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Population parameters and conservation implications for one of the world's rarest marine fishes, the red handfish (*Thymichthys politus*)

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Abstract

Population estimates are required for effective conservation of many rare marine species, but can be difficult to obtain. The critically endangered red handfish (*Thymichthys politus*) is a coastal anglerfish known only from two fragmented populations in southeast Tasmania, Australia. It is at a high risk of extinction due to low numbers, loss of habitat, and the impacts of climate change. To aid conservation efforts, we provide the first empirical population size estimates of red handfish and investigate other important aspects of the species' life history, such as growth, habitat association, and movement. We surveyed both red handfish local populations via underwater visual census on scuba over 3 years and used photographic mark-recapture techniques to estimate biological parameters. In 2020, the local adult population size was estimated to be 94 (95% confidence interval [CI] 40–231) adults at one site, and 7 (95% CI 5–10) at the other site, suggesting an estimated global population of 101 adults. Movement of individuals was extremely limited at 48.5 m (± 77.7 S.D.) per year. We also found evidence of declining fish density, a declining proportion of juveniles, and increasing average fish size during the study. These results provide a serious warning that red handfish are likely sliding toward extinction, and highlight the urgent need to expand efforts for ex situ captive breeding to bolster numbers in the wild and maintain captive insurance populations, and to protect vital habitat to safeguard the species' ongoing survival in the wild.

KEYWORDS

IUCN red list, mark-recapture, nursery habitat, reef, seagrass, threatened species

1 | INTRODUCTION

Knowledge of population demographics and life histories is fundamental to the successful and informed management of threatened species (Sutherland, 2008). Biological parameters such as population size, survival, movement, and growth represent important measures for assessing the success of conservation efforts (Caughley & Gunn, 1996). Monitoring these parameters can allow managers and researchers to determine if a population is changing through time, identify specific habitat requirements, and help avoid issues associated with shifting baselines, where population declines may go unnoticed (Pauly, 1995). An understanding of these parameters can also assist in teasing apart the impacts of pressures on a species, such as stochastic events, human impacts, natural variability in the population (e.g., births, deaths, movement), and the performance of conservation intervention (Krebs, 1995). However, accurately estimating these biological parameters can be difficult (Manning & Goldberg, 2010), especially when the species of interest is marine and rare (e.g., Bozec et al., 2011; Durso et al., 2011).

The handfishes (Brachionichthyidae) are an ancient family of anglerfish (Lophiiformes) consisting of 14 species, all of which are confined to Australian waters (Last & Gledhill, 2009). Members of this family possess modified pectoral fins resembling hands with which they use to preferentially "walk" across the sea floor instead of swimming. Handfishes exhibit various qualities that make them particularly vulnerable to extinction, such as lacking a dispersive pelagic larval stage, and high energetic cost to reproduction, investing in fewer, larger eggs that are guarded by the mother during development (Bruce et al., 1997; Last & Gledhill, 2009). These features have contributed to the handfishes being described as the most threatened family of marine fishes in the world (Stuart-Smith, Edgar, Last, Linardich, et al., 2020) with the IUCN's Red List assessments listing 7 of the 14 described species in the family as endangered or critically endangered (see Stuart-Smith et al. 2020a). Three species—the spotted handfish (*Brachionichthys hirsutus*), Ziebell's handfish (*Brachiopsilus ziebelli*) and the red handfish (*Thymichthys politus*)—are recognized as critically endangered internationally on the IUCN Red List (Edgar et al. 2020a; Last et al., 2020; Stuart-Smith et al. 2020b) and nationally on the Australian Environmental Protection and Biodiversity Conservation Act, with all three species being the subject of a formal Australian government recovery plan (Commonwealth of Australia, 2015).

Red handfish are small (<90 mm) and highly cryptic, inhabiting temperate coastal reefs less than 6 m deep, and are most often observed underneath algal canopies (Edgar et al., 2017; Last & Gledhill, 2009). Once known to exist on the north and east coasts of Tasmania (Last & Gledhill, 2009), and despite recent comprehensive searches for new populations of the red handfish (Edgar et al., 2015; Edgar et al., 2017), the species is now only known from two small populations in the southeast corner, in an area of habitat totaling approximately 4000 m^2 combined. It is considered particularly vulnerable to extinction, with various continuing pressures possibly contributing to suspected low population sizes, including habitat loss through overgrazing by a native urchin (*Heliocidaris erythrogramma*), various localized anthropogenic impacts, and potentially climate change (Bessell et al., 2022). Conservation efforts for the species only began in late 2018, and include headstarting (i.e., raising fish from eggs in captivity that are then released into the wild to bolster numbers) (see Thomas et al., 2019) as well as habitat restoration attempts through management of urchin numbers (Stuart-Smith et al., 2021). Although conservation strategies are in place for the species, currently reliable population estimates for red handfish are lacking. Informal estimates of population size have proposed that around 100 individuals remain in the wild (Stuart-Smith et al., 2021), though these have been based on expert opinion. No formal estimate of population size based on field research has been undertaken, despite recognition of the importance of this for effective conservation.

Mark-recapture is a common approach used to track individuals through time and can be used to obtain estimates of abundance. The approach considers encounter histories of marked individuals over multiple capture events and has been widely used for marine animals (e.g., Claassens & Harasti, 2020; Grossman et al., 2019; Harasti, 2016; Harasti et al., 2012; Martin-Smith, 2011; Shine et al., 2021; Van Cise et al., 2021). Depending on the model used, assessments can be made of population parameters, such as survival and probability of recapture (e.g., Cormack, 1964; Jolly, 1965; Seber, 1965), probability of entry to a population (e.g., Schwarz & Arnason, 1996), recruitment, and population growth (e.g., Link & Barker, 2005; Pradel, 1996). These types of studies often require large sample sizes, which can be challenging to obtain when working with rare or sparse populations, as is often the case with threatened species. Therefore, other measures, such as densities obtained from carefully designed quantitative surveys in key habitat, can be suitable alternatives to track population trends in rare and threatened species (e.g., Foster & Vincent, 2004; Sanchez-Camara et al., 2006), including handfish (e.g., Edgar et al., 2017; Lynch et al., 2022; Wong et al., 2018).

In addition to estimating abundance, mark-recapture studies allow for the assessment of species' movement patterns. Understanding the movement patterns of threatened species can be extremely valuable for conservation efforts. For example, knowledge that a species is highly mobile will allude to the need for a broader protection network, with the conservation of the species depending on the condition and protection of multiple sites (see Runge et al., 2014). Conversely, understanding that a species is mostly sedentary would suggest the species may be particularly prone to extinction from stochastic processes (e.g., Sekercioglu, 2007).

Non-invasive methods of marking are preferable for studies of threatened species that require individual identification, such as mark-recapture studies. One alternative to more traditional invasive approaches such as tagging is the use of natural marks or patterns of an animal, recognized from images of animals in the wild. This technique, known as photo-identification (photo-ID), has been applied to many marine species, including fishes (e.g., Araabi et al., 2000; González-Ramos et al., 2017; Martin-Smith, 2011; Read et al., 2003) and a related handfish. Studies of the spotted handfish (*B. hirsutus*) have utilized the unique spot patterns along the body of this species to successfully photo-ID individuals and to track their abundance, growth, and movement through time (Bessell, 2018; Moriarty, 2012). Because red handfish also display unique spots and patterns, an opportunity exists for application to this species for use in a mark-recapture study.

The primary aim of this study was to reduce uncertainty around the current population sizes of red handfish. The objectives of this study were to (1) establish the first estimates of the population size of red handfish in terms of both abundance (based on mark-recapture population models) and density (using counts per underwater survey), and to determine if these two approaches yielded similar results, and (2) using the field data collected for the population estimates, better understand other important aspects of the species' life history, such

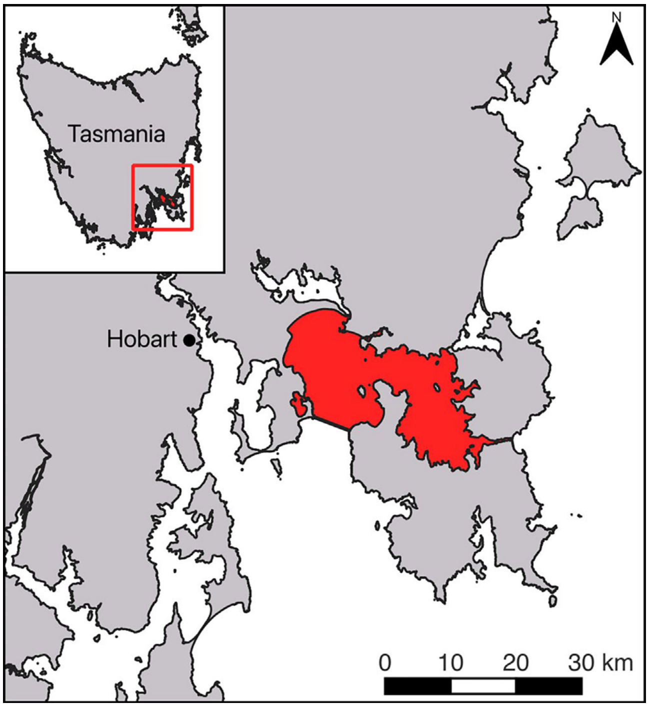

FIGURE 1 The study region in southeast Tasmania, Australia.

as growth, movement, and habitat use. These combined objectives sought to provide information to better guide conservation actions for red handfish.

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

The two study sites are located in southern Tasmania (Figure 1) close to shore, reaching a maximum depth of around 6 m, and consist of vegetated rocky reefs, and *Heterozostera nigricaulis* seagrass beds. Site locations are undisclosed due to concern for disturbance/impact or poaching (Bessell et al., 2022). Here we refer to these two populations as "Site 1" and "Site 2". Site 1 is primarily characterized by a high-complexity rocky reef with defined habitat boundaries of sand or bare rocky urchin barrens bordering the site (beyond which no red handfish have been observed in >15 years; T. Bessell, *pers obs*). It has an approximate total area of 1000 m^2. Site 2 is comprised of a low-complexity reef and large seagrass beds. It is located within a sheltered bay and is approximately 3000 m^2. The site's boundaries appear to vary seasonally, with suitable habitat often continuing around the bay onto a slightly more wave exposed shore.

We monitored red handfish at the two sites from 2019 to 2021 via two survey approaches. First, in summer 2019 and summer 2020, Reef Life Survey (www.reeflifesurvey.com) divers completed comprehensive censuses over 3 days that systematically searched for fish across most of the area of both sites. During these censuses, ~ 1 m $\times$ 50 m belt transects ($\sim$50 m^2) were placed in parallel, immediately adjacent to each other so that the entire seabed was searched at each site. Each belt transect was then searched for red handfish. Then, in 2020–2021, University of Tasmania divers monitored two fixed position transects at Site 1, and three fixed position transects at Site 2, every 2–4 weeks to assess changes in population size over time. These transects were 6 m $\times$ 50 m (300 m^2) belt transects (modified from Edgar et al. 2020b), with two divers each searching a 3 m $\times$ 50 m swath either side of the line. This disparity in transect search areas (300 m^2 for fixed position transects vs. $\sim$50 m^2 for the censuses) was in an effort to maximize time efficiency, area covered, and the number of fish sighted during the summer 2019 and 2020 censuses with multiple divers in the water at the same time. Over the 3 years, 141 transects were completed across the two sites, equating to 20,550 m^2 searched (Table 1) and totaling over 195 person-hours of underwater visual census effort.

When a red handfish was found, both sides of the fish were photographed, its length measured using calipers to the nearest millimeter, and a broad category of fine-scale habitat (either "seagrass," "red algae," "green algae," "brown algae," or "no cover") was recorded for the 0.5 m^2 area (0.5 m $\times$ 0.5 m, estimated visually) it was found within. In cases where fine-scale habitat was evenly split, the immediate surroundings (within approximately 5 cm) of the individual fish provided a tie-break. The fish's location was also recorded by a diver towing a tethered float with a GPS that was time-synchronized with the diver's camera to allow positioning of the location of each fish to within approximately <7 m (*see* Lynch et al., 2015; Schories & Niedzwiedz, 2012; Wong et al., 2018).

2.2 | Individual identification for mark-recapture abundance estimation

Red handfish have unique markings in the form of spots, blotches, and warty growths that allow for individual identification. Using these features, individual fish were identified from photographs taken of both sides of individuals observed during all censuses and surveys. Identifications were assessed manually by two independent researchers, aided by the computer-assisted photo-identification software *I^3S Classic* v4.02 (www.reijns.com/i3s), to reduce the possibility of incorrect identifications. Once an individual was identified, it was given a unique identification code, and images were stored in a database. Red handfish are not currently known to alter their spot patterns (some individuals observed multiple years apart display the same spot pattern), though some uncertainty exists around the stability of their patterns. Therefore, this remains a potential source of bias that may reduce resighting rates, and thus inflate abundance estimates.

Because the identification of red handfish individuals is based on photographs, we implemented a quality control protocol to remove poor-quality images from our database to reduce risk of misidentification (*see* Friday et al., 2000; Gowans & Whitehead, 2001; Read et al., 2003). Similar to the systems developed by Urian et al. (1999) and Read et al. (2003), we graded photographs on photographic quality (PQ). Images were assessed for focus and clarity, contrast of spots,

TABLE 1 Search effort for red handfish from 2019 to 2021.

	2019		2020		2021	
	Censuses[a]	Fixed transects[b]	Censuses[a]	Fixed transects[b]	Censuses[a]	Fixed transects[b]
Site 1 (1000 m^2)	18 (900 m^2)	–	7 (350 m^2)	2 (600 m^2)	–	13 (3900 m^2)
Site 2 (3000 m^2)	42 (2100 m^2)	–	27 (1350 m^2)	9 (2700 m^2)	–	23 (6900 m^2)

Note: The values given are the number of transects completed for each survey approach, and the area covered for each survey approach is reported in parentheses.
[a]Belt transects that comprised the censuses were ~50 m^2 each.
[b]Fixed position transects were 300 m^2.

angle of the fish relative to the photographer, and visibility of spot patterns, each on a scale of 1–5, with a lower value being assigned to better-quality images. The sum of the scores for these five criteria gave a final PQ score. Images with PQ scores greater than 9 were omitted from the database. Additionally, we omitted records where images of only a single side of a fish were available.

2.3 | Abundance and density analysis

Encounter histories of red handfish were created based on first sightings ("captures") and subsequent resightings ("recaptures") using photo-identification as a non-invasive "marking" tool. We pooled sampling effort by year and ignored resightings within each year for the purpose of abundance estimation. In addition to the PQ control protocols outlined earlier, we also excluded records of juveniles from our mark-recapture analysis because of uncertainty surrounding the stability of their markings and patterns (T. Bessell, pers. obs). We classify juveniles as fish <45 mm total length, based on maturity being reached at approximately >45 mm total length in individuals kept in captivity at around the 1.5-year mark (J. Stuart-Smith, pers. obs). Therefore, the population parameters we estimate using mark-recapture methods are for adult red handfish only.

We primarily analysed our mark-recapture data within the Programme MARK software (White & Burnham, 1999) using a POPAN parametrization of the Jolly-Seber model (Schwarz & Arnason, 1996). We used this model because (1) our primary objective was to estimate red handfish abundance and (2) the length of our study period allowed for births, deaths, immigration, and emigration, in addition to 42 headstarted juveniles that were released during the study (see below; Stuart-Smith et al., 2021). The POPAN formulation estimates rates of apparent survival (φ), resighting probability (p), probabilities of entry to the population ($pent$), and size of the "superpopulation" (N). The superpopulation parameter is an estimate of the total number of individuals theoretically present in the study area between the first and last capture occasions. Estimates of annual abundance (N_i) can then be derived from the models using estimated values for p. However, as with other Jolly-Seber models, some parameters risk being confounded as a result of being unable to estimate all parameters before an individual's first "capture" and after their last (Schwarz & Arnason, 1996). Thus, only abundance for the second year of our three-year study can be reliably calculated. Although we do report annual abundance for 2019 and 2021, we place most emphasis on estimates for 2020, which we consider most reliable.

Because of the species' limited dispersal capabilities (and longer-term photographic records from recreational divers), we were confident that no movement occurs between the two known red handfish populations. We therefore fit separate models for both Site 1 and Site 2, with the saturated models (i.e., all parameters being time dependent, marked as "t") for both sites being expressed as $\varphi_{(t)}\ p_{(t)}\ pent_{(t)}$. Subsequent candidate models consisting of parameters that were constant (i.e., the parameter did not vary with time) were marked with a dot ("."). We assessed goodness-of-fit (GOF) of our saturated models using Fetcher's variance inflation factor, $\hat{c}$ (Fletcher, 2012), because other built-in GOF routines within MARK were not available for our data. Generally, a $\hat{c}$ value of 3 or less indicates a reasonable fit (Lebreton et al., 1992). We also qualitatively tested the sensitivity of our models to incremental adjustments of $\hat{c}$ between the values 1.0–2.0, observing for changes in model rankings—a change in rankings following $\hat{c}$ adjustments indicates potential inadequacy of the final model. Following these GOF tests, parameters from the saturated model that could not be justified by the data were excluded, with the most parsimonious model for each site being selected based on AIC. A global population estimate was indirectly estimated by summing up the annual abundances estimated by the models for Site 1 and Site 2.

Importantly, the study spanned a preliminary "headstarting" effort, where eggs from two clutches were collected from Site 2 in 2019 and reared in captivity. Forty-two individuals were subsequently released back into the wild in 2020 (28 fish at Site 1, and 14 fish at Site 2; Stuart-Smith et al., 2021). Eighty surveys were conducted before this release (10 at Site 1 and 70 at Site 2), and 46 were conducted after release (15 at Site 1 and 31 at Site 2). Thus, any trends in abundance that we observe between 2020 and 2021 will include the effect of this direct intervention on population size. We only expected signs of this intervention to occur between 2020 and 2021 because this is when any reduced recruitment at Site 2 from egg removal may have become apparent, and when introduced juveniles (fish <45 mm long) at both sites may have become large enough for inclusion in the study.

As an additional measure of population size, we calculated the density of red handfish per 100 m^2 based on all the transect counts. This was calculated based on the following formula:

$$\text{Density (fish per 100 m}^2) = \left(\frac{\text{Number of sighted fish}}{\text{Transect search area } (m^2)}\right) \times 100 \quad (1)$$

Final densities at each site per year were an average of the calculated transect densities.

Then, to compare abundance estimates from the mark-recapture models with the calculated densities, we converted total abundance estimates from the mark-recapture study and population model to densities using the following formula:

$$\text{Mark-recapture derived density (fish per 100 m}^2) = \left(\frac{\text{Abundance estimate}}{\text{Site area } (m^2)}\right) \times 100 \quad (2)$$

To inform future monitoring efforts for red handfish, and to track trends through time, we conducted a power analysis to determine the number of repeated transects required to detect a significant density change using the "pwr" package in R (R Core Team, 2022). We only used density data collected from Site 2 in 2021 for this analysis to maintain a standardized transect area, because transect sizes varied in the previous years. We resampled the data 3000 times for up to 50 repeated transects, and calculated the resulting power using the pwr.t.test() function (with a significance level of 0.05) for detecting three scenarios of change in red handfish density: 30%, 50%, and 80%. We selected these scenarios based on the thresholds outlined by the IUCN's Red List Criteria for future reduction in population size (Criterion A3; see IUCN, 2012). We set our minimum acceptable power at 0.80 (Quinn & Keough, 2002).

2.4 | Length, growth, and movement analysis

Length, growth, and movement information was determined using data from resighted individuals. For these analyses we included all resighting records, including intra-year records, and records of juveniles where positive identification was beyond any doubt. However, length analysis only included data collected from Site 2 because of the extremely low population size at Site 1. Growth of resighted individuals was calculated by determining the difference in length between sightings.

After data for normality was checked, an ANOVA was used to test for differences in mean length, growth, and net movement values between groups (year, site, or size class), with the use of a Tukey's HDS post hoc test to distinguish between any significant differences. To test for differences between length-frequency distributions between years, we used a bootstrapped Kolmogorov–Smirnov test with 5000 samples using the ks.boot() function from the "Matching" package (Sekhon, 2011). Finally, the distance moved by a fish between resightings was determined manually using Google Earth Pro (www.google.com/earth).

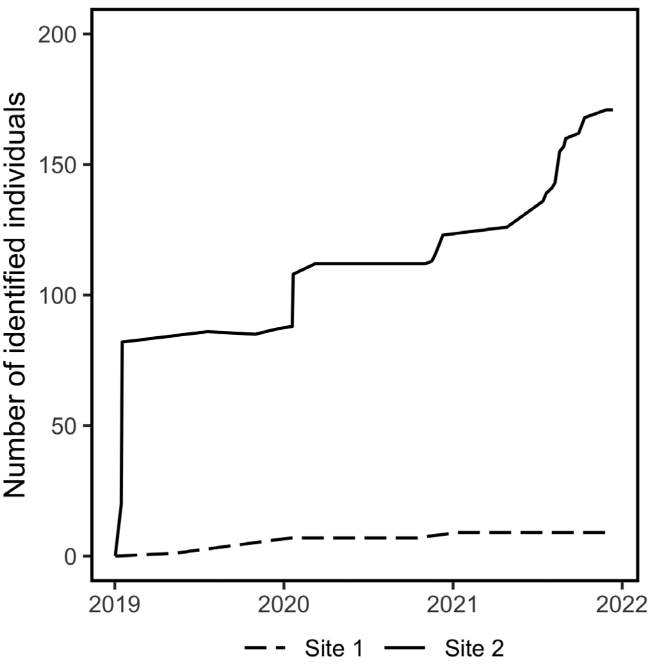

FIGURE 2 Discovery curve of individual adult red handfish from 2019 to 2021.

3 | RESULTS

3.1 | Abundance and density analysis

During our 3-year study, we made a total of 397 observations of red handfish: 22 at Site 1 and 375 at Site 2. After removing records of juveniles (fish <45 mm long), records of fish with only images of one side, and records with unacceptable photographic quality scores, 225 remaining observations (19 at Site 1 and 206 at Site 2) were available for mark-recapture analysis (Figures 2 and 3a,b). Of these remaining observations, a total of 184 individual fish sighted between 2019 and 2021 were identified (9 fish at Site 1 and 175 fish at Site 2), meaning that 18.2% of the database (41 observations) were resightings. Most resightings were of fish observed on two occasions; however, three individuals were sighted on four separate occasions. The largest time between the first and last sightings of a red handfish was 935 days, which was initially measured at 46 mm, and was 60 mm on its last sighting.

After intra-year resightings were removed, capture histories for 174 individuals (9 at Site 1 and 174 at Site 2) were available for use in building mark-recapture models (Supplementary Material). Both saturated mark-recapture models had reasonable GOF, with Fletcher-ĉ values of 1.95 and 2.81 for Site 1 and Site 2, respectively. Additionally, manual incremental increases of ĉ did not affect candidate model rankings for either site, and thus we were confident the saturated models sufficiently explained the data. From the set of candidate models (Supplementary Material), the models with no time effect for φ or *p*, but included a time effect for *pent* (i.e., $\varphi_{(.)}\ p_{(.)}\ pent_{(t)}$), were

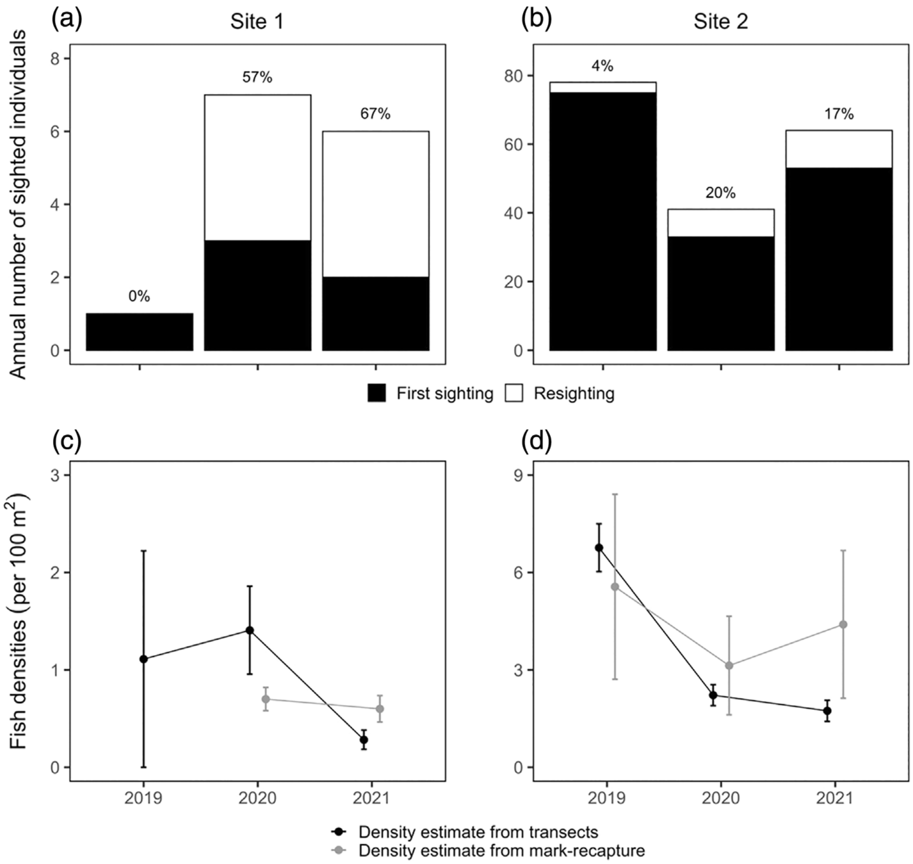

FIGURE 3 (a, b) Number of first sightings (black) and resightings (white) of adult red handfish. Percentages are the proportion of observations that were resightings each year. Note differing scales on the *y*-axis between Site 1 and Site 2. (c, d) Mean densities of red handfish using counts per underwater survey (black) and densities converted from mark-recapture abundance estimates (gray). Error bars are standard errors. See Table 1 for search effort. Note differing scales on the *y*-axis between Site 1 and Site 2.

TABLE 2 Jolly-Seber (POPAN) derived annual abundance estimates of adult red handfish from 2019 to 2021.

	Site 1		Site 2	
Year	Estimate ± S.E.	95% C.I.	Estimate ± S.E.	95% C.I.
2019	NA[a]	NA[a]	167 ± 85	65–429
2020	**7 ± 1**	**5–10**	**94 ± 46**	**38–231**
2021	6 ± 1	4–9	132 ± 68	51–343

Note: That estimates for the year 2020 (in bold) are the primary basis for conclusions, and caution is advised when interpreting the 2019 and 2021 estimates due to a lack of data from surrounding years on which to anchor estimates, and due to the addition of captive reared individuals to both sites in 2020 (therefore artificially increasing recruitment).
[a]Estimate not available due to only a single observation at this site in 2019.

chosen based on the AIC for both sites (Site 1: AICc = 27.25, AICc weight = 0.88, parameters = 4; Site 2: AICc = 139.13, AICc weight = 0.38, parameters = 5). The models indicated that the apparent survival (φ) of red handfish at Site 1 (0.63, 95% CI 0.29–0.87) was more than double the apparent survival at Site 2 (0.30, 95% CI 0.12–0.57; Table 2). Similarly, sighting probability (*p*) at Site 1 (0.99, 95% CI 0.99–1.00) was also more than double the sighting probability at Site 2 (0.47, 95% CI 0.12–0.85). The probability of an individual to enter the sampled population (*pent*) at Site 1 was estimated at 0.22 ± 0.14 (95% CI 0.06–0.58) for 2020, whereas at Site 2 *pent* was estimated at 0.33 ± 0.04 (95% CI 0.26–0.42) for the same year.

The total superpopulation size (*N*) of adult red handfish across the whole study period (from 2019 to 2021) was estimated to be 11 (95% CI 9–14) individuals at Site 1, and 315 (95% CI 200–812) individuals at Site 2. Derived estimates of abundance by site and year are reported in Table 2. The models estimated abundance in 2020 to be 7 adult fish (95% CI 5–10) at Site 1, and 94 adult fish (95% CI 40–231) at Site 2 (Table 2). This suggests a global adult population of 101 fish in 2020.

Density data from direct counts of individuals on transects also confirmed that the overall density at Site 1 was much lower than at Site 2 (Figure 3c,d). The highest mean (± SD) density at Site 1 was in 2020 with 1.41 ± 0.45 fish per 100 m^2, whereas at Site 2 it was 6.76 ± 0.74 fish per 100 m^2 in 2019. Our data do suggest a decline in red handfish density over the study period at both sites, though this is more obvious at Site 2, particularly from 2019 to 2020. Once converted into individuals per 100 m^2, density estimates derived from mark-recapture data were remarkably similar to those derived from underwater visual census (UVC) counts of fish observed on transects (Figure 3c,d), noting the potential for inaccurate abundance estimates in 2019 and 2021.

Power to detect significant population change through time based on the density data from UVC monitoring increased with the size of the population change to be detected and the sampling intensity used (the number of UVC transects). The power analysis indicated that at least twelve 50 m × 6 m (300 m^2) transects per site would be required per year to detect interannual population decline or increase

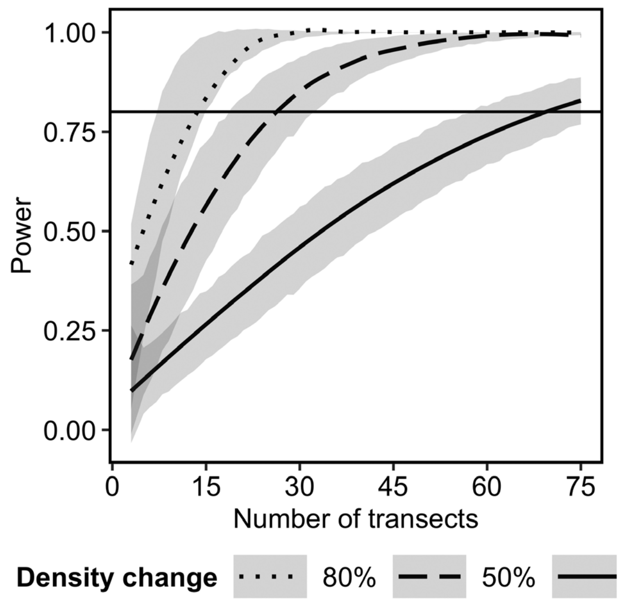

FIGURE 4 Simulated number of transects required (using 2021 density data from underwater surveys) for detecting red handfish population size changes under three scenarios of population decline. Shaded areas represent standard deviations. Horizonal line indicates a power threshold of 80%.

of 80% or more, with the conventionally accepted 80% power (Figure 4). To detect a 50% change in density at the same level of power, at least 27 transects per site would be required. However, to achieve 80% power of detecting a density change as small as 30%, a minimum of 70 transects per year would be required.

3.2 | Habitat association

The most frequently used habitat types (Figure 5) at Site 1 were brown and green algae, with 40.0% of the 20 observations of red handfish associated with each. The remaining 20.0% of observations at the site were in the open with no immediate surroundings (no cover). At Site 2, seagrass was the most frequently used habitat type, with over half (57.0%) of the 356 fish observations at the site hiding among seagrasses. A breakdown of habitat association by year and site can be seen in Figure S1. This was followed by brown algae (35.7%). Very few individuals were found in other habitat classifications, with only 3.9% not associated with any algal cover, 3.1% in red algae, and 0.3% green algae.

3.3 | Length, growth, and movement

Across all observations from Site 2, the mean (± SD) total length of red handfish was 58.6 ± 11.3 mm ($n = 375$) and ranged from 10.0 to 80.0 mm. Adult fish (>45 mm) made up 86.6% of all observations, whereas 13.4% of observations were of juvenile fish (<45 mm). Mean total length increased slightly over the 3 years, from 56.1 ± 12.0 mm ($n = 158$) in 2019, to 59.5 ± 11.3 mm in 2020 ($n = 84$), and 61.2 ± 9.8 mm ($n = 133$) in 2021 (ANOVA, $df = 2$, F9.07, $p \leq 0.001$), and a Tukey's HDS post hoc test determined that fish mean total length in 2019 was smaller than that in both 2020 and 2021.

A similar annual result was also found in yearly length-frequency distributions (Figure 6), with Kolmogorov–Smirnov tests detecting a difference between the 2019 and 2021 distributions ($p \leq 0.01$). No differences were detected between the 2019 and 2020 distributions ($p \geq 0.05$), or the 2020 and 2021 distributions ($p \geq 0.05$). Qualitatively, interannual size distribution differences could be seen in the proportions of smaller- to medium-sized fish between years. For example, the proportion of individuals over 70 mm (an arbitrary threshold) remained relatively stable between years, at 16.6% (25 fish), 21.3% (16 fish), and 17.4% (20 fish) in 2019, 2020, and 2021, respectively (Figure 6). However, the proportion of juveniles (<45 mm) decreased, dropping from 16.6% (25 fish) and 14.7% (11 fish) in 2019 and 2020 to only 6.1% (7 fish) in 2021.

Using our recapture data, growth was fastest in fish less than 50 mm, with rates slowing as fish grew larger (Table 3). The highest growth rates were recorded in the two smallest size classes, though there was a lack of observations of fish <40 mm in our dataset from which to reliably estimate growth at smaller size classes. The mean (± SD) growth rate across all size classes was 11.4 ± 26.0 mm per year ($n = 54$).

The mean (± SD) net movement rate of resighted fish was 48.5 ± 77.7 m ($n = 53$; Table 3). The greatest net distance moved by a fish was 99.5 m, although 12 of the 54 resighted individuals had moved less than 10 m, with one fish recorded only 0.3 m away from the original sighting (544 days later; noting GPS location error is larger than this distance). No differences in mean net movement were observed between the four 10-mm length classes from 40 mm to 80 mm (Table 3; ANOVA, $df = 3$, F1.36, $p \geq 0.05$), nor in mean net rate of movement (ANOVA, $df = 3$, F0.39, $p \geq 0.05$). However, movement was higher in fish whose time at large (i.e., the time between sightings) was greater than a year (mean = 37.4 ± 31.3 m, $n = 25$) compared to those whose time at large was less than a year (mean = 19.1 ± 18.5 m, $n = 33$; ANOVA, $df = 1$, F4.92, $p \leq 0.05$). We detected no movement between the two populations, although we did not conduct any searches for red handfish outside of the core study sites.

4 | DISCUSSION

This is the first study to collect quantitative field-based observations to estimate the global population of the critically endangered red handfish at its two known populations. We estimate abundance to be low; even at the highest 95% confidence limit at the population with the greatest number of fish, the mark-recapture model predicted no more than 231 adult individuals in 2020, making this species likely among the rarest of marine fishes in the world. A separate study of the detectability of red handfish in our transect-based survey methods has shown the method to be highly effective at locating

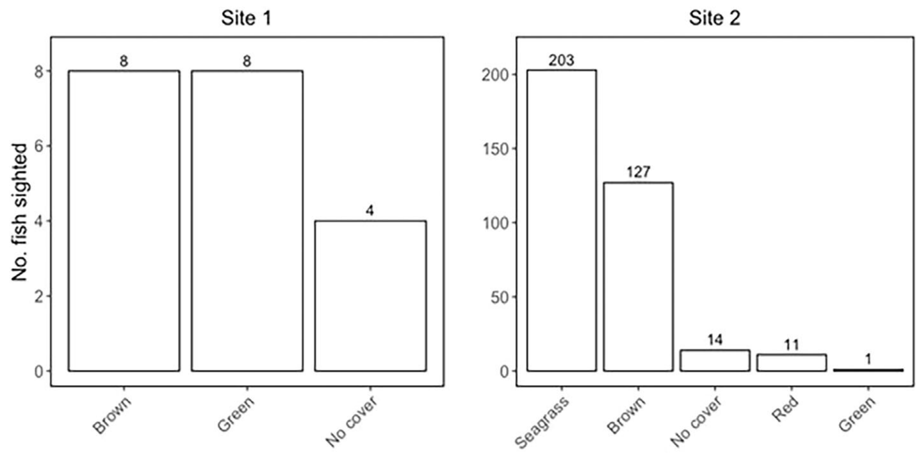

FIGURE 5 Habitat association of red handfish at the two known populations.

individuals when present (Bessell et al., 2023), giving confidence that the estimates of population size we report here are accurate.

Our mark-recapture density estimates were also comparable to density estimates based on underwater transect counts (Figure 3c,d). This concordance in estimates provides a reasonable level of confidence in the status of the species' population and suggests that either approach or ideally their combination can provide reliable estimates for tracking population trends through the future. Using density data as a metric of population size would be more cost-effective for future monitoring of the species, as it only requires the underwater survey data. Adding estimates of abundance requires the additional steps of taking and processing images, implementing photo-identification software, and running developing mark-recapture models, though it provides the added benefit of estimating survival.

Small population size is a substantial risk to the ongoing survival of the red handfish. Specifically, small populations suffer from a loss of genetic variation, an increased likelihood of inbreeding, and an increased susceptibility to stochastic and catastrophic events (e.g., Allentoft & O'Brien, 2010; Furlan et al., 2012; Grueber et al., 2010), all of which increase the risk of extinction. This highlights the need for management strategies for red handfish that increase numbers in the wild, such as establishing ex situ captive breeding and translocation programmes. These efforts would benefit from future research to formally estimate the minimum viable population (MVP; see Shaffer, 1981) size of the species, as this could act as a lower target for ongoing bolstering efforts.

Our results indicate the need for urgent intervention to prevent extinction. First, we observed a declining trend in observed fish density at Site 2 (the main stronghold for the population) from 2019 to 2020 (Figure 3d). This was halted (or possibly slightly reversed) after the release of 14 headstarted individuals in late 2020 (Stuart-Smith et al., 2021), with an increase in individuals in the 50–60 mm size classes indicating the possibility that headstarted fish were contributing to the population (rather than any increase occurring from immigrating adults). The headstarting effort and releases were intended to boost numbers, and indeed our results show some positive signs (albeit non-significant, and without any "control" populations to assess population trends in the absence of intervention). Furthermore, it is unknown whether the headstarted individuals were the only fish observed at Site 1 and thus prevented local extinction, or whether they had no impact on population numbers. Although headstarting has led to improved conservation outcomes in some marine species, including seals (Gerrodette & Gilmartin, 1990) and sea turtles (Heppell et al., 1996), there is uncertainty surrounding the effectiveness of the approach for fishes, which are known to be underrepresented in the conservation translocation literature (see Bajomi et al., 2010; Seddon et al., 2005). However, the purpose of this study was not specifically to evaluate the success of the 2020 release event, and clearly more research is needed to determine the efficacy of this approach for red handfish. With wide confidence intervals in population estimates in any given year, and without additional populations to provide "controls" or any knowledge of population trends in the absence of intervention, it is likely that headstarting will need to be continued for a number of years before it can be concluded to be successful or otherwise.

We recommend sustaining a release programme over a longer timeframe, and possibly with more individuals released at each population (in combination with habitat restoration). Morris et al. (2021) found that release programmes that were spread across multiple years were more likely to be successful, and that the number of individuals released significantly influences a programme's likelihood of success. We can use our results to help guide the number of fish to be released. For example, we estimated apparent survival (φ) at Site 2 (independent of a time effect) to be approximately 0.30. Assuming the mean clutch size per egg mass is around 60 fish, we could expect up to 18 fish per clutch to survive to 1 year old (if mortality is not higher in the first year, which it likely would be) and up to six of those to recruit to the adult population at 2 years old. Therefore, releasing 30 captively reared 1-year-old fish in this population might provide similar recruitment to approximately two egg clutches naturally hatching in the wild.

Second, the number of new juvenile fish observed at Site 2 declined, whereas mean fish size over the 3 years increased (as total abundance declined), indicating that the population grew older with progressively less recruitment during the study. It is likely that successful recruitment varies annually depending on the conditions

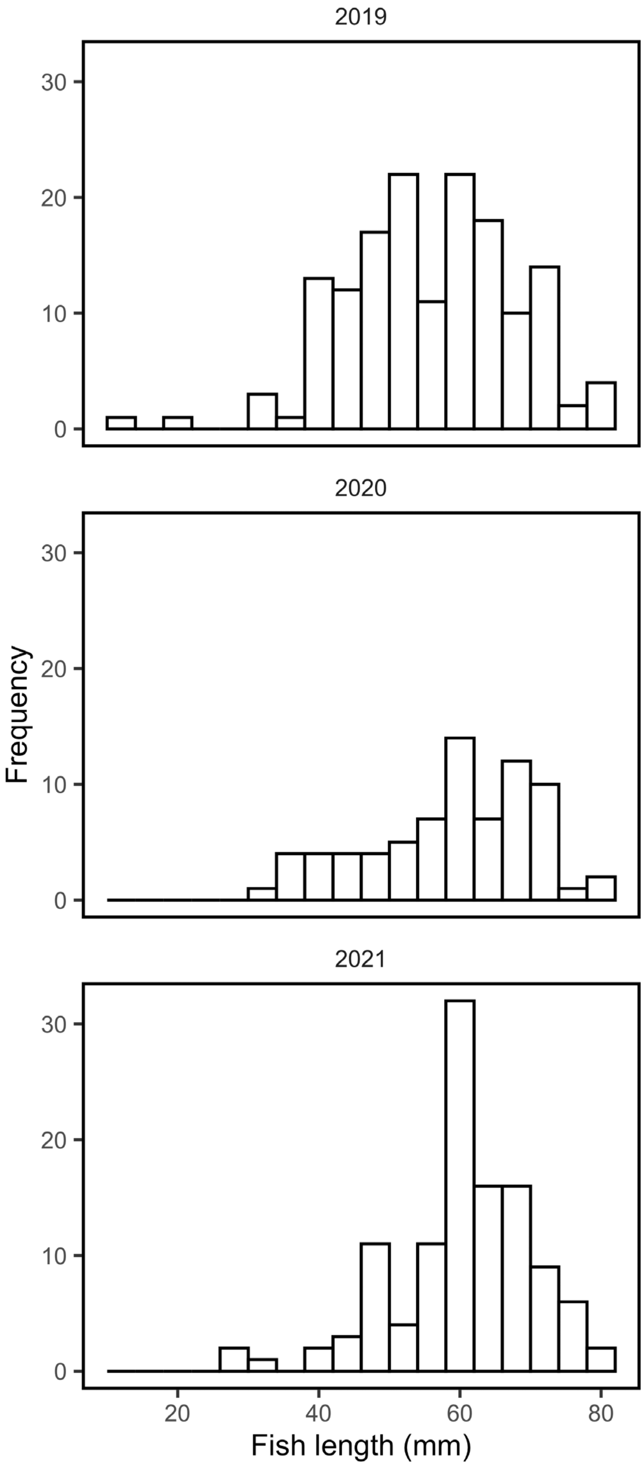

FIGURE 6 Length-frequency distributions of red handfish at Site 2 from 2019 to 2021.

(e.g., temperatures, habitat availability, stochastic events), and this apparent reduction could be attributed to successive poor recruitment years. We also cannot rule out that the collection of eggs for head-starting in 2019 led to reduced recruitment or the reduced number of juvenile (<45 mm) fish in 2021, even though natural mortality would presumably be far greater in the wild than in captivity. We note, however, that it is difficult to locate very small individuals during surveys, and have limited understanding of juvenile behavior or habitat use. The size of newly hatched individuals is ~5 mm (Stuart-Smith et al., 2021), but we did not observe any individuals smaller than 30 mm in our study. Although the poor ability of divers to detect fish <30 mm in the wild leaves room for uncertainty in patterns of recruitment, such fish are YOY, so they should appear in surveys within a year. As such, it seems clear that recruitment from the 2020 breeding season was lower than that from the 2018 and 2019 seasons. The downward population trends combined with an approaching "demographic cliff" of aging adults and few juveniles could lead to a rapid decline and local extinctions at one or both populations.

Another important consideration when interpreting our trends is the potential for natural spatiotemporal variability in the population or site-selection bias (Fournier et al., 2019). This bias is evident when researchers unknowingly begin monitoring a site during a peak abundance period for a population that naturally shows peaks and troughs. This would inevitably result in the detection of an initial population decline. Although this bias may be a possibility at Site 2 considering our short study (and thus the observed declines should be interpreted with caution), Site 1 has been visited and qualitatively monitored to varying degrees for almost 25 years. In fact, Site 1 was described as once containing "*hundreds of individuals*" in the 1990s (Last & Gledhill, 2009), and following a significant population decline at the site, is thought to have been home to fewer than 10 adults at any given time since around 2010. A potential cause of this decline was thought to be an increase in abundance of the native urchin *H. erythrogramma* at the site (Last & Gledhill, 2009), which has a demonstrated ability to overgraze macroalgae when in large numbers (Valentine & Johnson, 2005). The declines observed in our study at Site 2 should therefore be treated as a cause for concern, particularly considering an increased abundance of native urchins at the site was recently identified as among the greatest pressures to the species' ongoing survival at both sites (Bessell et al., 2022).

The abundances estimated by mark-recapture models may be impacted by biases or uncertainties that could affect their accuracy. One such bias may be introduced through misidentification of individuals, either by incorrectly judging one individual as two, or incorrectly judging two individuals as one. We aimed to control this bias to the best of our ability by having two independent researchers screen the database for resightings, as well as through the use of computer-assisted identification. We note, however, that Antennariidae, another family of Lophiiformes, have been known to change color (Pietsch & Arnold, 2020; Randall, 2005), and the closely related spotted handfish (*B. hirsutus*) have also displayed minor color changes (mostly slight fading of color and spots) while in captivity (Bessell, 2018). Although red handfish are not currently known to exhibit changes in their patterning, this remains a potential source of bias that may result in a lower resighting rate, and thus a potential overestimation of abundance. However, the concordance of our density estimates from mark-recapture methods with observations of densities from underwater transects (which do not rely on recognition of individuals) suggests

TABLE 3 Summary statistics of resighted red handfish by size class (with standard deviations in parentheses).

Size at first sighting (mm)	Number of resightings	Mean time at large (days)	Mean growth (mm)	Mean growth rate (mm/year)	Mean net movement (m)	Mean net movement rate (m/year)
30–39	1	681	36.0	19.3	–	–
40–49	9	390 (±329)	11.2 (±6.5)	20.1 (±16.1)	43.9 (±36.5)	48.2 (±35.8)
50–59	12	238 (±232)	3.6 (±4.2)	11.6 (±17.0)	19.8 (±27.2)	33.2 (±31.4)
60–69	23	375 (±297)	3.3 (±3.1)	11.1 (±36.4)	26.6 (±26.1)	66.8 (±117.9)
70–79	9	301 (±242)	1.8 (±3.2)	3.0 (±5.5)	26.1 (±17.9)	43.4 (±22.3)
All size classes	**54**	**352 (±284)**	**5.3 (±6.8)**	**11.4 (±26.0)**	**26.7 (±26.8)**	**48.5 (±77.7)**

that issues associated with failing to recognize individuals are unlikely to have greatly impacted our population estimates.

An additional potential source of bias is associated with the problem of small sample size. This may arise due to low animal densities, low probabilities of capture, or inadequate sampling design (White, 1982). Given rare and threatened species are often found in low densities, mark-recapture studies of these types of species are often hindered by this problem (Calvert et al., 2009; O'brien et al., 2005). For example, Harasti (2016) experienced a low abundance of White's seahorse (*Hippocampus whitei*) at two of his four study sites that prevented mark-recapture abundance estimation at those sites. Considering the risk for introduction of biases due to small sample size, the parameters predicted here, especially those for Site 1, should be interpreted with caution. Because our main objective was to produce statistically based abundance estimates, we place less emphasis on other parameters estimated by these models, even though understanding patterns in natural mortality could provide important additional information, if considered robust.

This was also the first study that made a concerted effort to explore movement in this species. The greatest observed net distance moved by an individual during our study was just under 100 m over approximately 1.5 years, though on average, most moved around 25 m between sightings (Table 3). For comparison, a similar study of the related (but larger) spotted handfish found mean movement to be around 210 m, and as high as 567 m in 1.5 years (Bessell, 2018; Moriarty, 2012). These movement data suggest red handfish have small home ranges (though this is possibly a product of the limited availability of suitable habitat), which highlights an important conservation consideration: low movement means the species is extremely vulnerable to site-specific impacts and stochastic events. This is further compounded by the species' poor dispersal capabilities due to having no larval phase and directly recruiting to the benthos after hatching (Bruce et al., 1997; Last & Gledhill, 2009), in addition to being limited to specific types of habitat. Therefore, the most effective conservation strategies for remnant red handfish populations at present will be highly site-specific, and should ideally be supported by dedicated protected areas at both sites with limited or no boating and fishing activity (which have been identified as being connected to important threats; Bessell et al 2021). For example, protective zoning has been documented to assist in the conservation of other rare and threatened species, including gray nurse shark (*Carcharias taurus*) (Lynch et al., 2013) and various species of anemonefish (Scott et al., 2011). Supplementing site protection with careful management of a range of direct sources of habitat destruction (e.g., via the habitat-grazing urchin *H. erythrogramma*, and urban development), will likely yield the greatest opportunity for the recovery of red handfish. We note, however, that the resighting rates reported here, and therefore the data from which net movement is determined, are relatively low (18.2%) for a small species with low mobility (though, Martin-Smith (2011) yielded comparable resighting rates of 21%–27% in a similar study of cryptic weedy seadragons [*Phyllopteryx taeniolatus*] in Tasmania). Given the scuba-based survey methods that we used in our study were recently found to be effective at detecting red handfish across different habitats (57%–97% detection probabilities; Bessell et al., 2023), our low resighting rate could be explained by a poor ability of the photo-identification software to recognize individuals using spot patterns, high rates of mortality, or migration.

An interesting finding of this study is the apparent importance of seagrass as a habitat for the species. Previously red handfish were thought to be associated with shallow rocky reef habitats, where it hides among a canopy of *Sargassum* spp. and *Caulerpa* spp. (Edgar et al., 2017; Last & Gledhill, 2009). However, over half of all observed individuals observed at Site 2 in this study were found hiding among seagrass. This was also true of the juveniles we observed, with 55.6% of all juveniles being found in seagrass. Seagrasses have been known to provide a nursery for juveniles of many species of fish (reviews by Pollard, 1984; Whitfield, 2017), and may play a similar role for red handfish. Although brown algal covered rocky reefs (e.g., *Sargassum* spp., and *Cystophora* spp.) are undoubtably still an important habitat type for the species, it seems likely that adjacent or interspersed algal covered reef and seagrass may provide a beneficial combination of cover from predators and suitable breeding habitat (observations of egg masses guarded by females at Site 2 have been exclusively on seagrass). Indeed, many (but not all) historical observation sites of red handfish, including by early European settlers in the 1800s (Last & Gledhill, 2009), were from locations that have both shallow reef and seagrass habitats present. An unpublished report from a study at Site 1 in 1999 also noted the presence of seagrass, with some handfish observed to have laid eggs among the seagrass (Green & Bruce, 2000; M Green pers. comm.). As this was the only known population of red handfish from the early 2000s until 2018, it is probable that the almost complete disappearance of seagrass alongside the reef at this location (albeit previously sparse; prior to monitoring of the red handfish population in 2010) had propagated the belief that the species was only found on rocky reef. Our findings are alarming given that seagrasses are declining globally (Waycott et al., 2009), in addition to seagrass extent in Tasmania having been estimated to have decreased by nearly 25% between 1950 and 1990 (Rees, 1993). Seagrass in the region is known to be influenced by tide, wind, light availability, water quality, as well as temperature (Macreadie et al., 2018). Considering Tasmania is a hotspot for ocean warming (Oliver et al., 2018; Ridgway & Dunn, 2007), and the role of seagrass as nursery for other fish species (Pollard, 1984), the probable importance of seagrass for red handfish (at least in its remaining populations) warrants management consideration.

Monitoring small, cryptic, and rare marine species is challenging due to low detection, often resulting in such species being underrepresented in biodiversity surveys (Ackerman & Bellwood, 2000; Bozec et al., 2011; Willis, 2001). This challenge can be hard to overcome, and therefore it may be necessary in extreme cases, as is the case for red handfish, for management decisions to be made using the limited data that are available. Given the limitations of collecting data for these types of species, and the importance of these data for conservation decision-making, there is a need to improve monitoring approaches for cryptic and sparse marine species, including exploring novel or modern approaches. For example, the use of environmental DNA (eDNA) methods is rapidly developing and has been applied to rare and cryptic species (Bessell et al., 2023; Nester et al., 2020; Nester et al., 2023). Additionally, artificial intelligence, coupled with image or video-based methods (e.g., autonomous underwater vehicles), may represent another approach to improving data collection capabilities (e.g., González-Rivero et al., 2020; Saleh et al., 2022), though this approach would be better suited to unvegetated habitats where animals are not concealed beneath the canopies of seaweeds.

This research confirms the severity of the red handfish's present status via a detailed estimation of current population size, based on the last known locations of the species and was a vital step for the conservation effort for this critically endangered species, providing a sound baseline for which future efforts of population protection and restoration can now be evaluated against. The low estimated abundances of red handfish are cause for concern and, coupled with a low movement capacity and an apparent decline in density over the 3 years, highlight the need for an urgent intensification of conservation action for the species. Our results provide clear evidence for the need for immediate intervention, alongside ongoing monitoring, preferably directly addressing the small population size species, and the need for managing its habitat. Specifically, we suggest:

1. Bolstering wild population numbers via headstarting and establishing a captive breeding programme;
2. Establishing insurance populations through the release of captive fish to new sites;
3. Establishing protected areas to manage critical habitat for red handfish populations and to potentially assist in buffering against current anthropogenic and climate change-associated ecological impacts, and;
4. Continued management of site-specific habitat-destroying processes, including improving understanding of their impacts, as well as active habitat and ecosystem restoration strategies.

Although other effective and important steps toward conservation exist (e.g., facilitation of in situ spawning via artificial spawning habitats, gene banks, estimating the minimum viable population) the recommendations mentioned earlier are likely the most direct and important options, and are therefore urgently needed to safeguard the species against extinction in the wild.

AUTHOR CONTRIBUTIONS

Tyson J. Bessell, Jemina Stuart-Smith, Rick D. Stuart-Smith, Neville S. Barrett, and Tim P. Lynch conceived the idea for the study. Tyson J. Bessell, J Jemina Stuart-Smith, Rick D. Stuart-Smith, and Olivia J. Johnson collected the data. Tyson J. Bessell analysed the data. All authors assisted in interpretation of results. Tyson J. Bessell led the writing of the manuscript. All authors contributed critically to manuscript development and gave approval for publication.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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