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REPORT

Population connectivity and the effectiveness of marine protected areas to protect vulnerable, exploited and endemic coral reef fishes at an endemic hotspot

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Abstract Marine protected areas (MPAs) aim to mitigate anthropogenic impacts by conserving biodiversity and preventing overfishing. The effectiveness of MPAs depends on population connectivity patterns between protected and non-protected areas. Remote islands are endemism hotspots for coral reef fishes and provide rare examples of coral reefs with limited fishing pressure. This study explored population genetic connectivity across a network of protected and non-protected areas for the endemic wrasse, *Coris bulbifrons,* which is listed as "vulnerable" by the IUCN due to its small, decreasing geographic range and declining abundance. Mitochondrial DNA (mtDNA) and microsatellite DNA (msatDNA) markers were used to estimate historic and contemporary gene flow to determine the level of population self-replenishment and to measure genetic and genotypic diversity among all four locations in the species range (south-west Pacific Ocean)—Middleton Reef (MR), Elizabeth Reef (ER), Lord Howe Island (LHI) and Norfolk Island (NI). MPAs exist at MR and LHI and are limited or non-existent at ER and NI, respectively. There was no obvious differentiation in mtDNA among locations, however, msatDNA revealed differentiation between the most peripheral (NI) and all remaining locations (MR, ER and LHI). Despite high mtDNA connectivity ($M = 259$–$1{,}144$), msatDNA connectivity was limited ($M = 3$–9) with high self-replenishment (68–93 %) at all locations. NI is the least connected and heavily reliant on self-replenishment, and the absence of MPAs at NI needs to be rectified to ensure the persistence of endemic species at this location. Other endemic fishes exhibit similar patterns of high self-replenishment across the four locations, indicating that a single spatial management approach consisting of a MPA network protecting part of each location could provide reasonable protection for these species. Thus, the existing network of MPAs at this endemic hotspot appears adequate at some locations, but not at all.

Keywords Endemic hotspot · Lord Howe Island · Marine protected areas · Management · Overfishing

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Introduction

Coral reefs worldwide have been impacted by disease, hurricanes, human overpopulation, eutrophication and global climate change (Hughes et al. 2003). However, fishing has had the most direct and wide-ranging influence

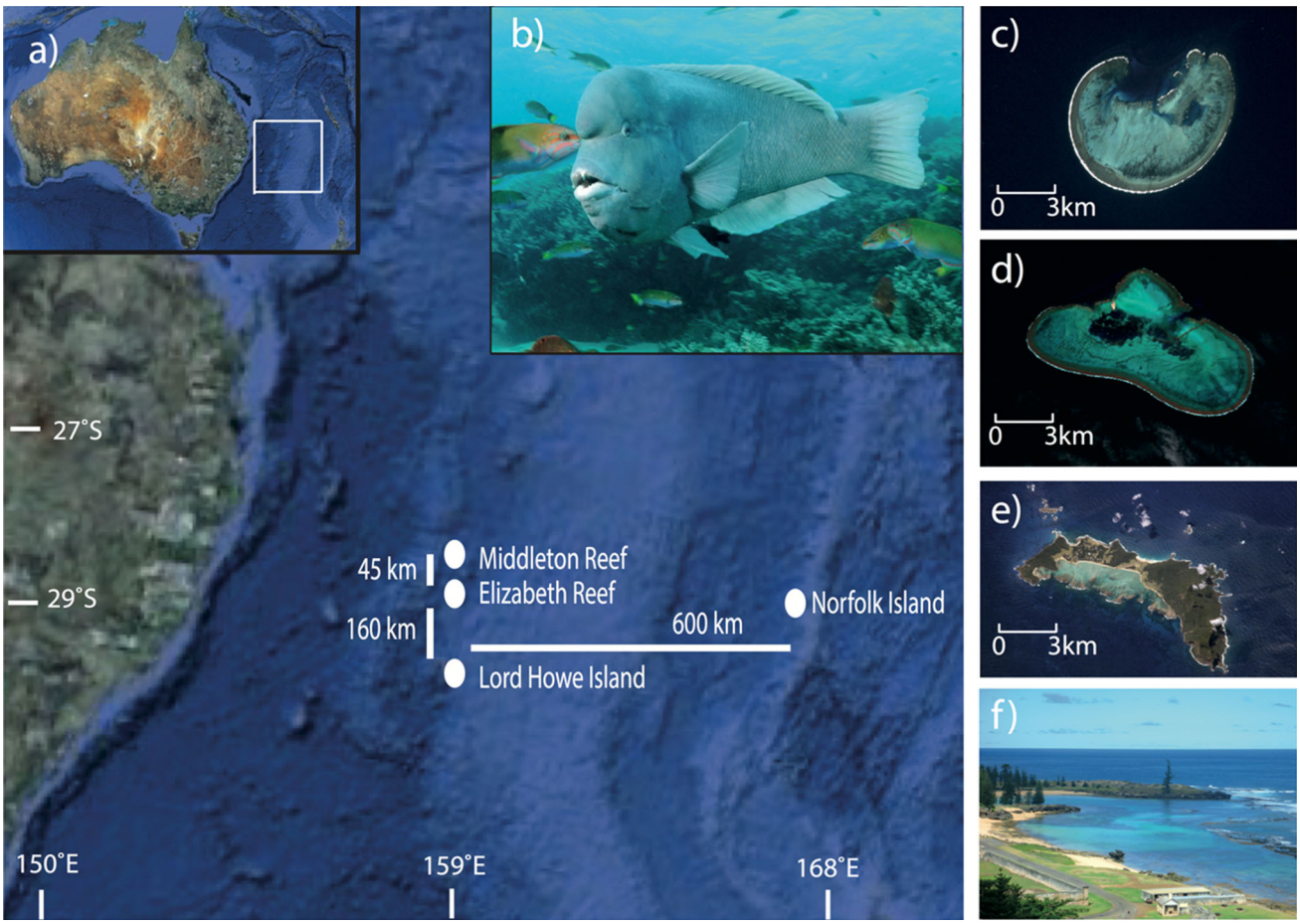

Fig. 1 Location maps and focal species (**a**) Google Earth image of eastern Australia showing Middleton Reef (MR), Elizabeth Reef (ER), Lord Howe Island (LHI) and Norfolk Island (NI) in the south-west Pacific Ocean. (**b**) *Coris bulbifrons* (Photo courtesy of Justin Gilligan). Aerial photographs of MR (**c**); ER (**d**), LHI (**e**) and NI (**f**; the bay measures 1 km in length)

on coral reefs and other marine ecosystems (Jackson et al. 2001). With anthropogenic pressures increasing (Steffen et al. 2007), natural resource managers have established marine protected areas (MPAs) to conserve biodiversity and protect fisheries stocks from overfishing. When designing MPAs, managers rarely have empirical evidence of levels of genetic connectivity among locations, forcing implementations based on "best guesses" (McCook et al. 2009).

Remote islands often represent rare examples of coral reefs with limited fishing pressure and thus provide a unique opportunity to assess how coral reef ecosystems function with limited human impacts. For example, the remote and lightly fished north-west Hawaiian Islands support significantly more fish biomass than the heavily fished main Hawaiian Islands (Friedlander and DeMartini 2002). Remote islands are also hotspots for coral reef fish endemicity (Jones et al. 2002), with a high proportion of their communities comprised of endemic species. While terrestrial endemics on remote islands are well known for their vulnerability to extinction (Whittaker 1998), much less is known about the vulnerability of their marine counterparts. The presence of endemic hotspots on isolated islands with lesser human impacts provides an ideal opportunity to examine inherent vulnerabilities of marine endemics.

In the Pacific, the locations with the greatest proportion of endemic coral reef fishes include: Hawaii (25 % endemism), Easter Island (22.2 %), the Marquesas (11.6 %), Lord Howe and Norfolk Islands (7.2 %) and Rapa Iti (5.5 %) (Randall 1998, 2001, 2007). The Lord Howe Island region in the south-west Pacific Ocean consists of four oceanic features: Middleton Reef (MR), Elizabeth Reef (ER), Lord Howe Island (LHI) and Norfolk Island (NI) (Fig. 1). These remote locations harbour tropical habitats dominated by scleractinian corals that transition into temperate habitats dominated by macroalgae (Johannes et al. 1983). The remoteness and transition between habitats makes these islands and reefs endemism hotspots for both coral and algae reef fishes. Lastly, these locations present

an ideal study system for genetic connectivity (i.e., gene flow) of endemic species since reef fishes occur on only four discrete islands/reefs that are separated by known distances (45–600 km).

The doubleheader wrasse (*Coris bulbifrons*, Randall and Kuiter 1982) is an iconic reef fish endemic to MR, ER, LHI and NI (Francis 1993). This large wrasse (maximum total length = 65 cm, Choat et al. 2006a) is targeted for food in recreational fisheries. It is locally abundant in sheltered habitats at MR (0.33/100 m^2), ER (0.28/100 m^2) and LHI (0.35/100 m^2) (Choat et al. 2006a; Hobbs and Feary 2007; Hobbs et al. 2009), but rare at NI (0.007/100 m^2*; authors pers obs*). The current network of MPAs provides diverse levels of protection to *C. bulbifrons*: MR is fully protected with no fishing allowed. ER allows recreational line and spearfishing of ten *C. bulbifrons* per person per day, but no commercial or charter fishing. However, there are very few boats capable of travelling out to ER and combined with poor weather for the majority of the year, few fish are thought to be caught at ER. LHI has MPAs (no take areas) and catch restrictions of one *C. bulbifrons* per person per day in areas open to linefishing (but no spearfishing is allowed). While fishing of *C. bulbifrons* does occur at Lord Howe Island, very few individuals are kept because there is a programme of catch and release. At NI, there are no MPAs and no catch restrictions for *C. bulbifrons*. Despite no protection or bag limits at NI, *C. bulbifrons* is not targeted due to the abundance of other higher quality fish.

C. bulbifrons is listed as vulnerable by the IUCN due to the (1) small area of occupancy (<2,000 km^2), (2) severely fragmented distribution (occurs at only four isolated locations), (3) declining area of occupancy and (4) declining number of mature individuals (Choat and Pollard 2010). Determining the temporal and spatial scales of genetic connectivity (gene flow) between the four locations where *C. bulbifrons* occurs is essential to establish how populations are maintained, replenished and in the event of a local extinction, what rescue options would be best. It is clear that this vulnerable species requires effective conservation management, especially in light of rapid population declines seen in other large wrasses following minimal fishing (Choat et al. 2006b).

Complete sampling throughout the entire range of a species distribution is rare in studies of coral reef fishes despite its importance to accurately estimate gene flow (historic and contemporary). Historic gene flow uses mtDNA to determine genetic exchange between populations that may have been isolated over thousands of generations (Hellberg 2009). Contemporary gene flow uses msatDNA to determine genetic exchange over a single or few generations by estimating either self-replenishment (i.e., contemporary timescales of 2–3 generations; inferred indirectly from a small sample size using genetic markers and subsequent assignment tests, in a population genetics context) or self-recruitment (i.e., current time scales of one generation; inferred directly by natural or artificial otolith tags, or nearly complete sampling of whole populations from various locations) to determine if populations are contemporarily open, closed or intermediate (e.g., Swearer et al. 1999; Planes 2002).

In this study, we estimate both historic and contemporary gene flow to establish which locations export and which locations import migrants and to identify genetic diversity of different subpopulations. The latter can serve as a potential indicator of genetic resilience (or lack thereof) to environmental change and extinction (Johannesson and Andre 2006). Such information will inform management agencies how to target conservation efforts by determining which location(s) are most vulnerable and therefore need the greatest levels of protection. Previous research on two other endemic species within this system (MR, ER, LHI, and NI) found concordant patterns in population genetic connectivity (van der Meer et al. 2012a, b, 2013a). Combining results from three endemic species that differ in biological and ecological traits provides a valuable framework to test population genetic connectivity across this endemic hotspot. Collectively, this information provides important guidance as to whether the same management approach could successfully protect a wide range of species.

Four primary aims underpin this study: (1) to estimate patterns of gene flow among locations/subpopulations of *C. bulbifrons* using mtDNA and msatDNA; (2) to estimate levels of self-replenishment (a proxy for self-recruitment) based on msatDNA assignment and exclusion analyses of *C. bulbifrons*; (3) to estimate *C. bulbifrons* population genetic diversities at all locations/subpopulations as a measure of genetic resilience to environmental change; and (4) to place the above results into a general framework that compares genetic estimates of patterns and levels of gene flow, levels of self-replenishment and genetic diversity, among different species from this endemism hotspot. This information will determine whether a single spatial management strategy is appropriate for conserving endemic reef fishes within the Lord Howe–Norfolk Island endemic hotspot.

Materials and methods

We combined estimates of historic (mtDNA) and contemporary (msatDNA) gene flow to provide a comprehensive overview of genetic dispersal over a range of timescales (Hellberg 2009; Leis et al. 2011). Using 17 polymorphic microsatellite loci, (van der Meer et al. 2013b) helped to compensate for small sample sizes

(Selkoe and Toonen 2006), while sampling all known locations left no unsampled "ghost" populations which can affect key contemporary genetic estimates (Beerli 2004). Our estimates for "self-replenishment" inferred indirectly from genetic markers are merely a proxy for self-recruitment, which is typically assessed using direct methods (e.g., natural or artificial otolith tags), such as those used by Swearer et al. (1999) and Jones et al. (2005). Lastly, differences in mortality (natural and anthropogenic) between locations can alter estimates of realised connectivity (Cowen and Sponaugle 2009). It is unclear if there are differences in natural mortality between the four locations, however, fishing mortality rates are probably low at all locations. If natural mortality rates are similar between the four locations, then the patterns of realised connectivity described here are likely to reflect patterns of larval dispersal. However, while fishing mortality is currently low at the four locations, future fishing mortality may pose a risk at some locations because the four locations have varying levels of protection in place.

Ethics statement

Fishes were collected by spearfishing and fin clipped or were anaesthetised underwater with clove oil, fin clipped in situ and released alive: MR ($n = 20$), ER ($n = 10$), LHI ($n = 37$) and NI ($n = 16$) (Permit Numbers: LHIMP08/R01, 003-RRRWN-110211-02, P11/0035-1.0; Animal ethics: A1605).

Study system

We sampled *C. bulbifrons* throughout its entire geographic range. MR, ER and LHI are referred to as the "western region" for *C. bulbifrons* because they occur on the same geographic feature (Lord Howe Island Rise) are relatively close to each other (Fig. 1) and support higher abundances (Choat et al. 2006a; Hobbs et al. 2009). In contrast, NI is referred to as the "peripheral location" for this species because it is the only location situated on a separate geographic feature (Norfolk Island Rise), which is isolated by more than 600 km of deep water from the western region (Fig. 1) and has a much lower abundance (*authors pers. obs.*). *Coris bulbifrons* inhabits shallow (<40 m) reef habitats and adults will not traverse deep oceanic waters to disperse between the four locations. However, *C. bulbifrons* has a relatively long Pelagic Larval Duration (PLD; mean duration 36 days; *authors pers comm*) suggesting that it is capable of dispersing between locations (e.g., Shanks 2009) especially when aided by the complex regional oceanographic currents (Suthers et al. 2011).

Gene flow between locations: mtDNA

mtDNA phylogenetic analysis

To identify any clear divisions in population genetic structure in *C. bulbifrons*, the non-coding (D loop) was sequenced following van der Meer et al. (2012a, b, 2013a). Fin clips from three *Coris gaimard* individuals were collected from Christmas Island (Indian Ocean) to use as an outgroup (Barber and Bellwood 2005). jModeltest (Posada 2008) identified a GTR+G model based on AIC ($\gamma = 0.271$). Three commonly used phylogenetic analyses [Maximum Likelihood (ML), Maximum Parsimony (MP) and Bayesian Inference (MrBayes, MB, BEAST)] were performed on aligned mtDNA sequence data. A Minimum Spanning Tree (MST) was generated based on output obtained from ARLEQUIN 3.5 (Excoffier et al. 2005) in order to explicitly identify shared haplotypes among *C. bulbifrons* from the four locations (MR, ER, LHI and NI).

Patterns of gene flow (mtDNA)

To obtain reliable estimates of mtDNA gene flow given low sample sizes, samples from ER were pooled with MR, which was appropriate because pairwise F_{st}, Discriminant Analysis of Principal Components (DAPC), STRUCTURE and GeneClass analyses could not genetically differentiate the two populations. Thus, *C. bulbifrons* mtDNA migration rates (M; number of migrants) were estimated among, and effective population sizes (θ) were estimated within, each of the three areas (MR–ER, LHI and NI) using MIGRATE-n 2.4.3 (Beerli 2004).

Gene flow between locations: msatDNA

Patterns of gene flow (msatDNA)

To determine spatial population partitioning based on msatDNA, we used three molecular analytical tools: (1) DAPC (Jombart et al. 2010) uses allelic states to discriminate between the four locations, yielding scatterplots of discriminant functions based on the spatial distributions of microsatellite genotypes. DAPC also provided posterior probabilities of population assignments for each individual. (2) A likelihood-based assignment method was used in GeneClass2 (Piry et al. 2004) to determine significant inter-location gene flow. (3) STRUCTURE V2.3 (Pritchard et al. 2000; Hubisz et al. 2009) places individuals into clusters that minimise Hardy–Weinberg Equilibrium (HWE) and can be used to identify contemporary gene flow among the four locations.

As above, to obtain reliable estimates of msatDNA gene flow given low sample sizes, samples from ER were pooled

with MR to estimate *C. bulbifrons* msatDNA migration rates (*M*; number of migrants) among, and effective population sizes (θ) within, each of the three areas (MR–ER, LHI, and NI) using MIGRATE-n 2.4.3.

Inferred levels of self-replenishment and recent migration

To determine self-replenishment and recent migration (both given as a percentage) among locations, we used BAYESASS v3 (Wilson and Rannala 2003) with a Markov Chain Monte Carlo (MCMC) method, consisting of a total of 11 million steps with a 2 million step burn in. Ten separate runs assessed convergence of the MCMC in order to evaluate the consistency of results obtained from these inferences.

Population genetic diversities

To explore differences between locations in molecular diversity, indices were calculated for mtDNA (haplotype diversity, *h*; nucleotide diversity, π) and msatDNA (genetic diversity, gd) for each location (and as a total of all pooled samples) in ARLEQUIN 3.5 (Excoffier et al. 2005). Haplotype and nucleotide diversities of the data were interpreted as either low with specified cut-off values of *h* and π (%) < 0.5 or high if values of *h* and π (%) were >0.5 (Grant and Bowen 1998).

Results

Gene flow between locations: mtDNA

Patterns of gene flow (mtDNA)

To determine gene flow between the four locations, 341 base pairs of mtDNA (D Loop) were sequenced for 81 *C. bulbifrons* individuals with a total of 56 polymorphic sites (parsimony informative = 37). A total of 13 spatially intermixed clades were identified (bootstrap values >50 %), with Clade 13 comprising 38 % of the entire sample ($n = 31/81$) suggesting that mtDNA gene flow exists between all locations occupied by *C. bulbifrons* (Fig. 2a). A Minimum Spanning Tree (MST) identified 56 haplotypes in total, many of which were unique ($n = 44$; Fig. 2b).

AMOVA of the mtDNA data revealed little structure among locations. Comparing the western region (MR, ER and LHI) with the peripheral location (NI) indicated no significant genetic variation between regions, $\Phi_{ct} = 0.002$ ($p = 0.752$); or among locations within regions, $\Phi_{sc} = 0.004$ ($p = 0.618$; Electronic Supplementary Material, ESM S1). All genetic variation occurs within locations, $\Phi_{st} = 0.002$ ($p = 0.553$; ESM S1), although this is not significant. Likewise, mtDNA pairwise Φ_{st} showed no genetic differentiation among any of the paired locations (pairwise $\Phi_{st} = 0.018$–0.012, $p = 0.234$–0.694; ESM S2).

MIGRATE-n analysis of mtDNA indicated high levels of historic gene flow between all locations (ER–MR, LHI and NI), with *M* values ranging from 291 to 1144 (Fig. 3a).

Gene flow between locations: msatDNA

Summary statistics

Of the 17 msatDNA loci that were examined: (1) nine of the 68 tests of HWE at the location level were significant before and only one after FDR (False Discovery Rate) correction (NI: Cb2; Benjamini and Hochberg 1995); (2) null alleles were identified only at one locus (ER: Cb5); and (3) 10 of the 272 locus-by-locus exact tests of linkage disequilibrium (LD) were significant before and only two after FDR correction (Cb13, Cb30).

Patterns of gene flow (msatDNA)

An AMOVA of msatDNA revealed significant genetic structure between populations from the four locations. AMOVA indicated significant structure in 7 (of 17) locus-by-locus analyses corrected for null allele frequency ($F_{st} = 0.001$–0.190, $p < 0.05$; ESM S3), corrected for standardised population differentiation ($F_{st} = 0.006$–0.268, $p < 0.05$; ESM S3) and in the global AMOVA as a weighted average over all microsatellite loci ($F_{st} = 0.025$, $p < 0.001$; ESM S1), with 97.53 % of the genetic variation existing within populations. In contrast to the AMOVA results, raw msatDNA pairwise F_{st} comparisons showed low non-significant genetic partitioning between populations ($F_{st} = 0.007$–0.027, $p > 0.144$), with the exception of LHI and ER ($F_{st} = 0.044$, $p = 0.003$) and LHI and NI ($F_{st} = 0.043$, $p < 0.001$; ESM S2). Excluding Null Alleles (ENA) corrected msatDNA pairwise F_{st} values showed no significant genetic differentiation between populations ($F_{st} = 0.011$–0.099, $p > 0.05$; ESM S2). The contrasting differences in genetic partitioning between the powerful AMOVA and less powerful pairwise F_{st}, most likely results from the low sample size of ER ($n = 10$) and subsequent lack of analytical power.

DAPC, GeneClass2 and STRUCURE all supported at least three geographically distinct populations (ER–MR, LHI and NI). DAPC, however, partitioned *C. bulbifrons* into four populations (ER, MR, LHI and NI) representing two regions: the western region (MR, ER and LHI) and the peripheral location (NI, Fig. 2c). Using the four locations as a priori population criteria, DAPC assigned 70–94 % of all individuals to the populations from which they were

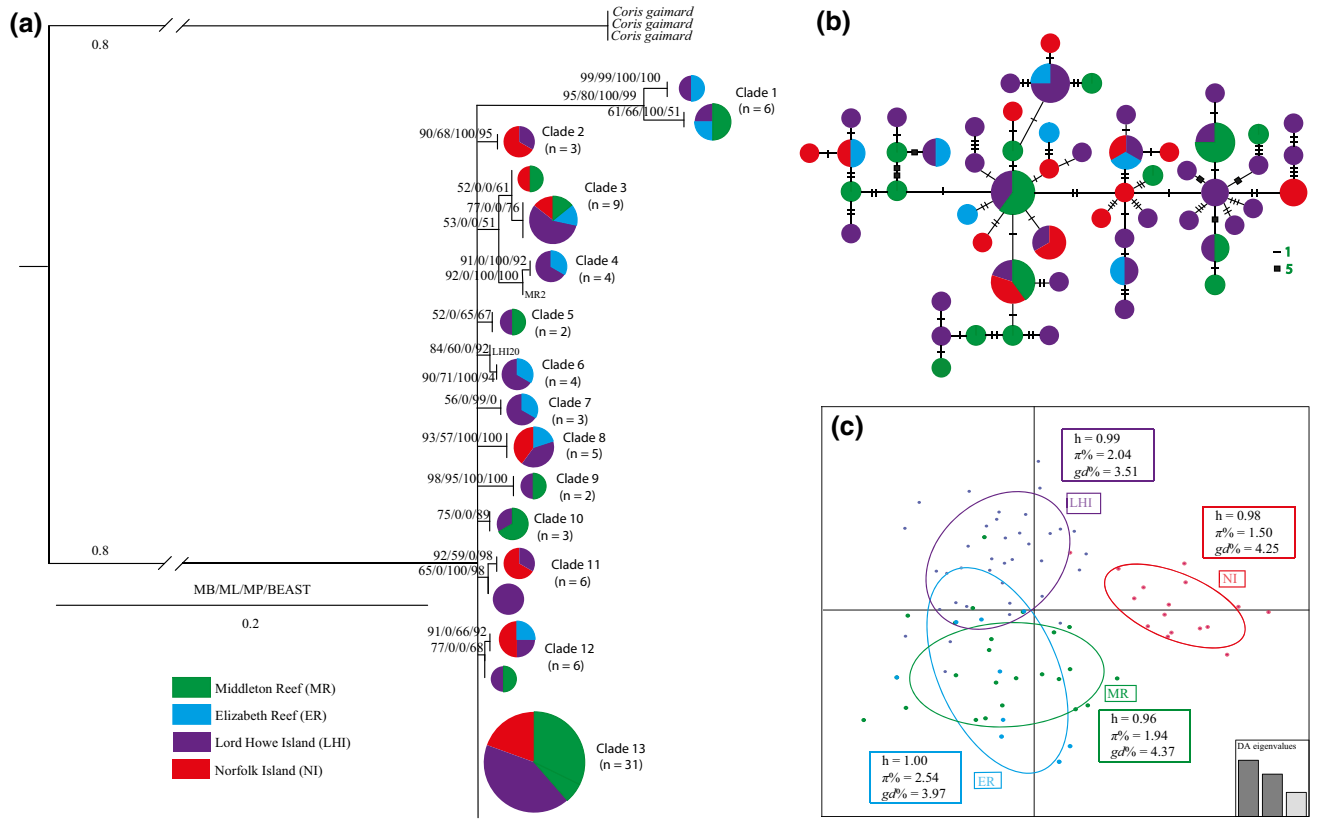

Fig. 2 *Coris bulbifrons* mtDNA and msatDNA analyses. **a** A phylogram of mtDNA (D loop) sequences from 81 *C. bulbifrons* individuals from Middleton Reef, Elizabeth Reef, Lord Howe Island and Norfolk Island. This represents the best Maximum Likelihood (ML) tree from 10 individual analyses. *Numbers on branches* indicate support for each clade, based on ML, Maximum Parsimony (MP), Bayesian Inference (MB) and BEAST analyses. **b** Haplotype minimum spanning tree (MST) with number of substitutions between haplotypes indicated on connectors. The *colours of the different fills* represent each of the four locations as shown on the key to the Figure. **c** A scatterplot of the Discriminant Analysis of Principal Components (DAPC) of the microsatellite data for the four locations where *C. bulbifrons* occurs globally, using geographic sample site as priors for genetic clusters. Individual genotypes appear as dots surrounded by 95 % inertia ellipses. Eigenvalues show the amount of genetic information contained in each successive principal component with the *x*- and *y*-axes constituting the first two principle components, respectively. Boxes within the DAPC plot indicate haplotype (*h*), nucleotide (π %) and genetic diversity (gd %) indices for *C. bulbifrons*

sampled (assignment per population, ER = 70 %, MR = 85 %, LHI = 92 %, NI = 94 %; Fig. 4). Geographical structure in msatDNA was confirmed by GeneClass2, where only 16 individuals were grouped with populations from which they were not sampled MR ($n = 3$), ER ($n = 4$), LHIL ($n = 6$) and NI ($n = 3$).

MIGRATE-n indicated gene flow several orders of magnitude lower using msatDNA when compared to mtDNA gene flow among populations (MR–ER, LHI and NI), with number of migrants (*M* values) ranging from 3 to 20 (Fig. 3b).

Inferred levels of self-replenishment and migrant exchange

Contemporary independence (i.e., gene flow among populations that is <10 %; Waples and Gaggiotti 2006) is suggested for five of seven population pair comparisons: exceptions being ER to LHI ($M = 14$ %) and MR to LHI ($M = 27$ %; Fig. 3c). Conversely, high levels of self-replenishment (68–93 %) were inferred at all four populations (Fig. 3c).

Population genetic diversities

Coris bulbifrons showed high haplotype (*h*), medium nucleotide (π %) and medium–high genotypic diversities (gd %) at all locations ($h = 0.98$–1.00, π % = 1.94–2.54, gd % = 3.51–4.37; Fig. 2c). The haplotype, nucleotide and genotypic diversities totalled across all locations were also high ($h = 0.99$, π % = 1.95, gd % = 3.84; ESM S1).

Discussion

Studying endemic species geographically restricted to a small number of discrete and remote locations offers

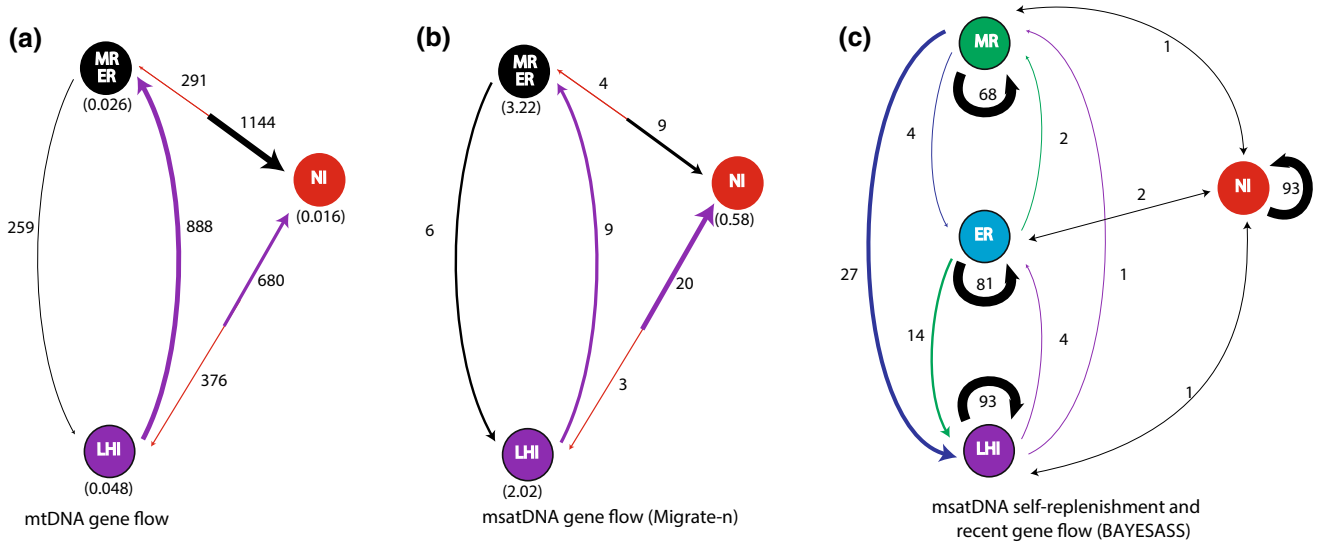

Fig. 3 Migration rates among *Coris bulbifrons* locations. **a** MIGRATE-n evolutionary gene flow (mtDNA) shown as *M* (number of migrants) and **b** MIGRATE-n contemporary gene flow (msatDNA) shown as *M* (number of migrants). For both **a** and **b,** the thickness of the *arrowed line* is directionally proportional to the number of migrants (*M*) and the *line colours* indicate the predominant direction of gene flow; population size (θ, within parentheses) is also shown for each location. **c** BAYESASS analysis of self-replenishment and recent migration rates (msatDNA) shown as a percentage

unique opportunities to examine gene flow throughout a species entire range. Island systems such as examined in this study provide valuable empirical data on gene flow (historic and contemporary) among isolated locations, separated by known distances and deep oceanic waters. Here, *C. bulbifrons* was found to have similar patterns and levels of mtDNA and msatDNA genetic connectivity, self-replenishment and genetic diversity as other endemic species from this area. This indicates that a single spatial management approach consisting of an MPA network protecting part of each location could provide reasonable protection for these species. Thus, the existing network of MPAs at this endemic hotspot appears adequate at some, but not all locations.

Gene flow among locations: mtDNA

MtDNA suggested a complete lack of spatial genetic structure for *C. bulbifrons*. This is likely the result of a small number of recruits per generation maintaining spatial genetic homogeneity (Shulman 1998; Planes 2002). Interestingly, the peripheral location (NI) shows no genetic break from the western region, in contrast with peripheral locations of other widespread reef fishes at larger spatial scales (Drew et al. 2008; Winters et al. 2010). Thus, mtDNA gene flow has apparently been sufficient or recent enough to suggest that all locations are connected over historic timescales as the presumed neutral mtDNA marker has not (yet) accumulated genetic differences under either genetic drift or selection.

Gene flow among locations: msatDNA

MsatDNA suggested spatial genetic structure for *C. bulbifrons* with high levels of self-replenishment (>68 %). The apparent discrepancy between mtDNA and msatDNA likely results from few recruits per generation maintaining mtDNA genetic homogeneity over historical timescales, whereas populations at isolated locations require substantial amounts of self-recruitment on contemporary timescales to maintain viable populations. This discrepancy between mtDNA and msatDNA is increasingly being documented in other coral reef fishes (e.g., Evans et al. 2010; Harrison et al. 2012) and within the LHI region (van der Meer et al. 2012a, b, 2013a). Interestingly, some individuals at the peripheral location (NI) show phenotypic differences (stripes and patterns around the eye, *authors pers obs*) suggesting that NI is at the very least, a genetically distinct and unique subpopulation (Drew et al. 2008) or at an early stage of peripheral speciation (sensu Rocha 2004; Bowen et al. 2013).

Currently, the MPAs in the western region (MR, ER and LHI) encompass suitable habitat for *C. bulbifrons* (and other coral reef fish) and when combined with greater abundance and higher levels of contemporary gene flow (i.e., larger number of migrants and lower self-replenishment), decreases the risk of local extinction and facilitates recovery should populations decline or go locally extinct. However, the lack of an MPA at the peripheral region (NI), low abundance and extremely low levels of contemporary gene flow between regions all increase the risk of local

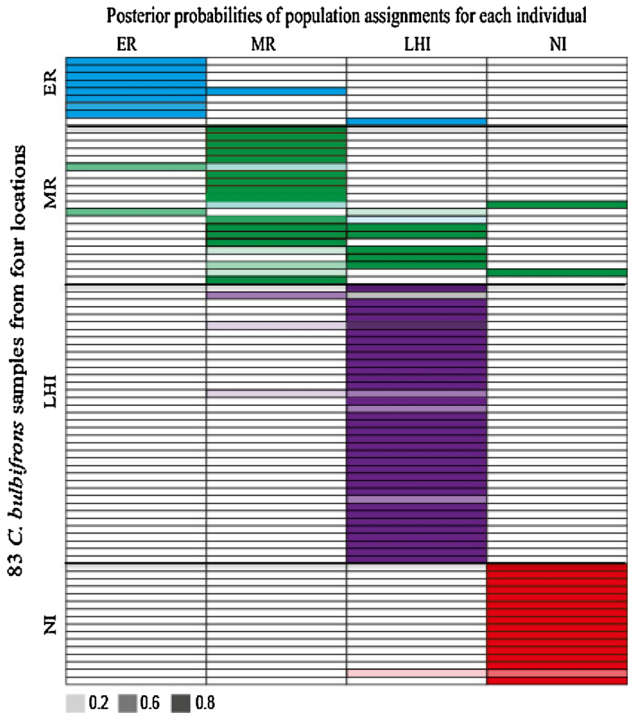

Fig. 4 Posterior probability of assignment of each individual genotype to four *Coris bulbifrons* populations as indicated by DAPC. The abbreviations of the possible assignment populations are given on the *x*-axis 83 genotypes are listed on the *y*-axis, along with the population from which they were sampled. *Light to dark shaded bars*, respectively, correspond to a 0.2–0.8 probability of assignment across all colour schemes

extinction and the potential loss of unique colour and genotype variants at this peripheral location. Lastly, high levels of self-replenishment (i.e., limited contemporary gene flow) at all locations and fishing pressure at ER (and in some areas at LHI) is concerning since populations may still decline even with minimal fishing effort (Choat et al. 2006b).

Population genetic diversities

C. bulbifrons showed high haplotype (*h*), medium nucleotide (π %) and medium–high msatDNA genotypic (gd %) diversities at all locations. Given that mtDNA diversity tracks nuclear genetic diversity in many marine species (Johannesson and Andre 2006), this is encouraging since maintaining genetic diversity is an IUCN priority (McNeely et al. 1990). High genetic and genotypic diversity provides the raw material for natural selection to act on over historical (Johannesson and Andre 2006) and contemporary timescales (Bell and Okamura 2005), decreases the risk of inbreeding depression (Reed and Frankham 2003) and allows greater adaptive capacity to better cope with the impacts of environmental change than species with low genetic diversity (Avise 2000). However, a genomic approach that identifies "outlier" loci that may be under selection is required, since loci under selection will have reduced genetic diversity within divergent populations for the relevant loci (Luikart et al. 2003).

Population connectivity in endemic fishes within the LHI region

The LHI (and NI) region is a hotspot for endemic coral reef fishes with the fourth highest percent endemism (7.2 %) in the Indo-Pacific (Randall 1998, 2001, 2007). Currently, an MPA network consisting of three isolated locations (MR, ER and LHI) aims to protect this unique diversity. Whilst the current network of MPAs within the western region may provide adequate protection for endemic reef fishes, the lack of protection at NI is concerning. Furthermore, many of the endemics at NI have low abundance (*author's pers obs*), which together with reduced input from the populations to the west (i.e., ER, MR and LHI), increases their vulnerability to local extinction. Given the elevated risk of extinction of endemics at NI and the genetic uniqueness of NI endemic populations, establishing protective measures (MPAs and fishing regulations) should be a management priority at this location.

Genetic studies across three taxonomically distinct groups having different ecologies (*A. mccullochi*—an anemone habitat specialist and generalist planktivore; *C. tricinctus*—a coral feeding specialist; and *C. bulbifrons*—an invertebrate feeding habitat generalist) and/or life histories (mean PLD: *A. mccullochi* = 12 days, *C. tricinctus* = 35 days, *C. bulbifrons* = 36 days, *authors. pers obs*) show similar patterns of population genetic connectivity and genetic diversity (van der Meer et al. 2012a, b, 2013a). This indicates that a single management strategy within this region may be appropriate for the design of MPAs to protect endemic reef fishes in the LHI–NI endemic hotspot. If other remote islands with high levels of reef fish endemism (e.g., Hawaiian Islands, Easter Island, the Marquesas, Rapa Iti) also show similar patterns of population genetic connectivity and replenishment among endemics, regardless of ecology and/or life history, then this advocates for the use of a single spatial management strategy to protect a wide range of species in these endemic hotspots (Toonen et al. 2011). A management strategy involving a network of MPAs that protects part of each genetically distinct population in the geographic range of endemics is likely to be effective at conserving the unique biodiversity of endemism hotspots.

Although isolation buffers remote locations from many anthropogenic impacts, it can also increase vulnerability because of limited contemporary genetic connectivity and replenishment among populations, as shown here. Given that remote reefs are also hotspots of endemism in coral

reef fishes (Jones et al. 2002), if widespread impacts occur, endemic species may be particularly vulnerable due to their small and fragmented geographic distribution. Island endemics have the highest rates of extinction in the terrestrial environment (Whittaker 1998), and globally coral reefs are experiencing a rapid increase in anthropogenic stresses (Steffen et al. 2007). These observations provide the impetus to establish broadly applicable management strategies that are effective in conserving multiple endemic species at endemic hotspots, in order to stem the likely loss of biodiversity that may result without such protective measures.

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