fishery,  $L_{\max}$  is the maximum size,  $T_{\max}$  is the mean of the oldest 20% of individuals, and  $\bar{L}$  is the mean length. Values are mean  $\pm$  maximum and minimum estimates

Roi life-history parameters North Kona (n = 78)	Value	Unit
$L_{\infty}$	47.9 ( $\pm 9.2$ )	cm
$K$	0.118 ( $\pm 0.02$ )	yr <sup>-1</sup>
$t_0$	-3.4	yr
$L_c$	25.0	cm
$L_{\max}$	49.0	cm
$T_{\max}$	17.4	yr
$\bar{L}$	34.6 ( $\pm 6.73$ )	cm

**Linearized catch curve.** A catch-curve was constructed to estimate total mortality based on a linear decline of individuals caught from age-based cohorts (Quinn & Deriso 1999). Based on assumptions of a closed population with constant recruitment, instantaneous mortality is modeled following continuous exponential growth where total loss of individuals is equal to total mortality. The log-frequency of catch of each age class is expected to increase until the age class is fully recruited to the fishery and then linearly decline with age.

Age-at-length was calculated using an age-length key based on fish collected from the study area from July to November 2011 (Table 1 in the present study; Donovan et al. 2013). The probability of each age for a given length interval (2 cm) was used to construct an age-length key by which individuals were then assigned an age by randomly selecting individuals from each length interval (Kimura 1977).

A linear model was fit to the cumulative log-frequency of age, and the slope of this line is equal to  $Z$ , the instantaneous mortality.

The percentage of annual mortality ( $A$ ) is calculated as follows:

$$A = 1 - e^{-Z} \quad (5)$$

**Alagaraja model.** Natural mortality was estimated by the Alagaraja (1984) method, which assumes that 99% of a cohort had died if it were exposed to natural mortality only:

$$M = \frac{-\ln(S)}{T_m} \quad (6)$$

where  $S$  is survival (0.05), and  $T_m$  is longevity.

Natural and the fishing mortality sum to the total mortality; thereby, the mortality due to fishing is calculated from the following relation:

$$Z = F + M \quad (7)$$

where  $Z$  is the total mortality,  $F$  is fishing mortality, and  $M$  is natural mortality.

The population growth parameters were obtained from Donovan et al. (2013), who conducted an age and growth study of West Hawai'i roi.

### Movements of roi

Roi were tagged to assess the response of surrounding populations to the removal at the treatment reef. Three buffer zones of 250 m were designated with a specific tag-type, color, and anatomical position on captured roi to facilitate underwater recognition of place of origin during subsequent underwater monitoring. In total, 67 roi from the areas adjacent to the defined removal sites were captured by pole and line ( $n = 7$ ), in diver-deployed barrier nets ( $n = 39$ ), and using a modified pole spear with a tag applicator tip ( $n = 21$ ). All individuals were tagged with a standard Hallprint tagging needle and dart tag (individuals caught with pole and line were measured and weighed) before being released at the capture location. Divers towed a float with a GPS in track mode during tagging and monitoring events. Tagging events were opportunistic from February to October 2011. Movements of tagged roi adjacent to and into the cleared area were noted during later monitoring events from June 2011 to July 2012. The geographic coordinates of tagged and recaptured roi were obtained by matching the recorded time of capture/re-sight with the logged GPS time-track. The spatial distribution of all tagged, re-sighted, or collected individuals were mapped in ArcGIS10 (ESRI 2011), and distances and directions of movement between tag and recapture locations were measured. Time duration between removal and re-sighting in the treatment zone was used to calculate the immigration rate of surrounding populations after initial removal.

All analyses were conducted in R 2.12.1 (R Development Core Team 2010), with tests considered significant at  $p \leq 0.05$ .

## RESULTS

Initial population abundance was measured by the number of individuals removed from the study site during the fish-down experiment (plus 2 remaining roi). Fishers removed 25 roi (totaling 22.5 kg) from the Puakō treatment reef during the fish-down effort in late April and early May 2011. The size distribu-

tion ranged from 28.8 to 44.3 cm (mean  $\pm$  SE:  $36.8 \pm 2.3$  cm) (see Table 3). In total, 24 roi were removed from the Ka'ūpūlehu treatment reef (totaling 21.7 kg) during 4 days from 15 to 18 August 2011, and the size ranged from 24.4 to 51.8 cm (mean:  $36.2 \pm 7.3$  cm). The measures of initial population abundance provide a direct estimate to evaluate the accuracy of the 3 fish monitoring methods.

### Comparison of three roi population abundance estimate methods

#### Leslie depletion model

Declines in CPUE during the fish-down effort were modeled using a linear regression to relate CPUE to cumulative catch. Relating the catch per fisher hour to the cumulative catch at Puakō produced a regression slope of  $-0.19$ . The  $x$ -intercept along the cumulative catch axis predicted an initial population abundance of 22.7 roi ( $16.9 \text{ ha}^{-1}$ ) (Fig. 2). Since fishing was modeled for only 6 d, natural mortality, recruitment, and immigration are assumed to be negligible. Likewise, for Ka'ūpūlehu, the Leslie depletion experiment predicted an initial population of  $11.8 \text{ roi ha}^{-1}$ .

#### Belt transect survey

A total of 19 visual surveys (each  $5 \times 25 \text{ m} = 125 \text{ m}^2$ ) were conducted during April and May 2010 to quantify the entire reef fish assemblage at Puakō. Roi

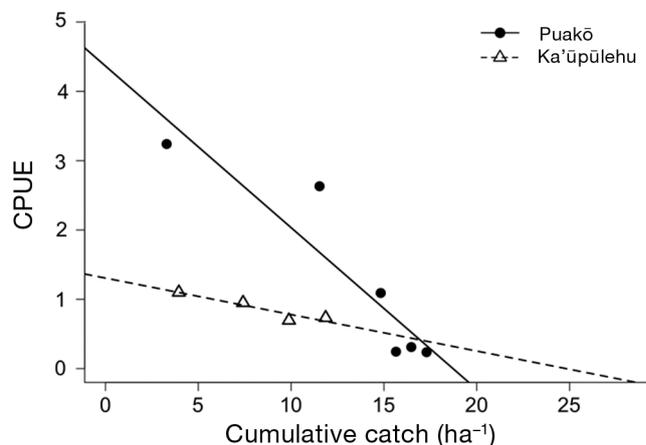


Fig. 2. Leslie depletion model for 25 roi removed from a 1.3 ha patch reef in Puakō, West Hawai'i (●, solid line) over 11 d from March to April 2011, and for 24 roi removed from Ka'ūpūlehu, West Hawai'i (Δ, dashed line) over 4 d in August 2011

occurred on 44 % of transects conducted at the treatment site before removal and accounted for 6.5 % of the total fish biomass and 0.4 % of the total assemblage numerical density at this location. The mean ( $\pm 1$  SE) population density of roi was 35.5 ( $\pm 9.3$ ) ind.  $\text{ha}^{-1}$ , and the mean biomass was 56.0 ( $\pm 6.7$ )  $\text{kg ha}^{-1}$ . At Ka'ūpūlehu, 24 transects were visually surveyed during October 2012. Roi were present on 46 % of the transects with an estimated density of 41.6 ( $\pm 0.9$ ) ind.  $\text{ha}^{-1}$  and biomass of 114.7 ( $\pm 4.0$ )  $\text{kg ha}^{-1}$ .

#### Tow-board survey

A survey of the size structure and distribution of the adjacent roi population (0.4  $\text{km}^2$  area encompassing both treatment and adjacent patch reef sites) was conducted before and after targeted removal. Overall, roi populations decreased in density by 59.8 % (from 9.2 to 3.7 ind.  $\text{ha}^{-1}$ ), though they maintained a similar size range, 18 mo after roi removal (Fig. 3, Table 2). The final tow-board survey occurred 1 mo following a community volunteer removal event in which 21 volunteer spear fishers captured 353 roi in

2 d within ~12 ha adjacent to the Puakō study site. Tow-board surveys of roi before and after the community volunteer removal event documented a sharp decrease in population density, from 7.3 to 3.7 roi  $\text{ha}^{-1}$  (Fig. 2).

The 3 methods for estimating roi population density yielded vastly different results (Table 3). The Leslie depletion model yielded the most accurate estimate of 16.9 roi  $\text{ha}^{-1}$  compared to the actual number of roi removed (20.2  $\text{ha}^{-1}$ ) during the fish-down experiment. The tow-board survey method underestimated roi density by 70.2 %, and the belt transect method overestimated roi by 75.7 %.

#### Roi population mortality

Roi population mortality was assessed by a variety of methods using growth parameters specific to North Kona roi populations (Table 1 in the present study; Donovan et al. 2013). Total mortality ( $Z$ ) estimates varied by method. The age-structured catch curve (Fig. 4) yielded an estimate ( $\pm 1$  SE) of  $Z = 0.14$  ( $\pm 0.03$ ). The Ault and Erhardt method yielded a sim-

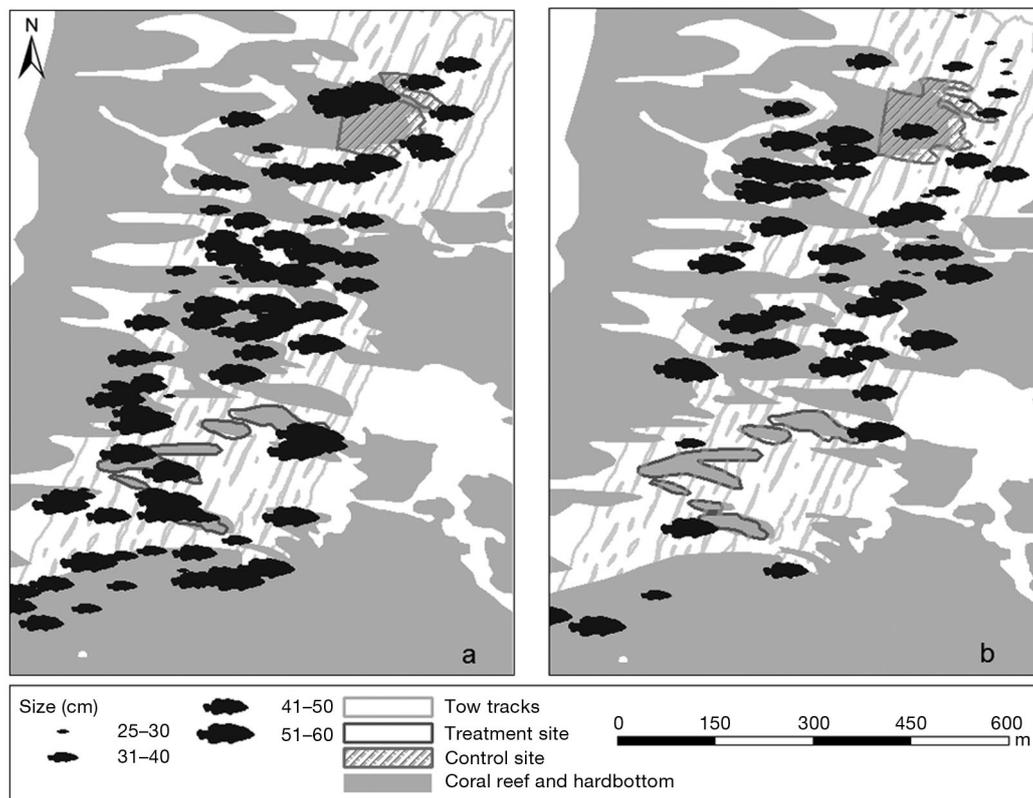


Fig. 3. Roi distributions for (a) tow-board Census 1 before removal at the treatment site and for (b) Census 5 after removal at the treatment site in Puakō, West Hawai'i

ilar estimate of  $Z = 0.14 (\pm 0.02)$ . The Beverton and Holt equation yielded a slightly lower estimate of  $Z = 0.12 (\pm 0.08)$ .

Natural mortality ( $M$ ) was calculated using Alagaraja’s method, which yielded  $M = 0.17$ . The annual fishing mortality rate was calculated using the Ault and Erhardt method (0.0 to 7.8%) and the Beverton and Holt method (0.0 to 5.8%; Table 4) with Alagaraja’s estimate of natural mortality.

**Comparisons of catchability at 2 locations**

CPUE in relation to cumulative catch was compared at Puakō and Ka’ūpūlehu (Fig. 2). The original roi density (mean  $\pm$  SE) at Ka’ūpūlehu ( $41.6 \pm 0.01$ ) was higher than at Puakō ( $35.5 \pm 9.2$ ) and the catchability, or  $q$ , declined more steeply at Puakō ( $q = -0.19$ ) compared to Ka’ūpūlehu ( $q = -0.03$ ) ( $F_{1,6} = 15.22, p < 0.01$ ), implying that catchability depends on the initial population density.

**Roi movements**

In total, 67 roi were externally tagged in 3 zones stratified by distance (250 m) surrounding the treat-

Table 2. Results of 5 tow-board population census rounds before (April 2011) and after the targeted fish-down event. The census is designed to cover the entire study area; therefore, the roi counts are summed. Numbers presented are totals ( $n = 1$ ) for each survey. Note that the final census round (October 2012) follows a community-wide volunteer removal event in the ~12 ha adjacent to the study site

Date	No. sighted	Density (ind. h <sup>-1</sup> )	Mean size (cm)	Size range (cm)
Apr-11	184	9.2	41.3 ( $\pm 8.2$ )	18–60
Jun-11	120	6	40 ( $\pm 7.9$ )	25–60
Nov-11	110	5.5	38 ( $\pm 8.8$ )	25–60
Jun-12	147	7.3	38 ( $\pm 9.5$ )	23–60
Oct-12	74	3.7	43 ( $\pm 10.6$ )	25–60

Table 3. Comparison of Puakō roi population density assessment methods and actual roi removed

Method	Area	n	Density estimate (ha <sup>-1</sup> ) ( $\pm 1$ SE)	Size range (cm) (mean $\pm$ SE)	% error
Tow-board	0.4 km <sup>2</sup>	1	6.0	18–60 (41.3 $\pm$ 8.2)	-70.2
Belt-transect	125 m <sup>2</sup>	19	35.5 (9.3)	18–55 (36.8 $\pm$ 2.3)	+75.7
Leslie depletion	0.013 km <sup>2</sup>	1	16.9	30–45 (37.5 $\pm$ 7.5)	-15.8
Roi removed	0.013 km <sup>2</sup>	1	20.2	30–45 (37.5 $\pm$ 7.5)	

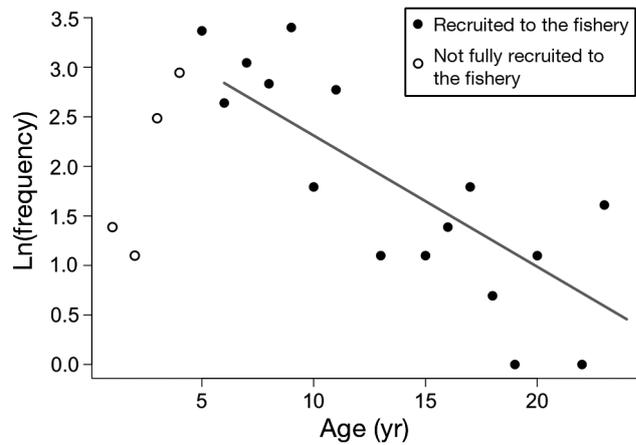


Fig. 4. Age-structured catch curve of North Kona roi collected from July to November 2011 ( $n = 203$ ). The log-frequency of catch of each age class is expected to increase until the age class is fully recruited to the fishery and then linearly decline with age. The slope of this line is equal to  $Z$ , the total mortality. Only fish  $\geq 5$  yr old (fully recruited to the fishery) were included in this analysis

ment reef (Fig. 5). Six roi were re-captured and 5 were re-sighted in 18 mo of monitoring. Distances traveled by roi averaged ( $\pm 1$  SD) 94.1 ( $\pm 38.4$ ) m and generally occurred from the periphery of the removal reef toward the center, with an immigration rate of 1 roi every 1 to 2 mo.

**DISCUSSION**

This study evaluated several methods for assessing the population density and mortality rate of a marine invasive fish (roi) species as well as the feasibility of roi removal as a management and restoration tool.

**Population estimate methods**

The 25 roi removed from the Puakō treatment site, plus the 2 remaining, represent the initial population abundance and is the reference point with which to compare 3 population estimate methods. In contrast to stock assessment comparisons in which the initial population number is not known, this depletion experiment provided a unique opportunity to directly compare the accuracy of estimate methods to the lower bound of the initial roi density at the removal reef.

Table 4. Mortality estimates based on intermediate and high estimates for  $L_{\infty}$  and  $K$  from Donovan et al. (2013)

Method	Total mortality, $Z$	% annual fishing mortality
Catch curve	0.14 ( $\pm 0.03$ )	$\sim 0.0$
Ault & Erhardt (1991)	0.14 ( $\pm 0.02$ )	0.0–7.8
Beverton & Holt (1956)	0.12 ( $\pm 0.08$ )	0.0–5.8

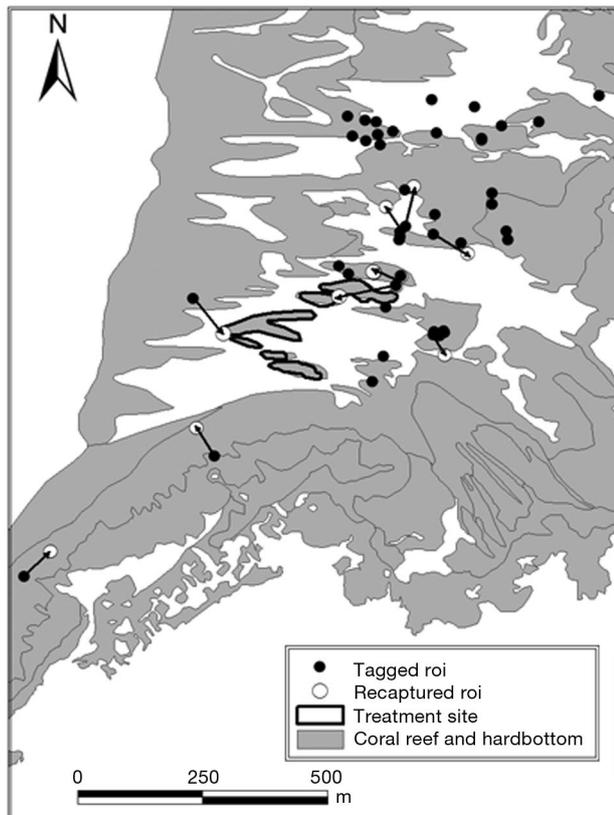


Fig. 5. Roi tag and recapture locations in 250 m zones surrounding the treatment reef in Puakō, West Hawai'i. Arrows indicate direction and distance traveled by roi from the original tag location

The Leslie depletion model yielded the most accurate population density estimate, with an error of only 15.8%. This method assumes a closed population, which was reasonable for the 6 d period of the experiments. It was also assumed that the catchability coefficient ( $q$ ) was constant, given that the same spear-fishers (i.e. same skill level) participated in the fish-down events.

One source of error in the depletion experiment may be that, as a result of the removals, some individuals may have become overly cryptic and were thus not counted during the removal exercise. If

there were more individuals, or if individuals emigrated out of the study area during removal activity, that would lessen the disparity between the depletion model and actual vs. alternate population estimates. It is unlikely that emigration was of a sufficient magnitude to confound fish-down results. The treatment reef was separated from adjacent areas by distinct sand channels, and the continued presence of wary wounded roi on the treatment reef might indicate that site attachment of individuals (Meyer 2008) is substantially stronger than the emigration from removal areas. Further, only the first 6 d of the fish-down effort were used in the depletion model, thus reducing this possible source of error. The similarity of the depletion model estimate with the actual numbers of roi removed during the fish-down experiment corroborates the models predicting initial population numbers by using catch and effort data.

The belt-transect method yielded the highest estimate of population abundance by far. Non-instantaneous surveys potentially over-count mobile species, as transects swum in  $\sim 15$  min allows observers to record mobile fishes that are initially occupying a larger area than the transect dimensions. However, since roi are among the slower-moving of the mobile predators, the relative bias due to mobility would be less pronounced in this species (Ward-Paige et al. 2010). Other sources of error in the belt transect method may be specific to the behavioral patterns of roi. The mean home range of the species was estimated to be 1236 m<sup>2</sup> (Meyer 2008), which would encompass multiple transects, increasing the probability of counting the same individual more than once during the  $\sim 1$  wk survey period, as the density of transects along patches of reef was quite high ( $\sim 15$  ha<sup>-1</sup>). Fixed-area visual survey methods may accurately determine abundances of new recruits and other cryptic species with small home ranges; however, population density estimates for large-bodied, territorial predators such as roi should consider the possible over-counting bias introduced with the fixed-area visual survey method for a small area heavily surveyed within a short ( $< 1$  wk) time frame (present study).

In contrast, the tow-board survey method underestimated roi population density at Puakō by more than half compared to the actual number of roi removed from the patch reef during the fish-down experiment. Roi behavior may be alerted by engine noise, the oscillation of the tow line in the water, and/or the presence of 2 highly visible divers towed behind a boat, and wary roi may seek shelter without being observed within 5 m to either side of the diver. This behavior of a semi-cryptic species in a complex habitat likely ex-

plains the drastic difference between tow-board surveys and belt-transect methods in which divers survey close to the reef and can identify sheltered roi that might otherwise remain out of view during tow-board surveys of the same area. More time is spent in a smaller area during belt-transect surveys, maximizing the chance of observing benthic-associated individuals (Stamoulis & Friedlander 2013). The use of tow-boards for assessing abundances of fish species such as roi that are accustomed to the threat signaled by boats and divers should account for the bias introduced by this conspicuous method. While the consistent use of either the belt-transect or tow-board method could provide a relative measure of roi density, caution should be used when expanding the density estimates obtained by either for use in management planning. Belt-transect results might grossly overestimate the threat posed by roi populations, and conversely, tow-board surveys might underestimate the threat. Both methods could be calibrated by comparison to estimates obtained using the Leslie depletion model (present study).

### Mortality and catchability

Total mortality ( $Z$ ) estimates for North Kona roi populations differed among stock assessment methods. The Beverton & Holt (1956) model is best applied to long-lived, slow-growing species such as roi, which explains the better fit compared to the Ault & Ehrhardt (1991) method that is applicable to short-lived tropical species. Previous work suggests that roi growth does not conform well to the von Bertalanffy growth function (VBGF), and therefore, models based on VBGF parameters should be interpreted cautiously (Donovan et al. 2013). Alternative methods, such as the re-parametrized VBGF (Francis 1988, Trip et al. 2008) and the double model (Porch et al. 2002), performed better for roi in West Hawaii. Although ages were calculated from site-specific growth parameters (Donovan et al. 2013), calculated age becomes less accurate as fish samples approach the mean asymptotic length (Quinn & Deriso 1999), introducing error when including the larger fish in assessment calculations.

The natural mortality rate ( $M$ ) estimated from the Alagaraja (1984) method (0.17) is low compared to  $M$  of 0.40 estimated from the native range of roi (Froese & Pauly 2011). However, most similar-sized groupers, besides *Epinehelus guttatus* (0.68), exhibit a lower  $M$  ranging from 0.18 to 0.30 (Polovina & Ralston 1987). The low  $M$  obtained in this study is reasonable

for Hawai'i roi because of their low vulnerability to predation, food fishing, and parasites (Meyer & Dierking 2011).

Likewise, the calculated fishing mortality ( $F$ ) estimate of ~0.0 to 8.0 % yr<sup>-1</sup> is low, though realistic for roi in Hawai'i given their avoidance as a food fish due to associations with ciguatera poisoning (Dierking & Campora 2009). However, despite the risks of ciguatera, roi are targeted in reported commercial landings. A total of 1472 kg were reported from 2004 to 2009, which comprised ~1% of all state inshore commercial landings (HDAR 2010). This catch may be partly from roi round-up tournaments (J. Giddens pers. obs.), and recreational catch is likely much higher than commercial catch for many reef species (J. Kittinger et al. unpubl.). Catch peaked in 2010 at 1920 kg, and North Kona contributed 1% of the total landings statewide (HDAR 2010). This relatively low commercial fishing pressure explains the low  $F$  for this population of roi.

Because catchability depends in part on the initial density (present study), efficacy of removal will vary by site. Fishing pressure may be high in localized areas where roi are targeted in focused efforts during community roi-roundup events and during individual fisher efforts haphazardly throughout the year. Given the low natural mortality of roi, it is still unclear what broad-scale effect volunteer removal has on populations of roi. A statewide roi population and fisheries assessment will elucidate the larger impacts of removal efforts. Likewise, this manipulative field experiment opens the opportunity to test the ecological effects of the introduced predatory grouper in Hawai'i (J. Giddens et al. unpubl.).

### Roi distribution and movements

The removal experiment suggests that it is possible to fish down and maintain depleted (<90%) populations with a sustained low level of targeted fishing effort. The slow immigration rate of 1 roi every 1 to 2 mo indicates that 2-monthly, 1 d fishing efforts are sufficient to maintain a locally depleted population. Fish assemblage surveys every 6 mo following removal show no roi at the treatment reef 2.5 yr following removal, as any new individuals were dispatched through routine maintenance dives throughout the study period. Given the low ingress of roi after 2 yr of tagging and monitoring, it is not likely that the additional community roi removal at an adjacent reef could have substantially impacted the immigration rate (Fig. 1).

These results suggest that long-term roi eradication is feasible for communities in Hawai'i. However, based on recurring SCUBA diving costs (compressed air, tank rental), fisher hours, and boat time, it was costly (~\$400 ha<sup>-1</sup>) to remove roi via the SCUBA-spear fishing method. Alternatively, volunteer-based roi round-up events have the potential to impact a larger reef area over a shorter period of time. For example, the community-wide roi removal event with 21 volunteer spear fishers dispatched 353 roi in 2 d in the ~12 ha adjacent to the Puakō study site. Note that these events might decrease catchability over a larger area, making it more difficult for SCUBA spear-fisher removal, as was observed for lionfish that learned to avoid fishers after culling events in the Caribbean (Côté et al. 2014). Tow-board surveys documented a sharp decrease in roi population density (from 7.3 to 3.7 roi ha<sup>-1</sup>) following the volunteer fishing effort. A community roi tournament costs approximately \$300 with food, 1 NGO (non-governmental organization) staff member, and supplies (C. Wiggins pers. obs.). Competitive roi tournaments are also expensive to conduct (costing approximately \$2800 for insurance, trophies, T-shirts, food, and entertainment; D. Tanaka pers. comm.), although the community-driven events fulfill social as well as ecological objectives. These events are community exchanges which likely reinforce the social institutions that lead to successful co-management of common resources (Basurto & Ostrom 2009, Kittinger 2013) and ease the fishing pressure on native species.

Experiments on lionfish removal at replicate patch reefs in the Caribbean documented that even partial culling, while requiring substantially less resources than complete eradication, could halt the erosion of native reef fish biomass (Green et al. 2013). Roi tournaments should prioritize accurate catch data collection to determine the broad-scale and site-specific effects of focused roi removal in Hawai'i and should be designed to complement targeted removal efforts to maximize efficiency.

The long-term effects of roi removal on the native reef fish assemblage are still unclear. This removal experiment presents the opportunity to assess the assemblage-level effects of roi in Hawai'i. Further, roi population dynamics can be examined in relation to the recipient ecosystem regime to identify characteristics that may have contributed to the successful invasion of roi over the past several decades. Defining the relative contributions of bottom-up vs. top-down control of roi populations might elucidate a threshold-specific target for management (Kelly et al. unpubl.).

For example, mesopredator release (Prugh et al. 2009) due to overfishing of top predators can lead to declining prey and local extinctions (Stallings 2009, Albins & Hixon 2013). Predation rates in the NWHI are high compared to the Main Hawaiian Islands, where roi dominate the piscivore guild (Friedlander & DeMartini 2002). Roi may be fulfilling a niche that is only opened by overfishing of the native predators. By comparison, in the Caribbean, larger predators such as sharks and groupers (Maljkovi et al. 2008) might be able to prey upon invasive lionfish or suppress foraging success through behaviorally mediated indirect effects, presenting a top-down biocontrol on lionfish populations (Côté et al. 2013). Similarly, in Hawai'i, awareness could be brought to the preservation of top predators and their role in suppressing roi populations.

In addition, the availability of prey may control roi populations. As generalist predators, roi may feed preferentially on those species most common on the reef (Dierking et al. 2009). Little is presently known about the recruitment patterns and the juvenile survival rates of roi in Hawai'i. Further research in these areas relating to the greater ecosystem regime would inform our general understanding of predatory fish invasion biology and elucidate efficient measures for roi population control.

For the public, the perceived decline in native reef fish may be disproportionately attributed to roi, compared to other anthropogenic sources such as run-off, eutrophication (Hamnett et al. 2006), and overfishing (Williams et al. 2008). Roi may be considered a 'scapegoat' in this regard. Nevertheless, stakeholder participation in invasive species management could be an avenue by which to raise awareness of near-shore reef environmental issues and to engage citizens in addressing these concerns. The momentum around roi removal might catalyze collective action towards sustainable resource use and strengthen the community attributes, such as social cohesion and knowledge sharing, that characterize resilient social-ecological systems (Basurto & Ostrom 2009, Ostrom 2009). There is a potential for the 'scapegoat' to become a catalyst for sustainability.

Our findings suggest that it is feasible to control roi populations at the local (<1.3 ha) patch reef scale. However, because the near-shore environment of Hawaii is characterized largely by contiguous reef habitats, there is difficulty in directly scaling up this experiment ecologically and economically. Removal efforts should be conducted over a broad spatial scale to determine any additional challenges to sustained roi depletion over contiguous habitats, such as

increased immigration rates from deep or adjacent reefs. A combination of the controlled fish-down method coupled with community-driven volunteer events may be the most cost-effective method for removing roi and, at the same time, raising fisher participation in community-based ecosystem management. Collaboration at the local and state level will be needed to efficiently reduce and maintain depleted roi populations for fisheries management and ecosystem restoration.

*Acknowledgements.* The authors thank Liz and Michael Morris's family and friends and all of the community volunteers and supporters of marine conservation in Hawai'i. Special thanks to Charles Birkeland, William Walsh, and the Kona Division of Aquatic Resources. Thanks to spear fishermen Kawika Auld and Brian Thomas. Thanks to The Nature Conservancy Marine Team: Russell Amimoto, Kydd Pollock, Zach Caldwell, Rebecca Most, and Ily Iglesias, and thanks for field/tech support from Joe Laughlin and Paolo Usseglio. Thanks to Mary Giddens and Matthew Iacchei for technical support. Finally, we thank Michel Kulbicki and 2 anonymous reviewers for their comments. This material is based upon work supported in part by the National Science Foundation Graduate Research Fellowship (DGE-1329626), National Oceanic and Atmospheric Administration Hawai'i Coral Reef Initiative (NA09NOS4260242), the NOAA Restoration Center, the PADI Foundation (7886), and The Puako Community Association.

#### LITERATURE CITED

- Alagaraja K (1984) Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian J Fish* 31: 177–208
- Albins MA, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ Biol Fish* 96:1151–1157
- Ault JS, Ehrhardt NM (1991) Correction to the Beverton and Holt Z-estimator for truncated catch length-frequency distributions. *ICLARM Fishbyte* 9:37–39
- Balon EK, Brutten MN (1986) Introduction of alien species or why scientific advice is not heeded. *Environ Biol Fish* 16: 225–230
- Basurto X, Ostrom E (2009) Beyond the tragedy of the commons. *Economia delle Fonti di Energia e Dell'ambiente* 52:35–60
- Beverton RJH, Holt SJ (1956) A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *Rapp P-V Reun Cons Int Explor Mer* 140:67–83
- Bienfang PK, Parsons ML, Bidigare RR, Laws EA, Moeller PDR (2011) Ciguatera fish poisoning: a synopsis from ecology to toxicity. In: Walsh, PJ, Smith SL, Fleming LE, Solo-Gabriele H, Gerwick WH (eds) *Oceans and human health: risks and remedies from the sea*, Chap 14. Elsevier Science Publishers, New York, NY
- Bozoc YM, Kulbicki M, Laloë F, Mou-Tham G, Gascuel D (2011) Factors affecting the detection distances of reef fish: implications for visual counts. *Mar Biol* 158:969–981
- Briggs JC (1999) Coincident biogeographic patterns: Indo-West Pacific Ocean. *Evolution* 53:326–335
- Côté IM, Green SJ, Hixon MA (2013) Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biol Cons* 164:50–61
- Côté IM, Darling ES, Malpica-Cruz L, Smith NS, Green SJ, Curtis-Quick J, Layman C (2014) What doesn't kill you makes you wary? Effect of repeated culling on the behavior of an invasive predator. *PLoS ONE* 9:e94248
- DeMartini EE, Friedlander AM (2004) Spatial patterns of endemism in shallow-water reef fish populations of the northwestern Hawaiian Islands. *Mar Ecol Prog Ser* 271: 281–296
- Dierking J (2007) Effects of the introduced predatory fish *Cephalopholis argus* on native reef fish populations in Hawaii. PhD dissertation, University of Hawaii at Manoa
- Dierking J, Campora CE (2009) Ciguatera in the introduced fish *Cephalopholis argus* (Serranidae) in Hawai'i, and implications for fishery management. *Pac Sci* 63:193–204
- Dierking J, Meyer A (2009) Prey regurgitation in the grouper *Cephalopholis argus*. *J Appl Ichthyology* 25:600–602
- Dierking J, Williams ID, Walsh WJ (2009) Diet composition and prey selection of the introduced grouper species peacock hind (*Cephalopholis argus*) in Hawai'i. *Fish Bull* 107:464–476
- Division of Fish and Game (1956) Annual report of the Board of Agriculture and Forestry, Territory of Hawai'i. Fiscal Year 1 July 1955 to 30 June 1956. The Board, Honolulu
- Donovan MK, Friedlander AM, DeMartini EE, Donahue MJ, Williams ID (2013) Demographic patterns in the Peacock grouper (*Cephalopholis argus*), an introduced Hawaiian reef fish. *Environ Biol Fishes* 96:981–994
- ESRI (2011) ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, CA
- Francis R (1988) Maximum-likelihood estimate of growth and growth variability from tagging data. *N Z J Mar Freshw Res* 22:43–51
- Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar Ecol Prog Ser* 230:253–264
- Friedlander AM, Brown E, Monaco ME (2007) Defining reef fish habitat utilization patterns in Hawai'i: comparisons between marine protected areas and areas open to fishing. *Mar Ecol Prog Ser* 351:221–233
- Friedlander AM, Keller K, Wedding L, Clarke A, Monaco M (eds) (2009) A marine biogeographic assessment of the Northwestern Hawaiian Islands. NOAA Technical Memorandum NOS NCCOS 84. Prepared by NCCOS's Biogeography Branch in cooperation with the Office of National Marine Sanctuaries Papahānaumokuākea Marine National Monument, Silver Spring, MD
- Froese R, Pauly D (2011) FishBase, version (12/2011). [www.fishbase.org](http://www.fishbase.org) (accessed on 15 August 2012)
- Green SJ, Dulvy NK, Brooks AML, Akins JL, Cooper AB, Miller S, Côté IM (2013) Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecol Appl* 24:1311–1322
- Hamnett M, Lui M, Johnson D (2006) Fishing, ocean recreation, and threats to Hawai'i's coral reefs. Social Science Research Institute, University of Hawai'i at Manoa, HI
- HDAR (Hawai'i Division of Aquatic Resources) (2010) Commercial marine landings summary trend report. Department of Land and Natural Resources, State of Hawai'i, Honolulu, HI

- HDAR (2011) Administrative rules. Department of Land and Natural Resources, State of Hawai'i, Honolulu, HI
- Hayes T, Hourigan TF, Jazwinski SC, Johnson SR (1982) The coastal resources, fisheries and fishery ecology of Puakō, West Hawai'i. Hawai'i Coop Fish Res Unit Tech Rep 82: 153–156
- Holzwarth SR, Demartini EE, Schroeder R, Zgliczynski BJ, Laughlin JL (2003) Sharks and jacks in the Northwestern Hawaiian Islands from towed-diver surveys 2000–2003. NOAA Pacific Islands Fisheries Science Center, Honolulu, HI, [www.pifsc.noaa.gov/library/pubs/HolzworthARB543\\_Final.pdf](http://www.pifsc.noaa.gov/library/pubs/HolzworthARB543_Final.pdf)
- Hourigan TF, Reese ES (1987) Mid-ocean isolation and the evolution of Hawaiian reef fishes. *Trends Ecol Evol* 2: 187–191
- Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Kimura DA (1977) Statistical assessment of the age-length key. *J Fish Res Board Can* 34:317–324
- Kittinger JN (2013) Participatory fishing community assessments to support coral reef fisheries co-management. *Pac Sci* 67:361–381
- Kulbicki M, Cornuet N, Vigliola L, Wantiez L, Mou-Tham G, Chabanet P (2010) Density estimates of coral reef fishes: transect length matters. *J Exp Mar Biol Ecol* 387:15–23
- Leslie PH, Davis DHS (1939) An attempt to determine the absolute number of rats on a given area. *J Anim Ecol* 8: 94–113
- Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species. A selection from the Global Invasive Species Database. First published as special lift-out in *Aliens* 12, December 2000, updated and reprinted version November 2004. The Invasive Species Specialist Group (ISSG), a specialist group of the Species Survival Commission of the World Conservation Union (IUCN), Auckland
- Maljkovi A, Van Leeuwen TE, Cove SN (2008) Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs* 27:501–505
- Meyer A (2008) *Cephalopholis argus*: an ecological comparison of the species in introduced and native populations. PhD dissertation, University of Hawai'i, Manoa, HI
- Meyer A, Dierking J (2011) Elevated size and body condition and altered feeding ecology of the grouper *Cephalopholis argus* in non-native habitats. *Mar Ecol Prog Ser* 439:203–212
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Front Ecol Environ* 6:485–492
- Mora C (2008) A clear human footprint in the coral reefs of the Caribbean. *Proc Biol Sci* 275:767–773
- Ostrom E (2009) A general framework for analyzing the sustainability of complex social-ecological systems. *Science* 325:419–422
- Parkes G, Moreno CA, Pilling G, Young Z (1996) Use of the Leslie stock depletion model for the assessment of local abundance of patagonian toothfish (*Dissostichus eleginoides*). *CCAMLR Sci* 3:55–77
- Polovina J, Ralston S (1987) Tropical snappers and groupers biology and fisheries management. Westview Press, Boulder, CO
- Porch CE, Wilson CA, Nieland DL (2002) A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenetic changes in growth rates. *Fish Bull* 100:149–152
- Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. *Bioscience* 59:779–791
- Quinn TJ, Deriso RB (1999) Quantitative fish dynamics. Oxford University Press, Oxford
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Randall JE (1987) Introduction of marine fishes to Hawaiian Islands. *Bull Mar Sci* 41:490–502
- Ricker W (1975) Computation and interpretation of biological statistics and fish populations. *Bull Fish Res Board Can* 191:1–382
- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Am Zool* 37:621–632
- Stallings CD (2009) Predator identity and recruitment of coral-reef fishes: indirect effects of fishing. *Mar Ecol Prog Ser* 383:251–259
- Stamoulis KA, Friedlander AM (2013) A seascape approach to investigating fish spillover across a marine protected area boundary in Hawai'i. *Fish Res* 144:2–14
- Trip EL, Choat JH, Wilson DT, Robertson DR (2008) Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. *Mar Ecol Prog Ser* 373:97–109
- Vignon M, Sasal P, Galzin R (2009) Host introduction and parasites: a case study on the parasite community of the peacock grouper *Cephalopholis argus* (Serranidae) in the Hawaiian Islands. *Parasitol Res* 104:775–782
- Walsh W, Cotton S, Barnett C, Couch C, Preskitt L, Tissot B, Osada-D'Avella K (2013) Long-term monitoring of coral reefs of the main Hawaiian Islands. Final report, 2009 NOAA Coral Reef Conservation Program. Hawai'i Island monitoring report NA09NOS4260100, 10/01/2009–12/31/2012. Division of Aquatic Resources, Department of Land & Natural Resources, Honolulu, HI
- Ward-Paige C, Flemming-Mills J, Lotze HK (2010) Over-estimating fish counts by non-instantaneous visual censuses: consequences for population and community descriptions. *PLoSOne* 5:e11722
- Williams ID, Walsh WJ, Schroeder RE, Friedlander AM, Richards BL, Stamoulis KA (2008) Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environ Conserv* 35:261–272

Editorial responsibility: Tim McClanahan, Mombasa, Kenya

Submitted: December 10, 2013; Accepted: June 13, 2014  
Proofs received from author(s): September 9, 2014