








## RESEARCH ARTICLE

# Larval dispersal and fishing pressure influence recruitment in a coral reef fishery

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**Handling Editor:** Qiang He**Abstract**

1. Understanding larval connectivity patterns in exploited fishes is a fundamental prerequisite for developing effective management strategies and assessing the vulnerability of a fishery to recruitment overfishing and localised extinction. To date, however, researchers have not considered how regional variations in fishing pressure also influence recruitment.
2. We used genetic parentage analyses and modelling to infer the dispersal patterns of bumphead parrotfish *Bolbometopon muricatum* larvae in the Kia fishing grounds, Isabel Province, Solomon Islands. We then extrapolated our Kia dispersal model to a regional scale by mapping the available nursery and adult habitat for *B. muricatum* in six regions in the western Solomon Islands, and estimated the relative abundance of adult *B. muricatum* populations in each of these regions based on available adult habitat and historical and current fishing pressure.
3. Parentage analysis identified 67 juveniles that were the offspring of parents sampled in the Kia fishing grounds. A fitted larval dispersal kernel predicted that 50% of larvae settled within 30 km of their parents, and 95% settled within 85 km of their parents. After accounting for unsampled adults, our model predicted that 34% of recruitment to the Kia fishery was spawned locally. Extrapolating the spatial resolution of the model revealed that a high proportion of the larvae recruiting into the Kia fishing grounds came from nearby regions that had abundant adult populations. Other islands in the archipelago provided few recruits to the Kia

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fishing grounds, reflecting the greater distances to these islands and lower adult abundances in some regions.

4. *Synthesis and applications.* This study shows how recruitment into a coral reef fishery is influenced by larval dispersal patterns and regional variations in historical fishing pressure. The scales of larval connectivity observed for bumphead parrotfish indicate that recruitment overfishing is unlikely if there are lightly exploited reefs up to 85 km away from a heavily fished region, and that small (<1 km<sup>2</sup>) marine-protected areas (MPAs) are insufficient to protect this species. We recommend greater efforts to understand the interactions between larval dispersal and gradients of fishing pressure, as this will enable the development of tailored fisheries management strategies.

#### KEYWORDS

*Bolbometopon muricatum*, fisheries management, genetic parentage analyses, larval dispersal, local knowledge, modelling, recruitment, Solomon Islands

## 1 | INTRODUCTION

In the past decade, experimental studies on the dispersal of reef fish larvae have provided insights into the intrinsic vulnerabilities of coral reef fish metapopulations (Bonin et al., 2016; van der Meer et al., 2015), helped to justify the establishment and dimensions of marine-protected areas (MPAs; Almany et al., 2007; Baetscher et al., 2019; Harrison et al., 2012; Jones et al., 2009) and validated biophysical models of larvae dispersal (Bode et al., 2019). This research has sought to establish the degree to which fish populations are demographically 'open' or 'closed', as this underpins our understanding of the appropriate ecological scales for management (e.g. Jones, 2015; Pelc et al., 2010; Sale et al., 2005). Populations are demographically open where there is limited localised retention of larvae and the mean larval dispersal distances are long (i.e. hundreds of kilometres; e.g. Herrera et al., 2016; Nanninga et al., 2015). Conversely, closed populations occur where a large proportion of the dispersing cohort are locally retained, where populations are isolated and where mean larval dispersal distances are short (i.e. tens of kilometres; e.g. Almany et al., 2007).

A fish population that is demographically closed has the ability to sustain itself and can therefore be managed at its spatial scale of demographic closure, but such populations will also be vulnerable to recruitment overfishing (Begg et al., 1999; Walters & Martell, 2004) and localised extinction at that scale. Once depleted, they are unlikely to be rescued by the arrival of larvae from distant intact populations (Bonin et al., 2016; van der Meer et al., 2015). In a demographically open population, localised extinction is unlikely since an overfished population can be rescued by dispersal from distant stocks. However, the ecological rationale and motivation for implementing small-scale management measures, such as small MPAs, is weakened (Mills et al., 2010), and overfishing in adjacent areas can undermine local conservation actions (Almany et al., 2013; Costello

et al., 2015). Consequently, understanding the match (or mismatch) in the scales of larvae dispersal and fishing pressure for exploited fisheries would help assess the sustainability of a stock and assist with the development of suitable management interventions (Mills et al., 2010).

Direct empirical estimates of larval dispersal are dominated by studies on small reef fishes (e.g. Bonin et al., 2016; Herrera et al., 2016; Pusack et al., 2014; Shulzitski et al., 2016), particularly species that are reliably associated with specific benthic habitats such as anemones and sponges (e.g. D'Aloia et al., 2015; Pinsky et al., 2017). To date, the limited available empirical data on larvae dispersal patterns in commercial (fishery) species come from genetic parentage studies on tropical coral trout species (*Plectropomus maculatus*, *P. leopardus* and *P. areolatus*) and snapper *Lutjanus carponotatus* that were undertaken in Australia and Papua New Guinea (Almany et al., 2013; Harrison et al., 2012; Williamson et al., 2016). Evidence has also been gathered from kelp rockfish *Sebastes atrovirens* in temperate waters in America (Baetscher et al., 2019) and snapper *Chrysophrys auratus* in New Zealand (Le Port et al., 2017).

The first two tropical studies (Almany et al., 2013; Harrison et al., 2012) were conducted over relatively small spatial scales (10 s of km), as was the temperate rockfish study (the longest observed dispersal event was 5 km). Both tropical studies suggested that dispersal distances were relatively short, and that self-recruitment was common. They have consequently been widely cited to support the assumption that networks of MPAs can serve as effective fisheries management tools by exchanging and exporting demographically meaningful amounts of larvae (e.g. Green et al., 2015). However, their experimental designs were too small to encompass much variation in fishing pressure, although, in each case, the studies were embedded in a spatial gradient of fishing intensity.

Later studies on coral trout expanded the spatial scale of these sampling projects, however, and drew more complex conclusions.

These analyses revealed common larval exchange for both *P. maculatus* and *P. leopardus* over much larger distances—even bidirectional exchange between reefs that were 200 km apart (Williamson et al., 2016). Empirical evidence, statistical analysis and biophysical oceanographic modelling (Bode et al., 2019) all concluded that long-distance dispersal should be relatively common in these two reef fish species. Consequently, the demographic scale of these populations and the spatial extent of their fishery stocks are far larger than initially thought.

In this study, we used genetic parentage analysis to examine the larval dispersal patterns of the giant bumphead parrotfish *Bolbometopon muricatum* in Solomon Islands. *B. muricatum* is a commercially valuable species that reaches >1 m in length and 50 kg in weight (Hamilton & Choat, 2012). The maximum recorded ages of *B. muricatum* in the western Solomon Islands are 29 years (Taylor et al., 2018). In Solomon Islands, *B. muricatum* pair spawn during the last lunar quarter within foraging sized schools of 20–60 adults, with larvae spending 25 days in the pelagic phase before settling into *Acropora* colonies in sheltered lagoons at 1 cm in length (Hamilton et al., 2017; Taylor et al., 2018).

*Bolbometopon muricatum* has many life-history characteristics that make it vulnerable to severe population declines and local extinctions: Schools of *B. muricatum* sleep in predictable shallow water locations, making them lucrative targets for night spearfishers and resulting in hyperstable *B. muricatum* fisheries, where catches can remain high despite declining populations (Hamilton et al., 2016). Juveniles inhabit sheltered lagoonal reefs that are prone to degradation (Brown & Hamilton, 2018; Hamilton et al., 2017), and *B. muricatum* has a long lifespan and late maturation (Taylor et al., 2018). *B. muricatum* has been overfished across much of its range (Hamilton & Choat, 2012) and is currently listed as vulnerable (VU) on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Chan et al., 2012).

Historical and current levels of exploitation of *B. muricatum* vary across the Solomon Islands, with rapid population declines starting shortly after cash markets develop for the species (Hamilton et al., 2019). In this study, we used genetic parentage analyses and modelling to infer the dispersal patterns of *B. muricatum* larvae in the Kia fishing grounds, Isabel Province, Solomon Islands. We then mapped the available nursery and adult habitat for the species in six regions in the western Solomon Islands, and estimated the relative abundance of adult *B. muricatum* populations in each of these regions based on historical and current fishing pressure. This enabled us to extrapolate our dispersal model for the Kia fishing ground to a regional scale and ask the following questions: (1) How demographically closed is the Kia *B. muricatum* fishery? (2) How do the scales of larval dispersal overlap with the scales of human exploitation across the Solomon Islands? (3) What bearing does this have for the management of this species and the risk of recruitment overfishing and local extinction?

## 2 | MATERIALS AND METHODS

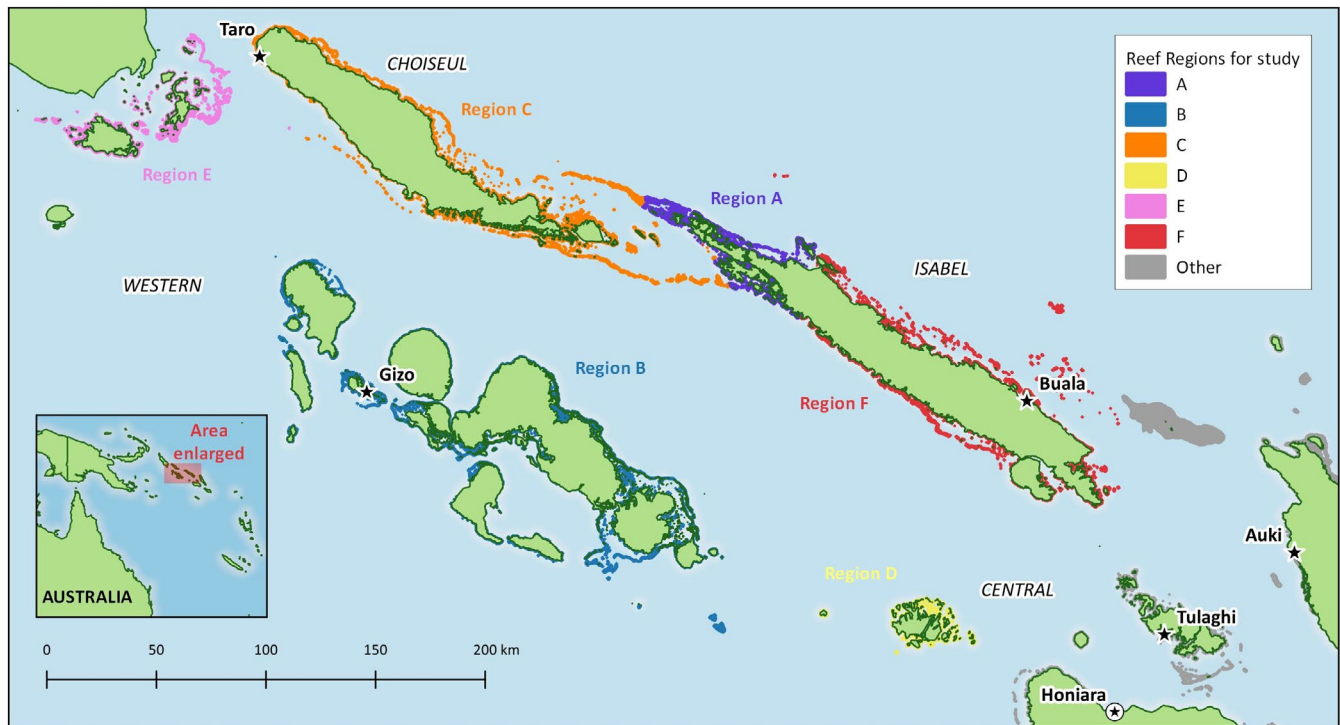
### 2.1 | Environmental setting

Our empirical research was conducted over 177 km<sup>2</sup> of reefs in the Kia District of Isabel Province, Solomon Islands (Region A) from February 2012 to October 2013. We extrapolated our dispersal model for the Kia fishing grounds to include an additional 1,176 km<sup>2</sup> of reefs in five other locations (Region B, C, D, E and F) in the western Solomon Islands (Figure 1). Reefs in Region B–F were located 0–282 km away from the Kia fishing grounds. The study area contains, in total, 34 different types of reef habitat, and 15 of these reef habitats were present in the Kia District (Andrefouet et al., 2006). For presentation purposes, we aggregated 15 different types of reef habitat in the Kia District into five major reef types: back, fore, fringing and patch reefs, as well as subtidal reef flats (Figure 2).

The Kia region supported a recently commercialised, high-yield *B. muricatum* night spearfishery that has been the focus of previous research (e.g. Hamilton et al., 2016, 2017; Taylor et al., 2018). In 2012, two fisheries centres were operating in the Kia District, the Bahana Provincial Fisheries Centre (BPFC) and a private fisheries centre in Babahairo (Hamilton et al., 2016). The fishing grounds in the Kia District were divided into areas of high and low historical fishing pressure based on interviews with 22 expert spearfishermen from Kia (Hamilton et al., 2016; see Supporting Information; Appendix S1). The fishing grounds and the capture location of every adult and juvenile *B. muricatum* sampled in this study are shown in Figure 2. Zone 1 had experienced high levels of spearfishing pressure and had low abundances of adult *B. muricatum*, whereas Zones 2 and 3 had experienced low levels of spearfishing pressure and had high abundances of adult *B. muricatum* (Hamilton et al., 2016).

### 2.2 | Demography and collection of tissue samples

The growth rates and reproductive characteristics of the *B. muricatum* population in Region A have been comprehensively studied (Taylor et al., 2018), and for mature *B. muricatum*, sex is easily identifiable based on macroscopic examination of gonads (Hamilton et al., 2008). Here, we define juvenile *B. muricatum* as fish that ranged from 55 to 642 mm and ages of approximately 0–6 years, and adult *B. muricatum* as fish that ranged from 650 to 1,190 mm and ages of approximately 7–29 years (see Supporting Information; Appendix S2; Taylor et al., 2018). Tissue samples from 3,924 *B. muricatum* (1,110 females, 1,020 males, 102 adults of unknown sex and 1,692 juveniles) were collected from the Kia fishing grounds (Region A) between February 2012 and October 2013 (Figure 2). Of these, 2,655 fin tissue samples were obtained from *B. muricatum* sold to the Bahana and Babahairo fisheries' centres. Trained fisheries officers preserved tissue samples in individually labelled 2-ml vials filled with 80% ethanol, removed otoliths from a subsample of fish and



**FIGURE 1** The study area within the Solomon Islands. Coral reef habitats are colour coded into multiple regions: Kia fishing grounds (Region A), Western Province (Region B), Choiseul Province (Region C), Russell Islands (Region D), Shortland Islands (Region E) and eastern Santa Isabel Island (Region F). Reefs outside of these six regions are indicated as 'other' and were not considered in the study

collected information on the location of capture, length, weight, sex and gonad weight of each *B. muricatum* landed (Hamilton et al., 2016; Taylor et al., 2018).

Two thousand six hundred and fifty-five *B. muricatum* that were purchased by local fisheries centres consisted of 2,232 adults and 423 juveniles. Additional 1,269 juvenile tissue samples were collected between April and August 2013 by 30 Kia and Babihro spearfishers who were paid SBD \$10 (USD 1.25) for every juvenile *B. muricatum* that they bought to a fisheries centre for processing. The decision to sample juvenile *B. muricatum* was endorsed by the Kia House of Chiefs after initial attempts to capture juvenile *B. muricatum* alive at night on SCUBA proved unsuccessful. We estimate that these 1,269 juveniles represented less than 2% of the juvenile *B. muricatum* present in the Kia fishing grounds in 2013 (see Supporting Information; Appendix S3). One Kia spearfisher captured 544 juvenile *B. muricatum*, after observing that *B. muricatum* in the 100–400 mm size range often slept in a 'green branching coral', which was later identified as *Acropora echinata*.

### 2.3 | Genetic techniques and parentage analysis

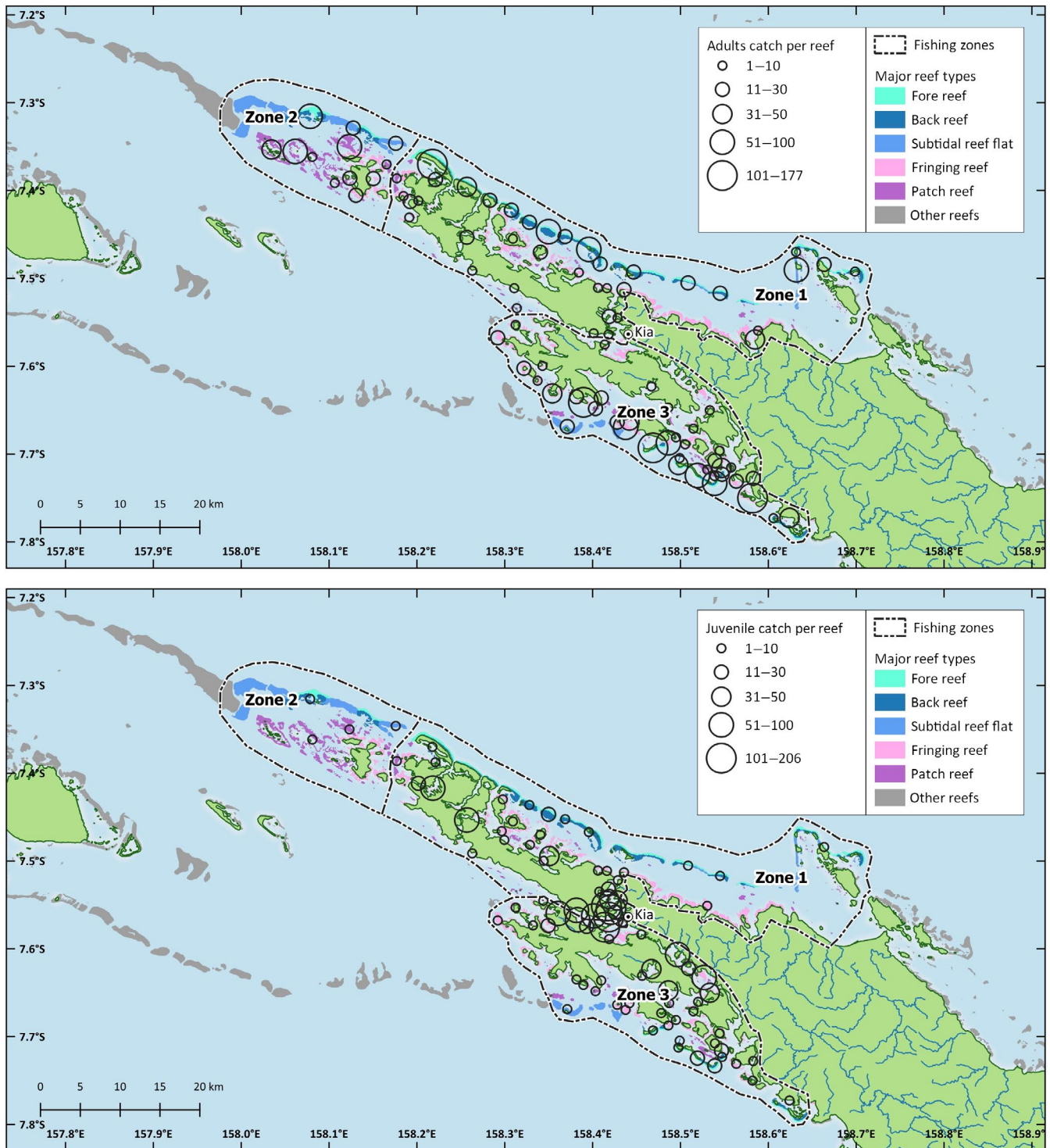
Genomic DNA was extracted from approximately 2 mm<sup>2</sup> of fin tissue following the protocol described in Harrison et al. (2014). For each individual, a series of four multiplex polymerase chain reactions (PCRs) were performed to amplify 28 polymorphic microsatellite

loci (Lozano-Cortés, 2014), with individual genotypes scored in GENEMAPPER v4.0. Further details of these loci and the genotyping procedure are described in Priest et al. (2015).

The number of genotyped individuals ( $N$ ), number of alleles ( $N_a$ ), observed heterozygosity ( $H_o$ ) and expected heterozygosity ( $H_e$ ) was estimated from all samples and for each locus using GenAlEx v6.5 (Peakall & Smouse, 2006, 2012). The exact test of Hardy–Weinberg and the score test for heterozygote deficiency were performed in Genepop on the Web (Raymond & Rousset, 1995; Rousset, 2008) alongside Weir and Cockerham's (1984) estimate of FIS. Probability test for linkage disequilibrium was performed for each pair of loci using the log likelihood ratio statistic in Genepop based on 10,000 dememorisations, 5,000 batches and 10,000 iterations. Significance levels of 0.05 were adjusted for a given false discovery rate of 10% to account for multiple testing (Benjamini & Hochberg, 1995). The presence of null alleles was determined from 700 randomly selected individuals in Microchecker (van Oosterhout et al., 2004) based on the estimator of Brookfield (Brookfield, 1996).

### 2.4 | Parentage analysis and accuracy tests

All collected juveniles were screened against the total pool of adult samples to reveal parent–offspring relationships, which were identified using a maximum likelihood approach implemented in the software program FAMOZ (Gerber et al., 2003; Marshall et al., 1998).



**FIGURE 2** Capture locations of 2,232 adult (>650 mm total length, upper panel) and 1,692 juvenile (<650 mm total length, lower panel) *Bolbometopon muricatum* that tissue samples were obtained from within Region A. Three fishing zones (identified by expert interviews) are delineated by dashed lines. Zone 1 was heavily fished whereas Zone 2 and Zone 3 were lightly fished

The program computes log of the odds ratio (LOD) scores for assigning individuals to candidate parents based on the observed allelic frequencies at each locus. Simulated datasets with known parent-offspring relationships were used to determine a critical LOD score

for assigning parentage and to assess Type I and Type II errors following the procedure described in Harrison et al. (2014). The minimum LOD score thresholds for single-parent assignments were identified from simulations as 8.8 and 15.0 for the assignment to parent-pairs.

The resulting probability of assigning a juvenile to a parent that was not its true parent, knowing that the true parent was not sampled, was 2.0% (false positive—type I error). Conversely, the probability of a true parent–offspring pair not being identified knowing that the true parent was sampled was less than 12.3% (false negative—type II error). Despite the high number of loci, low polymorphism in microsatellite loci precluded higher accuracy in the parentage analysis. The high rate of type II errors indicates that other true parent–offspring are likely to exist in our data; however, low polymorphism precludes our ability to identify them confidently. The low rate of type I errors indicates we can be confident that the assignments made are true parent–offspring pairs and representative of dispersal distances in this system.

## 2.5 | Fitting dispersal kernels to genetic parentage data

Larval dispersal kernels were fit to the parentage assignment dataset following the methods outlined in Bode et al. (2018). In brief, larval dispersal was assumed to follow a distance-based relationship, where  $s_{ij}$  is the number of larvae that settle in nursery habitat patch  $j$  that were spawned on reef  $i$ , calculated by:

$$s_{ij} = f \cdot N_i \cdot \rho(d_{ij}), \quad (1)$$

where  $N_i$  is the abundance of adults on reef  $i$ ,  $f$  is the constant per capita fecundity of the species,  $d_{ij}$  is the shortest in-water distance between locations  $i$  and  $j$  and  $\rho(d)$  is a probability density function that represents a dispersal kernel. In our case, we estimated the abundance of adults on each reef using the area of adult habitat identified for each reef, multiplied by the average density observed in each zone from underwater visual census (UVC) surveys undertaken in 2012 (Hamilton et al., 2016; see Supporting Information; Appendix S4). Larval output from each reef was therefore proportional to local abundance. To estimate this abundance, we used the specific abundance estimate for sampled reefs, and we estimated the density on unsampled reefs to be the average density on the sampled reefs. Uncertainty in these estimates was incorporated in our bootstrap resampling procedure described below.

Our candidate kernels were generalised Gaussians with integer exponents  $\beta$  (i.e. the Laplacian function when  $\beta = 1$ , the standard Gaussian when  $\beta = 2$  and the Ribbens function when  $\beta = 3$ ):

$$\rho(d) = \frac{\beta e^{-(\alpha/\beta)d}}{2\alpha\Gamma(1/\beta)}. \quad (2)$$

Any proposed larval dispersal kernel (or even a biophysical larval dispersal model; Bode et al., 2019) can be used to create a multinomial vector of predicted settlement proportions  $\mathbf{q}_j$  at reef  $j$ , where each element of the vector  $i$  is defined as:

$$q_{j,i} = \frac{s_{ij}}{\sum_i s_{ij}}. \quad (3)$$

Of course, the parentage assignment dataset only offers unambiguous information about the minority of juveniles (generally between 1% and 30%) that could be assigned to an adult. To construct the probability that a sampled juvenile on reef  $j$  was assigned to an adult on reef  $i$ , we modify Equation 3 by  $\theta_i$ , the proportion of adults on reef  $i$  that was genotyped:

$$\hat{q}_{j,i} = \frac{(1 - (1 - \theta_i)^2) s_{ij}}{\sum_i s_{ij}}, \quad (4)$$

and the probability that a sampled juvenile on reef  $j$  could not be assigned to any adults in the genotyped set is:

$$\hat{q}_{j,x} = \frac{\sum_i (1 - \theta_i)^2 s_{ij}}{\sum_i s_{ij}}, \quad (5)$$

Using these probabilities, we can calculate the kernel function and parameterisation that maximises the (log) likelihood of observing the parentage assignment dataset for *B. muricatum*. We searched for the best-fit scale parameter  $\frac{1}{\alpha}$  across values between  $10^{-6}$  and  $10^3$ .

The parameters in this estimator contain substantial uncertainty, and we propagated this uncertainty through to our estimates of larval dispersal. First, we fit the kernel to 250 bootstrap resamples of our dataset (with replacement, at the reef level), to include the uncertainty introduced by our set of parentage sample sites. To incorporate the consequences of uncertainty in the estimates of adult abundance across the region, we allowed the abundance on each of these reefs to vary independently, using lognormally distributed variation with a mean of one and a standard deviation of 0.5. Our analyses assume no errors in the assigned parentage data—either false negatives or false positives. Both may be present in the data. We do not expect this assumption to bias our estimates of the dispersal kernel, since the errors are equally likely at every distance from the natal reefs.

## 2.6 | Modelling nursery and adult habitat for *B. muricatum* across Solomon Islands

Reef maps from the Millennium Coral Reef Mapping Project were used to quantify the availability of *B. muricatum* habitat across the western Solomon Islands (Figure 1). The overall study region contained 15,524 separate reef polygons, which were classified into 34 different types of reef habitat. The complex arrangement of the Solomon Islands archipelago means that in-water distance between two reefs can differ dramatically from the Euclidean distance. Distances between each of the polygons were therefore based on the shortest in-water distance, which we calculated by applying Dijkstra's algorithm to an adaptively sized grid placed across the region. Edges between grid points that traversed land were excluded.

We divided the reef polygons into six different regions that were chosen on the basis of both oceanographic and biological factors (Figure 1). The regions were physically separated by large channels

and distances, and therefore likely to be more demographically isolated. They have also been exposed to differing levels of fishing pressure. Despite a lack of physical features separating them, we defined a separation between Regions A and F to allow a closer focus on Region A, where the parentage assignment was undertaken. Region A was further divided into three zones (Figure 2). In each of these regions, we used the mapped habitat types to identify the amount and location of juvenile nursery habitat and adult habitat. Based on underwater observations of the species (Hamilton et al., 2016, 2017) and its association information gained from the parentage sampling, we classified reefs as juvenile habitat if they were deep lagoons; enclosed lagoons or basins; lagoon pinnacles; and shallow lagoons and lagoonal terraces. Adult habitat comprised barrier, fringing, basin, bank, slope and flat reef of all types; reef channels; reef terraces (excluding lagoonal terraces); and fore reefs. We used the combined area of adult reef habitat types to estimate the number of larvae produced by each of the 15,524 mapped reefs. All other habitat types were assumed to produce no larvae. Larval output in adult habitat was assumed to be proportional to population, which we assumed was proportional to the habitat area, after accounting for historical levels of fishing pressure. Each of the six regions was classified by the level of historical and current fishing pressure they had experienced based on observations that R.H. and J.P. have made in these six regions since the 1990s and available UVC surveys (i.e. Hamilton et al., 2016, 2019). Regions B and D, and Zone 1 of Region A were classified as heavily fished; Regions C, E and F, and Zones 2 and 3 of Region A were classified as lightly fished. Per unit area, lightly fished regions were assumed to produce 10 times the larval output of heavily fished regions, based on quantitative studies that have shown that the abundance of adult *B. muricatum* in heavily exploited locations such as Region B has declined by over 90%, with associated reductions in the size distribution (Hamilton et al., 2019). Within the Kia fishing grounds, we estimated inter-reef distances using the shortest in-water distance. Exchanges between all zones were confirmed by parentage assignments. For the larger region, we assumed that inter-reef distances were Euclidean (i.e. point-to-point, not 'as the fish swims'), since the overall distances were much larger than deviations caused by the location of the islands.

### 3 | RESULTS

#### 3.1 | Microsatellite genotyping and locus characteristics

Data presented here contained 28 polymorphic loci with 0.4% missing data (Supporting Information; Table S1). The mean number of alleles per locus was 9.0 and ranged from 3 to 14 alleles. Similarly, the average observed heterozygosity was 0.43 and ranged from 0.02 to 0.79. Each locus was tested for departure from Hardy–Weinberg equilibrium where 17 loci showed deviation from theoretical predictions after correction for multiple testing. Estimates of Weir and Cockerham's  $F_{IS}$  were positively skewed with an average  $F_{IS}$  of

$0.018 \pm 0.012$  SE across all loci. Amongst 378 pairwise comparisons, six locus pairs showed evidence of linkage disequilibrium after correction for multiple testing and no locus showed evidence of null alleles. Deviations from Hardy–Weinberg equilibrium and linked loci are indicative of null alleles in microsatellite or population processes such as inbreeding. However, simulation test showed that retaining all 28 loci increased the overall accuracy of the parentage analysis with an optimum LOD threshold of 8.8 to minimise the number of false-positive and false-negative assignments.

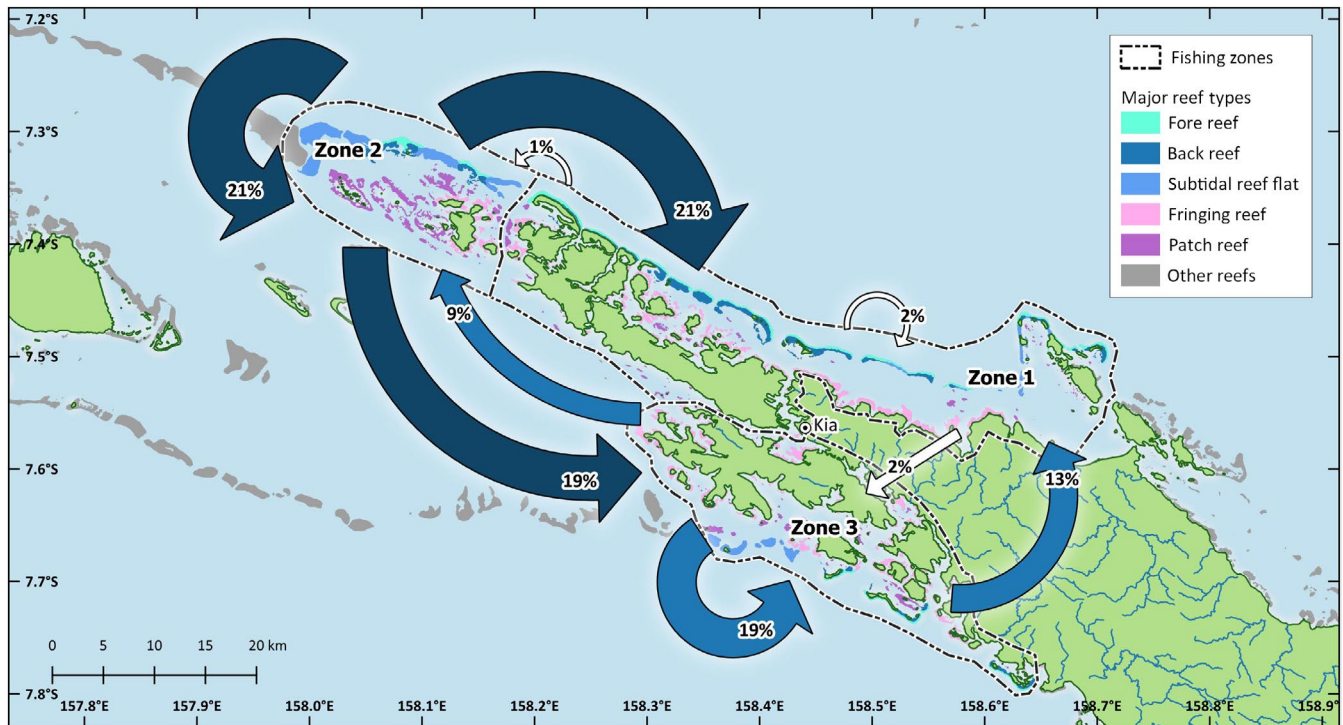
#### 3.2 | Larval dispersal within the Kia fishing grounds

Parentage analysis identified 67 juveniles that were the offspring of single parents sampled at 35 reefs in the Kia fishing grounds and these 67 juveniles ranged in size from 89 to 640 mm total length and came from 26 reefs (Supporting Information; Table S2). The maximum in-water distance between sampled adult and juveniles was 78 km. After accounting for unsampled adults, our model predicted that this represents 34% self-recruitment within the Kia fishery. The relative degree of self-recruitment and connectivity between the three Kia fishing zones are shown in Figure 3. Zone 1 had very low levels of self-recruitment and limited connectivity to Zone 2 or 3, reflecting the low adult populations in this heavily fished zone.

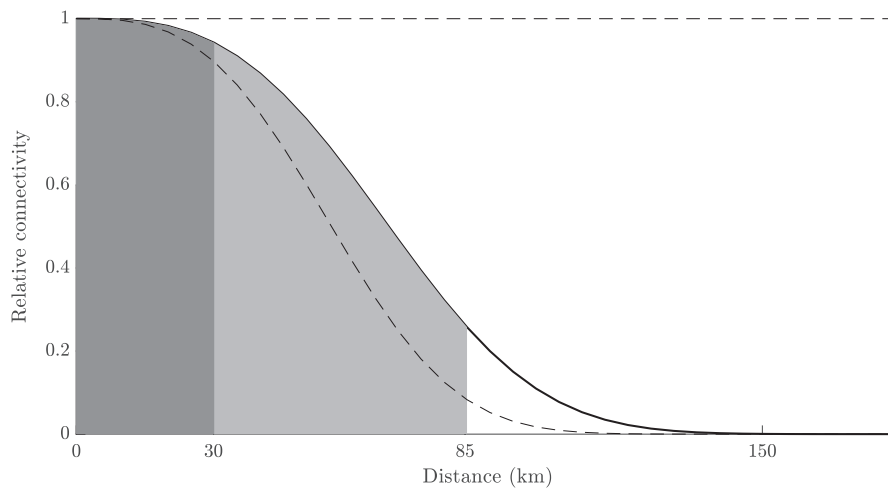
Our best-fit dispersal kernel predicted that 50% of larvae settled within 30 km of their parents, and 95% settled within 85 km of their parents (Figure 4). The lower bound of our uncertainty about the scale of larval dispersal kernel was relatively certain, but the upper bound was highly uncertain. Essentially, we could not discount (at a confidence level of 2.5%) the possibility that *B. muricatum* dispersal was effectively homogeneous across the sample region.

#### 3.3 | Extrapolating the dispersal model beyond the Kia fishing grounds

Using the best-fit larval dispersal kernel, we extrapolated the proportion of recruitment into Region A that could be attributed to the wider metapopulation. In doing so, we have extended the fitted kernel beyond the spatial scale of the parameterisation data, and to an oceanographic scale where new processes (e.g. oceanic circulation such as the North Vanuatu Jet) will add uncertainty to regional predictions of larval transport. Our results predict both strong and weak regional connections (Figure 5). Approximately half of the recruitment to Region A came from Isabel Province, with most of that being regional self-recruitment from adults in Region A itself. The remainder of the larvae (49%) are sourced from Choiseul Province (Region C), across the narrow Manning Strait. Because the strength of connectivity declines rapidly with distance, most of these recruits come from reefs off the north and eastern coasts of Choiseul. Other islands in the archipelago—the Western Province (Region B), Russell Islands (Region D) and Shortland Islands (Region E) contribute very little to recruitment on Isabel. This reflects a combination of both



**FIGURE 3** Modelled larval recruitment patterns of *Bolbometopon muricatum* within the three zones of the Kia fishing grounds, Isabel Province, Solomon Islands. Values are estimated using the best-fit larval dispersal kernels to the parentage data. Arrows represent the dispersal of larvae between zones and self-recruitment (return of larvae to their natal zone), expressed as percentages of total larval recruiting into each zone. For example, of the larvae that recruited to zone 3, 19% were self-recruits, 19% came from zone 2, 2% came from zone 1, and 60% came from outside the Kia fishing grounds



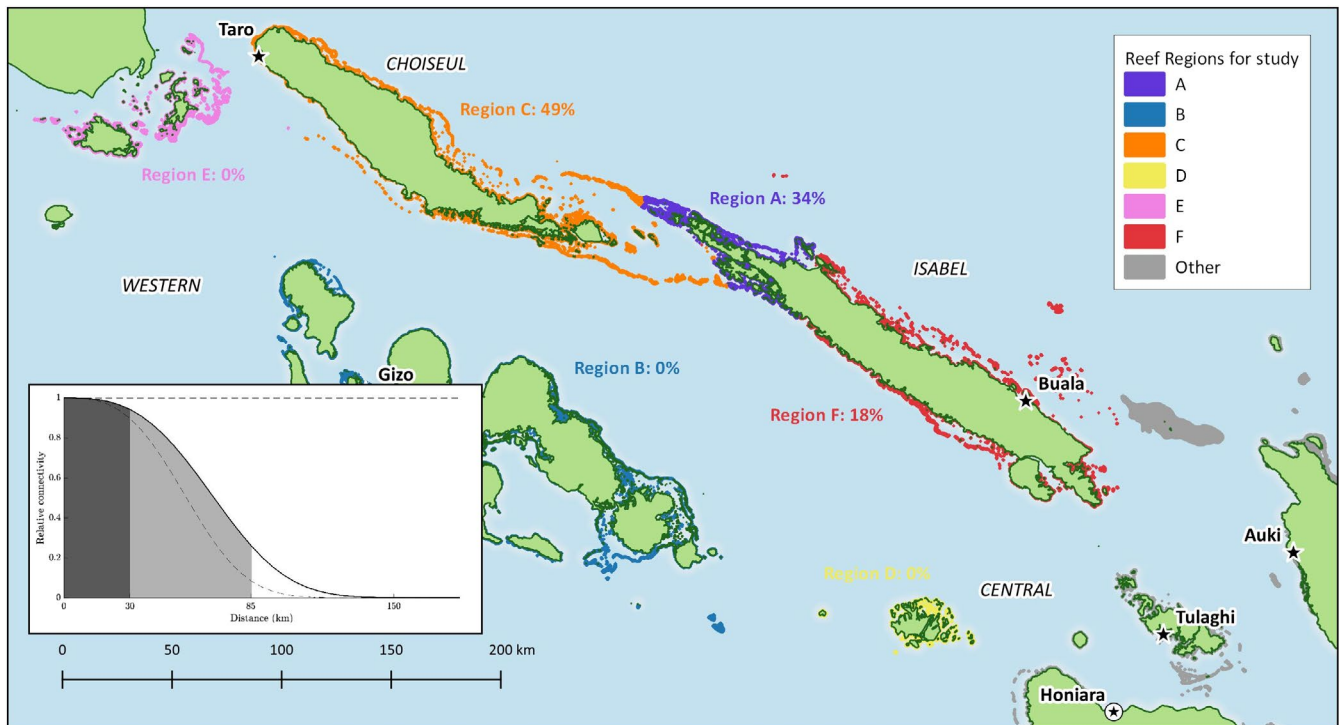
**FIGURE 4** Best fit Ribbens dispersal kernel for *Bolbometopon muricatum* larvae from Isabel Province, Solomon Islands. The best fit parameters are  $\beta = 3$ , and  $1/\alpha =$  in Equation 2. Kernels were estimated from the observed parent-offspring pairs within and between the Kia fishing zones. The solid black line is the maximum likelihood fit, while dashed lines show 95% confidence intervals. Note that the upper bound is essentially flat, indicating that dispersal may be very long-distance for this species. Grey-shaded areas indicate the distances within which 50% and 95% of larvae are predicted to settle

the greater distance to these islands than Choiseul (i.e. Shortland Islands) but also their lower adult abundances (e.g. Western Province, Hamilton et al., 2019).

The 10:1 ratio of adult density in lightly versus heavily fished areas is based on a combination of expert opinion and data from Kia

and Roviana fisheries (Hamilton et al., 2016, 2019). To estimate the sensitivity of the results to this assumption, we recalculated both the regional exchange figure (Figure 5) and the zonal exchange figure (Figure 3) using relative densities of 2:1 and 20:1. These changes do not greatly change the regional exchange results (see Supporting





**FIGURE 5** Relative contribution of different regions to recruitment of *Bolbometopon muricatum* larvae into the Kia fishing grounds (Region A), Isabel Province, Solomon Islands. For example, we estimate that southeast Isabel Island (red reefs) contribute 18% of the larvae recruiting to the Kia grounds. Inset plot reproduces the best-fit larval dispersal kernel, appropriately scaled

Information; Appendix S5). The contribution of Region C, for example, varies between 45% and 49%, and remains the major contributor in both cases. Similarly, the contributions of regions B, D & E are negligible in all cases. The variation does have a marked effect on the zonal exchange results (see Supporting Information; Appendix S5). Self-recruitment in zone 1, for example, which has lower densities of the species, varies markedly (from 1% to 9%) between the lowest and highest relative *B. muricatum* densities. We note, however, that the data on relative abundance are reliable at this scale in particular, supporting our best guess (1% self-recruitment in this case).

## 4 | DISCUSSION

In this study, we combine genetic parentage analysis and modelling to describe the larval dispersal patterns of the giant bumphead parrotfish *B. muricatum*. We identified 67 juvenile fish in the Kia fishing grounds that were the offspring of parents from those fishing grounds, and fit a dispersal kernel based on the sampling location of adult and juvenile fish. The model predicted that most *B. muricatum* larvae settle within 30 km of their parents, with stronger inter-regional connectivity from lightly exploited populations. This is the first time that a larval dispersal kernel has been estimated for a parrotfish, and only the fourth time that a dispersal kernel has been calculated for a commercially valuable reef fish. The mean dispersal distance of *B. muricatum* larvae fall between the lowest (14 km) and

highest (190 km) mean dispersal distances reported for different coral trout species (Almany et al., 2013; Williamson et al., 2016).

By subdividing our study area into three zones, we were able to observe how fishing pressure had impacted larval exchange within the Kia fishing grounds. Although all three zones exchanged larvae, the heavily fished Zone 1 produced substantially lower amounts of larvae than the lightly fished Zones 2 and 3. After accounting for unsampled adults, we calculated that 34% of juveniles sampled were the offspring of adults in the Kia fishing grounds. By expanding our dispersal model to cover five other regions in the Solomon Islands, we estimated that many of the unassigned juveniles in the Kia fishing grounds (66%) were the offspring of adult subpopulations in the lightly fished Regions C and F. None of the regions (B, D, or E) that are located more than 100 km away from the Kia fishing grounds supplied larvae into the Kia fishery, regardless of whether they represented lightly or heavily exploited regions.

Our findings have several important implications regarding the management of *B. muricatum* and its local extinction risk. Firstly, the larval dispersal kernel of *B. muricatum* should buffer subpopulations against recruitment overfishing and localised extinctions, as overfished stocks can be 'rescued' by the larvae that are produced by adult subpopulations up to 85 km away.

There are two important and obvious caveats to this positive conclusion. Regional rescue is only possible if lightly exploited spatially separated adult subpopulations exist, and it is only possible if the overfished region in question has adequate and intact nursery

habitat (Brown & Hamilton, 2018; Hamilton et al., 2017). Roviana Lagoon is in the Western Province of Solomon Islands (Region B) and provides an example of where an overfished *B. muricatum* fishery is potentially being restocked by distant *B. muricatum* populations. Between the mid-1980s and 2018, the Roviana *B. muricatum* population declined by over 90%, yet despite sighting very low numbers of adult *B. muricatum* in UVC surveys of Roviana Lagoon in 2018, juveniles of varying size and age classes were present. This ongoing recruitment into the Roviana fishery may reflect the rescue effect, with one potential source of larvae being the large (15 km<sup>2</sup>) MPA adjacent to the uninhabited island of Tetepare, which lies approximately 40 km to the south of Roviana Lagoon and has high abundance of adult *B. muricatum* (Hamilton et al., 2019). However, as dispersal may vary strongly through time, multiple lightly exploited populations are likely necessary to rescue heavily fished populations of *B. muricatum* (Catalano et al., 2021; Harrison et al., 2020).

Secondly, while the dispersal kernel for *B. muricatum* could save local stocks from recruitment overfishing, it also highlights the fact that small MPAs are unlikely to be an effective strategy for conserving *B. muricatum* stocks. Although MPAs are a popular fisheries management tool in the Pacific, most are <1 km<sup>2</sup> (Mills et al., 2010; Weeks et al., 2010), a magnitude smaller than the estimated home ranges of adult *B. muricatum* (Green et al., 2015) and several magnitudes smaller than the median dispersal distance of *B. muricatum* larvae. In the case of *B. muricatum*, the spatial separation between nursery areas and adult foraging habitat further limits the ability of small MPAs to effectively manage this species.

Although small MPAs are a poor management option for *B. muricatum* (Hamilton et al., 2019) and many other large mobile reef species (Bellwood et al., 2019), there are several practical measures that would help conserve *B. muricatum* across its range: (a) protect recruitment habitat by minimising development in catchments that are adjacent to fragile nursery grounds (Hamilton et al., 2017); (b) establish and enforce a 650 mm minimum size limit to protect immature fish and limit the amount of commercial fishing in lagoons (Hamilton et al., 2019; Lavin et al., 2021); (c) encourage governments to place moratoriums on harvesting *B. muricatum* once stocks are overfished; and (d) when socially and politically feasible, establish networks of large MPAs that encompass linked juvenile and adult habitat (Green et al., 2015).

The ability of regional fish populations to subsidise and enable the recovery of overfished stocks is a critical question for both biodiversity conservation and human well-being. However, the question is made scientifically challenging by the contrastingly small size of pelagic larvae, and the vast spatial scale of the regions of interest. To estimate recovery potential, we were forced to assume a great deal of spatial and temporal ecological homogeneity. For example, fish population densities, reproductive output and oceanographic patterns will fluctuate in space and time. These changes will alter dispersal patterns, but are not included in our results. Even with these factors held constant, our estimate of the larval dispersal kernel contains considerable uncertainty (Figure 4); while our best estimates suggest that most larval dispersal occurs within 30 km of the natal location, it is possible that dispersal is occurring over a much larger

scale. While this range means that our estimates of proportional contributions (Figure 5) must be understood to be only approximate, it does not alter our primary qualitative conclusions about the large role played by regional populations in recruitment and recovery to the Kia fishing grounds. Most of the uncertainty suggests that dispersal distances may be longer than our best guess, and longer average dispersal distances will only increase the importance and role of these regional sources.

The scale of *B. muricatum* larval dispersal, as measured here, is one of the few positive aspects of this species' life-history and fishery attributes. Its intermediate scales of larval connectivity increase the likelihood of overfished *B. muricatum* subpopulations being restocked by lightly exploited subpopulations, up to 85 km away. Nevertheless, this species dependency on fragile lagoonal nursery habitat (Hamilton et al., 2017), its longevity (Taylor et al., 2018) and the fact that it sleeps exposed in shallow water at night (Hamilton et al., 2016) are life-history characteristics that make *B. muricatum* highly susceptible to overexploitation.

Given that global food security increasingly relies on coastal fisheries, greater effort is necessary to develop and enforce fisheries management measures that will enhance the persistence of exploited species. The development of orthodox fisheries management strategies relies on species-specific life-history information such as growth rates and size at maturity. Our results illustrate the importance of augmenting this information with knowledge on larval dispersal patterns. In particular, the vulnerability of fisheries species is critically dependent on the contrasting scales of larval dispersal and fishery exploitation.

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## CONFLICT OF INTEREST

The authors have declared no conflicts of interest.

## AUTHORS' CONTRIBUTIONS

R.J.H., G.R.A., J.H.C. and M.B. conceived the ideas and designed methodology; R.J.H., G.R.A., J.P. and C.G. collected field samples; P.S.-A. and D.L.-C. conducted laboratory analyses; D.L.-C., P.S.-A., H.B.H., M.B., N.P., M.L.B. and P.A.W. analysed the data; M.B. conducted the modelling components; R.J.H. and M.B. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.fxpvnv0sh> (Hamilton et al., 2021).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of the article at the publisher's website.

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