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Biology

Limited genetic structure among broad-scale regions for two commercially harvested, tropical deep-water snappers in New Caledonia

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Abstract We estimated the spatial population connectivity of *Etelis carbunculus* and *E. coruscans* based on measures of population genetic structure using the mitochondrial DNA control region. We collected samples from three areas separated by a minimum of 200 km around New Caledonia. We identified two separate genetic groups for *E. carbunculus* and a single group for *E. coruscans*. There were many singleton haplotypes distributed among geographic regions, indicating minimal spatial differentiation in genetic structure between regions for each species, although one of the genetic groups for *E. carbunculus* was in only two of the three regions. Conservation and management directives should consider both species as a single genetic stock among these three widespread regions. Our results provide evidence that stock structure might be less variable in the South Pacific than reported elsewhere, possibly indicating that trans-boundary management may be required in this region for deep-water snapper fisheries. Further refinement (including taxonomy) is required for *E. carbunculus* to characterize the different lineages observed.

Keywords Deep-water snappers · Mitochondrial DNA control region · Population structure · South Pacific · Spatial differentiation · Trans-boundary management

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Introduction

Measuring population connectivity and assessing the role of dispersal in maintaining genetic diversity in marine ecosystems are fundamental to understanding fish population dynamics, community structure, the resilience of populations to harvest [1–3], setting effective management strategies [4–6] and establishing conservation priorities [6, 7]. In the case of commercially important, tropical deep-water snapper species, it is generally assumed that sub-populations are highly structured arising from the largely presumed sedentary adult phase [8–10] when occurrence is strongly associated with physical features such as seamounts and deep-sea ridges [11]. Despite this assumption, some connectivity among populations should arise from larval dispersal. For instance, lutjanid larvae are often pelagic up to approximately 40 days after hatching, depending on the species and habitat configuration [12, 13].

Global tropical deep-water snapper fisheries target many species simultaneously; however, the two prominent

genera targeted are *Pristipomoides* and *Etelis*. The fisheries operate at depths between 150 and 400 m; *Etelis* spp. are usually caught at 250–400 m. Both *E. carbunculus* and *E. coruscans* have a high market value (approximately US$20 kg^{-1}), which is almost comparable to tuna per kilogram (Adams and Chapman, unpublished data, 2004). For many countries in the Asia–Pacific region, such as Japan and Hawaii, the red colour is a sign of wealth and good luck, giving a cultural importance to these snappers. Economically, the high market value of these fishes gives opportunities for developing countries to explore an export market internationally, but also helps ease the pressure of coastal fisheries at a local scale.

During the early and mid-1980s, many Pacific Island countries and territories investigated the potential development of deep-water snapper fisheries (Adams and Chapman, unpublished data, 2004). This period directed effort towards the application of efficient and effective fishing techniques, but research into the biological and ecological sustainability factors for the fishery was practically non-existent. Hence, population structure and dynamics were largely assumed from standard fisheries management algorithms to estimate sustainable yields (Adams and Chapman, unpublished data, 2004) [14, 15]. The combination of insufficient scientific information on biology and market propaganda promoting the fish as a food commodity, problematic infrastructure development and support in most developing countries made it less lucrative for fishers to continue (Adams and Chapman, unpublished data, 2004) [16] and in many instances these fisheries have reduced in size since the mid-1990s (Adams and Chapman, unpublished data, 2004).

In New Caledonia, the deep-water snapper fishery has persisted since the mid-1980s, but it has not expanded due to competition with the more lucrative and well-promoted Pacific tuna fishery that gained dominance in the early 1990s (Adams and Chapman, unpublished data, 2004). Currently, the fishery targets eteline species, particularly *E. carbunculus* and *E. coruscans*. Unfortunately, there is limited data describing the ecology and life history for either species to parameterize sustainable-catch models [17].

Understanding the structure and connectivity of these species' populations is required to quantify the mechanisms, behaviour and potential for stock resilience to fishing. Population genetic assessments applied to commercially important fish populations have identified isolation in tuna [18–20], sharks [21] and coastal and deep-water snappers [22–24], and population genetic assessment is now an accepted stock-separation tool [6, 10]. Such studies can also measure the variability associated with the genetic structure and connectivity among sub-populations, which is not necessarily concordant with the larval stage duration and potential dispersal of the species. For example, Ovenden et al. [13] suggested that the gold-banded snapper *Pristipomoides multidens* has distinct population structure for some areas in central and east Indonesia, despite the short distance (191 km) between sub-populations being well within the species' estimated dispersal range. More recent studies using mitochondrial DNA and allozyme markers for two lutjanids, *Lutjanus erythropterus* and *L. malabaricus*, in Indonesia that co-occur with *P. multidens* revealed discrete genetic populations, also suggesting isolation [13, 24] despite their assumed high dispersal ability. In contrast, Shaklee and Samollow [25] showed that six populations of the crimson snapper *P. filamentosus* had similar allozyme frequencies across the entire Hawaiian Archipelago, suggesting a single genetic stock fishery. In the South Pacific there has been no examination of the genetic structure of deep-water snapper populations.

In New Caledonia, deep-water snapper fisheries occur in three geographically separate areas. This provides the opportunity to test the hypothesis that distinct genetic populations of deep-water snappers occur in areas separated by several hundreds of kilometres. For *E. carbunculus* and *E. coruscans*, we isolated and quantified the mitochondrial DNA control region to estimate population genetic structure and connectivity from the three areas where fisheries occur. No formal assessment of genetic population structure for these species has been done in New Caledonia. Currently, the authority responsible for managing each of the deep-water snapper fisheries in New Caledonia differs depending on geographical location, and our results represent the first broad-scale assessment of stock structure and have immediate relevance for determining the necessity for managing populations as shared resources.

Materials and methods

We collected fin and muscle tissue from 90 *E. carbunculus* and 90 *E. coruscans* individuals (180 total) using aseptic techniques either in situ or in a wet laboratory; the technique we used was the least destructive for fish specimens, minimizing damage for re-sale. We stored all samples in dimethyl sulfoxide (DMSO). We sampled six locations for each species from three regions of New Caledonia, the Northern Province (NORD, north-east coast), Southern Province (SUD, south-west coast) and the Loyalty Islands (ISLE, far-east region) where deep-water snapper are harvested regularly (Fig. 1).

DNA extraction

We extracted DNA from a 5-mm^2 plug of tissue cut from the end of each fin sample. All samples were incubated at

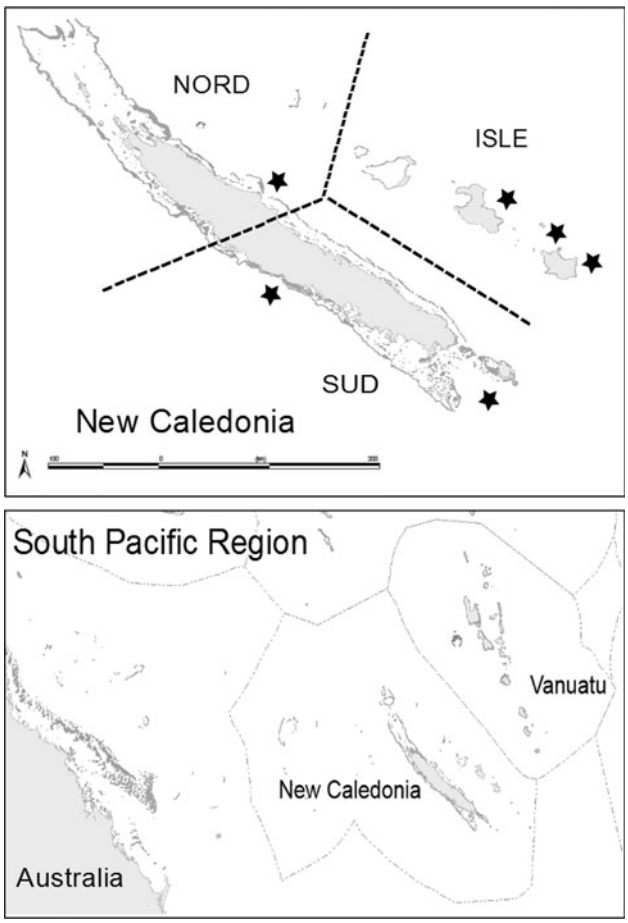

Fig. 1 Map of New Caledonia. Shaded areas indicate locations where samples of *Etelis carbunculus* and *E. coruscans* were collected from the three regions with artisanal fisheries that regularly catch deep-water snappers

56 °C overnight in 420 µl of Tissue Digest (DXT) and 4.2 µl DX Digest enzyme and DNA extracted using the Corbett X-tractor Gene (Qiagen) automated standard tissue/swab protocol following the manufacturers' instructions. We eluted DNA in 50 µl of elution buffer. We amplified the 5′ end of the control region (or D-Loop) via polymerase chain reaction (PCR) using primers Pro889U20 (CCW CTA ACT CCC AAA GCT AG) and Tdkd1291L21 (CCT GAA ATA GGA ACC AAA TGC) [13, 30]. We did PCR amplifications on a GeneAmp 9700 thermocycler (Applied Biosystems) in 25 µl reactions containing 1 µl of DNA extract, 2.5 µl of FastStart Taq DNA polymerase PCR buffer with $MgCl_2$, 2.5 µl dNTPs (2 mM), 1 µl of each primer (10 pm/µl), 1 µl of BSA (10 mg/ml) and 1.5 U of FastStart Taq DNA polymerase (Roche Diagnostics). Cycles were as follows: 95 °C for 4 min, 35 cycles of 94 °C for 15 s, 50 °C for 30 s, 72 °C for 30 s, and a final extension of 72 °C for 10 min. We visualized amplification products under ultra-violet light using ethidium bromide stained agarose gels and sequenced them in both directions using BigDye™ Terminator version 3.1 (Applied Biosystems) following the manufacturer's protocol. We analysed the sequenced PCR products on an Applied Biosystems 3130xl genetic analyser using DNA Sequencing Analysis Software version 5.3.1 (Applied Biosystems).

Analysis

We identified haplotypes using the program Sequencher version 4.6 (Gene Codes), that we further tested in TCS 1.18 [26] and aligned in Clustal X 1.83 [27] using default parameters (gap opening = 10, extension penalties = 0.2). We calculated the divergence among haplotypes using MEGA4 [28]. We constructed statistical parsimony networks in TCS 1.18 [26] to examine intraspecific genetic relationships and Bayesian phylogenetic analysis for interspecific relationships. We applied Modeltest version 3.06 [29] to obtain the evolutionary model best fitting the data based on the information–theoretic Akaike's information criterion (AIC) [30] for phylogenetic application (*P. multidens* was the phylogenetic out-group). We did a Bayesian analysis using a 4 × 4 nucleotide model with gamma estimation for 1 000 000 generations (25 % burn-in) in Mr Bayes software [31, 32]. We observed stationarity in the data in two independent runs, and retained every 100th generation over 1 000 000 generations to avoid autocorrelation. We determined the genetic differentiation among locations within each of the identified species groups using Nei's [33] uncorrected measure of nucleotide differentiation (d_{xy}), which along with Nei's nucleotide diversity (π) and haplotypic richness (H) were calculated using Arlequin 3.5 [34]. We tested the hierarchical distribution of genetic variation among locations (SUD, ISLE and NORD) with an analysis of molecular variance (AMOVA) [35] in Arlequin version 3.5.1.2 [34] based on the number of pair-wise nucleotide differences [36].

Results

A partial fragment (383 base pairs) of the mitochondrial DNA control region was aligned for 90 *E. carbunculus* and 90 *E. coruscans* individuals from three regions of New Caledonia (Table 1); the northern (NORD), the southern (SUD) and the loyalty islands to the east (ISLE). The aligned sequences produced 100 haplotypes: 35 for *E. coruscans* and 75 for *E. carbunculus* (the latter subsequently identified as two separate clades). Sequence divergence among haplotypes ranged from 0 to 5 % within lineages, 11–18 % among lineages and 37–44 % between the study species and the out-group *P. multidens*.

We obtained two statistical parsimony networks for *E. carbunculus,* hereafter referred to as HapGroup 1 and

Table 1 Sampling locations, sample sizes (n) and summary statistics for *Etelis coruscans* and *E. carbunculus*

Population	Sample ID	n	H	π
E. coruscans	SUD	30	16	0.010
	NORD	30	17	0.012
	ISLE	30	15	0.008
E. carbunculus (HapGroup1)	SUD	30	27	0.026
	NORD	26	19	0.026
	ISLE	14	11	0.024
E. carbunculus (HapGroup2)	NORD	4	4	0.007
	ISLE	16	12	0.007

The identification code for each population is included. Summary statistics include: H = number of haplotypes, π = nucleotide diversity

HapGroup 2, that could not be joined with statistical confidence, indicating two isolated lineages or even different species (Fig. 2a, b). The network also shows individuals from HapGroup 2 are only present in the NORD and ISLE regions, and most frequently in the latter (Fig. 2b). In contrast, HapGroup 1 is represented in all three regions with greater genetic variation, and a high frequency of hypothetical haplotypes (Fig. 2a). Bayesian probabilities support the presence of two divergent lineages within *E. carbunculus* (Figs. 2a, b, 3). Sequence divergence between the two lineages (11–18 %) is greater than within the lineages (0–2 %), and both are equally distant to *E. coruscans* (11–18 %). We therefore treated HapGroups 1 and 2 as separate species, but recognize that further taxonomic work is required.

The two HapGroups for *E. carbunculus* and *E. coruscans* exhibit connectivity among regions as shown by the sharing of haplotypes and mixed geographic origins for haplotypes in the statistical parsimony networks (Fig. 2a–c). In addition, the global F_{ST} values obtained by AMOVA were low and not statistically different from zero for each of the three datasets (F_{ST}: 0.008, −0.016, −0.023, for *E. coruscans* and HapGroups 1 and 2, respectively) and the three locations were negligible in explaining the genetic variation in these datasets (among-group variation: 0.8, approximately 0 and approximately 0 %, for *E. coruscans*

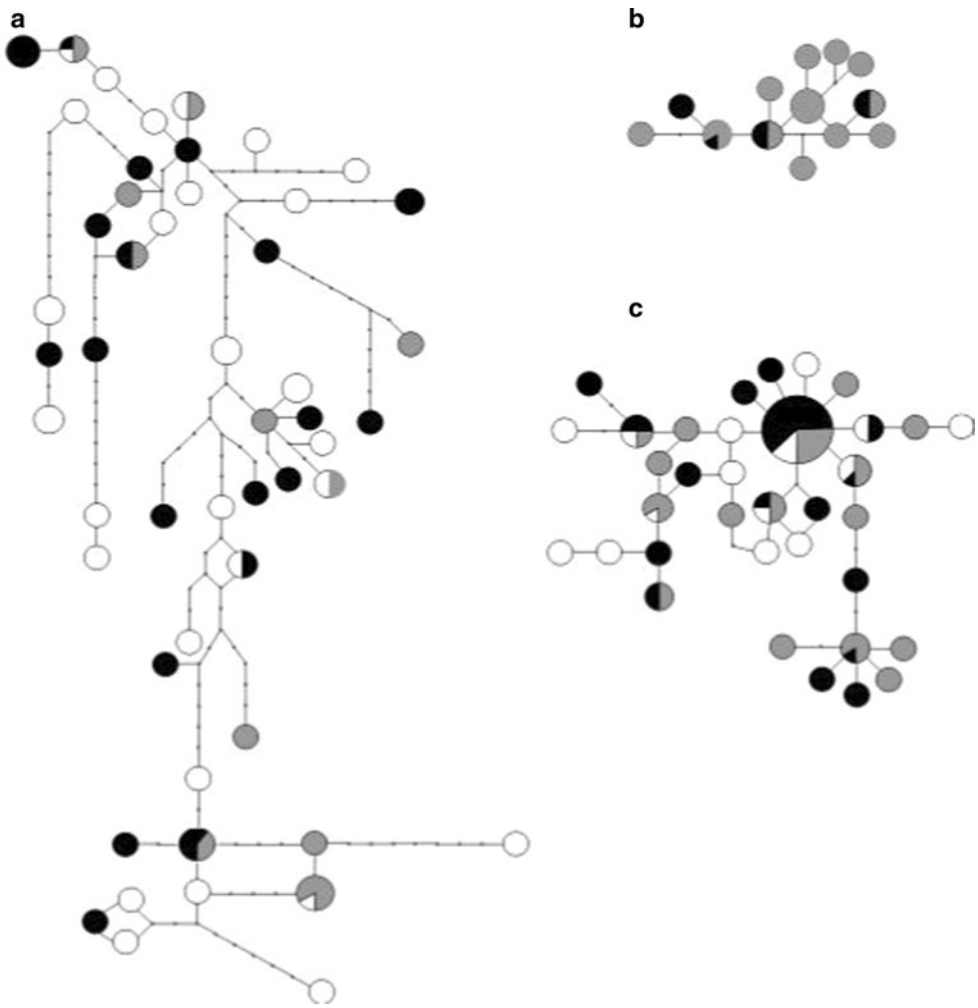

Fig. 2 Statistical parsimony networks for the mtDNA control region of haplotype groups 1 (**a**) and 2 (**b**) for *E. carbunculus*, and for *E. coruscans* (**c**). *Circle* size represents the number of individuals exhibiting a haplotype and *pies* represent the three different sampling locations. *Large circles*: *white* SUD, *black* NORD, *grey* ISLE, *small clear circles* hypothetical haplotypes. Connections depict a single mutation

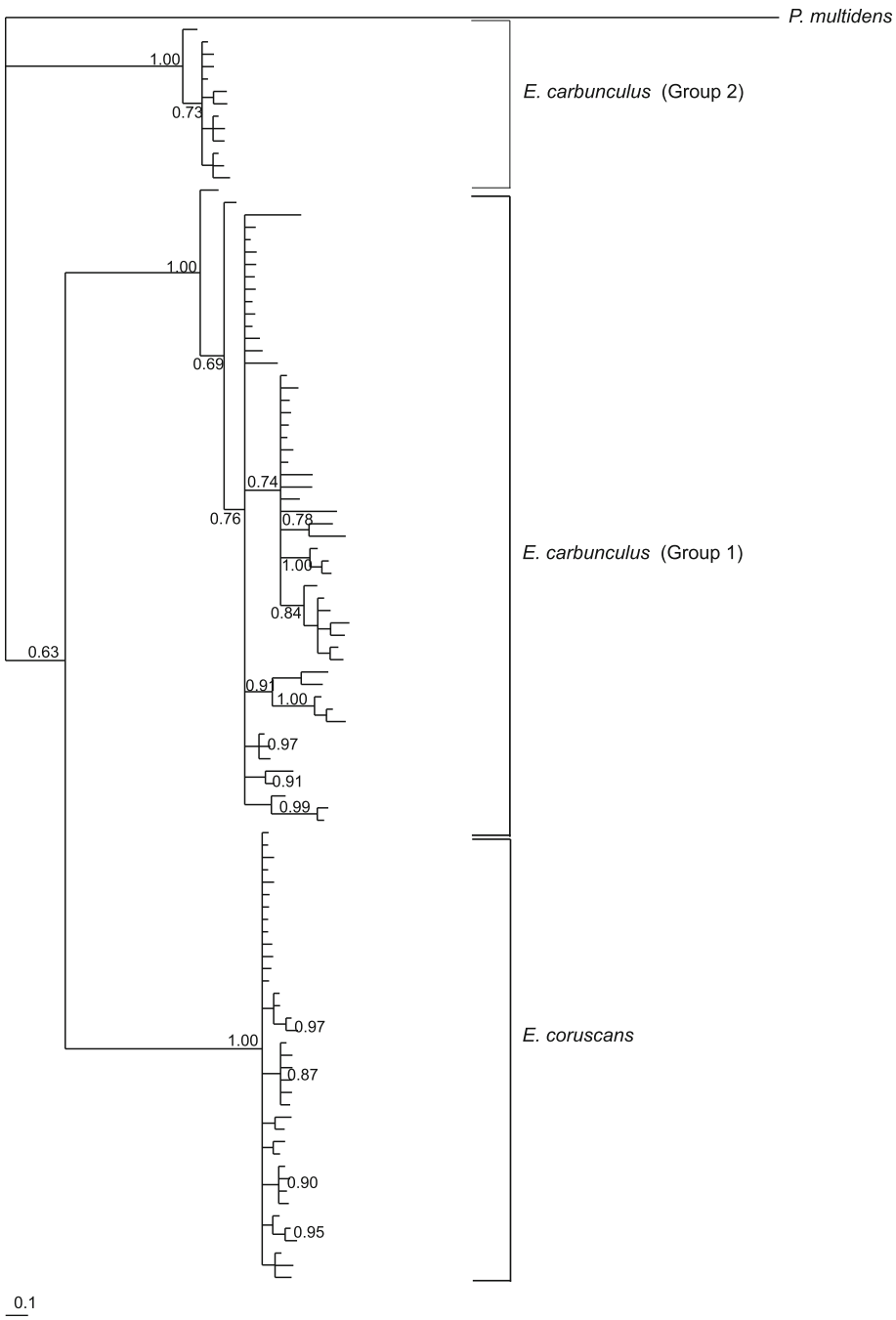

Fig. 3 A phylogenetic tree for the species *E. carbunculus* and *E. coruscans* of the mtDNA control region. We used *Pristipomoides multidens* to represent the out-group of closest relation. Bayesian probabilities are displayed above and below the nodes

and HapGroups 1 and 2, respectively). *E. coruscans* exhibits one dominant haplotype that is present in high frequency among all regions (Fig. 2c). However, 27 of the 35 haplotypes were in single individuals throughout the regions. We detected some isolation or divergence within this species, with one clade of haplotypes only occurring in the NORD and ISLE regions. This species displays low nucleotide diversity compared to *E. carbunculus* (HapGroup 1) and a less complex network, with both recent and deeper radiations visible. We detected few hypothetical haplotypes (7) in this network.

Genetic diversity and population connectivity are high for *E. carbunculus* (HapGroup 1). At least two regions shared seven of the 62 haplotypes, with the remaining 55 haplotypes occurring in single individuals mixed throughout the regions (Table 1; Fig. 2a), and there are many hypothetical haplotypes for this group. In contrast, HapGroup 2 shows strong connectivity between the NORD and

ISLE regions, dominated by the ISLE region with closely related haplotypes throughout the group (Fig. 2b).

Discussion

Our results highlight two important characteristics of the deep-water snapper fishery in New Caledonia: (i) the fishery has potentially been catching a putative third species erroneously identified as *E. carbunculus* and (ii) there is connectivity among a single stock for each of the species studied. The two divergent lineages within the *E. carbunculus* species group have not been distinguished taxonomically; however, a recent study describing a new species *E. marshi* erroneously identified in most literature as *E. carbunculus* [37] supports our separate-species hypothesis. Further taxonomic classification is required to distinguish HapGroups 1 and 2 as separate species and confirm that at least one is the newly described *E. marshi*. The three lineages we identified had moderate to extensive connectivity among regions. This conclusion is supported by the low F_{ST}, sharing of haplotypes and mixed geographic origins of haplotypes observed in all groups. The reproductive behaviour and the potentially prolonged pelagic larval phase of most lutjanids, including *Etelis* spp. [12, 13], suggest a high potential for connectivity and gene flow between sampled regions through larval dispersal. Our results also indicate that we did not fully capture the genetic diversity in *E. carbunculus*, which might be due to a large population size maintained by extensive mixing among regions for this species. Additional sampling is warranted to describe more completely the genetic diversity in this species and the extent of mixing.

Adult deep-water snappers are presumed to have a strong affinity to seamounts similar to *Beryx splendens* and *Hoplostethus atlanticus* at depths greater than 200 m [38] on which they depend for foraging and refuge. From the three regions we sampled in New Caledonia, the SUD and ISLE regions have more seamounts scattered in the currently exploited fishable areas, whereas region NORD is dominated by external reef slopes. The occurrence of HapGroup 2 in the NORD and ISLE regions suggests that this species exhibits different dispersal properties or that the SUD environment is sub-optimal. However, its absence in some locations could also be an artefact of the smaller sample size arising from the unexpected sampling of two lineages/species.

The snappers *P. multidens* and *P. filamentosus* are sympatric with *E. carbunculus* and *E. coruscans* [13, 39]. We decided to use *P. multidens* as our phylogenetic outgroup based on the compatibility of analytical techniques and abundant available genetic information. However, our results contrast those obtained previously for *P. multidens* in Australasia and South-East Asia, where substantial genetic structuring and isolated sub-populations exist for areas <200 km apart and well within the larval dispersal range [39]. Instead, our results were more congruous with those obtained for *P. filamentosus* across the Hawaiian Archipelago that suggested a single genetic stock [25].

We conclude that the three lineages are comprised of genetically similar sub-populations across the major regions of New Caledonia. In addition to taxonomic verification of the third lineage, we recommend increasing the sizes and range of sampling to stretch farther west of the Exclusive Economic Zone (e.g., Chesterfields and Fairway) to refine our results. Further sampling to the east would also identify the connectivity of New Caledonian stocks with those of Vanuatu, providing the information necessary for determining if more politically complex trans-boundary management of the species is required. Future studies should incorporate more detailed analysis using more rapidly evolving nuclear markers such as microsatellites and bomb radiocarbon-dating techniques, which would enable the identification of individuals and the potential assignment of those to their geographic range. This would give more insight into the genetic heritage of populations over space and time. In light of our results, we recommend that the management of this resource should consider all species as single populations for stock management until demonstrated otherwise. Currently, all three regions are governed by separate management authorities, so amalgamation of targets and organisation of the separate fisheries seems prudent to maximize sustainability targets.

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