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Phylogeography of commercial tuna and mackerel in the Indonesian Archipelago

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ABSTRACT.—While numerous population genetics studies have investigated phylogeographic patterns of coral reef organisms in the Coral Triangle, few have addressed whether fishes in the pelagic environment exhibit concordant patterns of genetic subdivision. We analyzed approximately 400 base pairs of the mitochondrial control region to compare population structure and phylogeography of five pelagic tuna and mackerel within a subset of their geographic ranges (i.e., the Indonesian Archipelago). Focal species include frigate tuna [*Auxis thazard* (Lacépède, 1800)], kawakawa [*Euthynnus affinis* (Cantor, 1849)], skipjack tuna [*Katsuwonus pelamis* (Linnaeus, 1758)], Indian mackerel [*Rastrelliger kanagurta* (Cuvier, 1816)], and narrow-barred Spanish mackerel [*Scomberomorus commerson* (Lacépède, 1800)]. Observed patterns of regional genetic subdivision were consistent with the role of Pleistocene vicariance in structuring populations. Divergence dates of all pelagic fish lineages dated to the Pleistocene epoch. Concordant barriers to larval dispersal found near Sumatra, Sulawesi, and Papua suggested that the Halmahera and Mindanao eddies and the Indonesian flowthrough may be contemporary forces maintaining genetic divergence between demes of pelagic fishes. Given the economic importance of these species, we suggest that the scale of management for pelagics in Indonesia be re-evaluated to reflect regional differences in the genetic composition of fishes.

The Coral Triangle, which includes the marine environments of Indonesia, the Philippines, Papua New Guinea, Solomon Islands, Malaysia, and East Timor, represents the global epicenter of marine biodiversity (Myers et al. 2000, Hughes et al. 2002, Roberts et al. 2002, Briggs and Bowen 2013). The exact processes generating patterns of increased species diversity in this region are unclear (Barber and

Bellwood 2005, Barber 2009, Bellwood and Meyer 2009), with multiple competing theories to explain the concentration of species diversity within this region of the world (e.g., Ekman 1953, Ladd 1960, Woodland 1983). However, vicariance is considered one of the key mechanisms driving population subdivision and lineage diversification in a wide variety of taxa within the Coral Triangle. 53

The Indonesian Archipelago represents a major biogeographic barrier between the Indian and Pacific Ocean provinces (Briggs 1974). During the Pleistocene, sea level fluctuations of up to 130 m exposed the Sunda and Sahul shelves, restricting waterways within the archipelago and isolating Indian and Pacific populations of marine species (Porter 1989, Voris 2000). Limited larval exchange between oceans, in conjunction with genetic drift and natural selection, facilitated genetic subdivision of demes. In addition to numerous biogeographic studies (e.g., McManus 1985, Woodland 1986, Springer and Williams 1990), a key line of evidence supporting Pleistocene vicariance between Indian and Pacific coral reef ecosystems comes from studies of genetic connectivity and phylogeography. While there are counterexamples in which Indo-Pacific phylogeographic structure is not observed in marine taxa (e.g., Klanten et al. 2007, Horne et al. 2008, Reece et al. 2010), there are numerous studies from the Coral Triangle that demonstrate largely concordant patterns of genetic structure in a wide variety of marine taxa (e.g., Williams and Benzie 1998, Benzie 1999, Lessios et al. 2001). Such concordant patterns may reflect signals of allopatric divergence from the Pleistocene (see Carpenter et al. 2011 and Barber et al. 2011 for review).

Genetics studies have also shown the role of ocean currents in reinforcing lineage divergence in the Coral Triangle. Ocean currents were once presumed to facilitate long distance dispersal and genetic homogeneity in marine systems (Sale 1991, Roberts 1977). Not only have marine populations proven more closed than initially expected (e.g., Jones et al. 1999, 2005, Almany et al. 2007), evidence has emerged to suggest that currents can inhibit larval dispersal and genetic connectivity. Barber et al. (2002) initially suggested the role of the Western Boundary Currents in limiting east to west larval transport across the Maluku Sea, a pattern later confirmed by Barber et al. (2006). Additional studies on mantis shrimp (Barber et al. 2011) as well as giant clams (Ravago-Gotanco et al. 2007, DeBoer et al. 2008, Kochzius and Nuryanto 2008, Nuryanto and Kochzius 2009), echinoderms (Crandall et al. 2008b), and fishes (Timm et al. 2008, Ackiss et al. 2013) have confirmed the role of currents in driving population subdivision. Recent biophysical modeling studies have also confirmed patterns of limited connectivity between Indo-Pacific demes (Kool et al. 2011).

The majority of phylogeography studies in the Coral Triangle have focused on either reef-associated or inshore taxa. To date few studies have investigated whether pelagic species encounter the same dispersal barriers as reef-dwelling organisms. Pelagic fishes are expected to exhibit weak population structure due to high dispersal potential, migratory behavior and large effective population sizes (Graves 1998, Ely et al. 2005). The few studies that have examined population structure of pelagic species in the Coral Triangle provide some evidence of east-west genetic subdivision among demes of pelagic fishes (Perrin and Borsa 2001, Rohfritsch and Borsa 2005, Sulaiman and Ovenden 2010). However, discordant geographic sampling across multiple unrelated studies makes direct comparison of these results challenging. As such, it remains unclear whether vicariance events and oceanographic processes that

Table 1. Biological data for focal species: *Auxis thazard*, *Euthynnus affinis*, *Katsuwonus pelamis*, *Rastrelliger kanagurta*, and *Scomberomorus commerson*. Data include maximum length (max. length) in centimeters, pelagic environment, depth range in meters, and spawning periodicity (Collete and Nauen 1983, Collette 1995, Pauly et al. 1996, Riede 2004).

Species	Maximum length (cm)	Pelagic environment	Depth range (m)	Spawning periodicity
<i>A. thazard</i>	65	Neritic	50–?	Seasonal
<i>E. affinis</i>	100	Neritic	0–200	Seasonal
<i>K. pelamis</i>	110	Oceanic	0–260	Year round
<i>R. kanagurta</i>	35	Neritic	20–90	Seasonal
<i>S. commerson</i>	240	Neritic	10–70	Seasonal

promote population divergence in reef-dwelling species have subdivided the seemingly homogenous pelagic habitat in the same way as coral reef habitats.

We designed a phylogeographic study of five commercially important pelagic fishes. Focal species are members of the family Scombridae, including frigate tuna [*Auxis thazard* (Lacépède, 1800)], kawakawa [*Euthynnus affinis* (Cantor, 1849)], skipjack tuna [*Katsuwonus pelamis* (Linnaeus, 1758)], Indian mackerel [*Rastrelliger kanagurta* (Cuvier, 1816)], and narrow-barred Spanish mackerel [*Scomberomorus commerson* (Lacépède, 1800)]. While all five species are associated with pelagic environments (Collette and Nauen 1983), they vary in a number of biological characteristics including spawning periodicity, maximum size, and depth range (Table 1). We sampled within a subset of the entire geographic range for all species, focusing on the Indonesian Archipelago, a region well known for the presence of phylogeographic barriers and some of the world's highest landings of principal market tuna and mackerels (Majkowski 2007). We analyzed the hypervariable mitochondrial control region to investigate the role of both historical and contemporary processes such as Pleistocene sea level fluctuations and physical oceanography in generating regional patterns of lineage diversification within the archipelago. Knowledge of population structure and phylogeography may be used to inform fisheries management and conservation efforts for commercial pelagic species in Indonesia.

METHODS

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We collected tissue from the pectoral fins of *A. thazard* ($n = 135$, 11 localities), *E. affinis* ($n = 188$, 12 localities), *K. pelamis* ($n = 177$, 12 localities), *R. kanagurta* ($n = 178$, 11 localities), and *S. commerson* ($n = 127$, 9 localities) throughout the Indonesian Archipelago (Fig. 1, Table 2). Tissue samples were acquired in artisanal fish markets during 2005 and 2006 and preserved in 95% ethanol. Whenever possible, we collected all five species from the same markets to maximize the comparability of the datasets. Due to the small size of fishing vessels, lack of refrigeration and the high cost of petrol, artisanal fishermen only operate within waters 20–30 km from the fish markets. Local fishing activity reduces the possibility that fish sampled were shipped from other locations. We will consider these 20–30 km regions around fishing ports as separate sampling localities or demes in subsequent analyses.

We extracted DNA from tissue samples using a 10% Chelex (BioRad) solution (Walsh et al. 1991). We then amplified a 374–403 base pair fragment of control region using the primers CRA and CRE (Lee et al. 1995). Polymerase chain reaction (PCR) utilized the following thermocycler parameters: an initial hold at 94 °C for 5 min, 38 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 60 s, followed by 72 °C for 7



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Figure 1. Map of the Indonesian Archipelago showing sampling localities of pelagic tuna and mackerel (black circles). Numbers correspond to sample localities listed in Table 1.

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min. PCR products were visualized on a 1% agarose gel. PCR products that amplified were cleaned by adding 5 ml of product to 5 units of Shrimp Alkaline Phosphatase (Biotech Pharmakon) and 5 units of Exonuclease I (GE Healthcare), incubating products at 37 °C for 30 min and 80 °C for 15 min. Cleaned PCR products were sequenced using BigDye terminator chemistry (Applied Biosystems, Inc.). We sequenced PCR products in the forward and reverse directions on an ABI 377 DNA sequencer. Sequences were proofread and aligned using Geneious v5.6 (Drummond et al. 2011).

We calculated molecular diversity and neutrality statistics for each species, including nucleotide diversity (π), haplotype diversity (h), Fu's F_s , Tajima's D , and Fu and Li's D^* . Neutrality statistics can be used to uncover demographic phenomena and to detect selection in cases where patterns of DNA polymorphism deviate from those predicted by the Wright-Fisher neutral model of evolution (Fu and Li 1993, Tajima 1989, Fu 1996, Fu 1997). Simulation studies comparing the statistical power of such neutrality statistics revealed that F_s provides a powerful assessment of population expansion, while D^* performs best when assessing background selection (Fu and Li 1993, Fu 1997). Following empirical work by Crandall et al. (2008a), we calculated these statistics to determine the relative importance of background selection and population expansions in demes of pelagic fishes.

We assessed phylogenetic relationships among sequences using haplotype networks and neighbor-joining trees, and plotted how patterns of genetic variation changed across geographic space. Haplotype networks based on pairwise distances between haplotypes were generated using Arlequin and R, and formatted using Adobe Illustrator. We generated neighbor-joining trees in PAUP (Swofford 1993). We estimated the average sequence divergence between clades, evaluating values >7% (McCune and Lovejoy 1998) for evidence of cryptic speciation or species misidentification. Finally, we plotted the frequency of distinct clades (with bootstrap support of 75% or higher) in each sampling locality as pie diagrams to illustrate the geographic distribution of genetic variation.

We tested for statistically significant population structure by estimating global and pairwise estimates of the fixation indices F_{ST} and Φ_{ST} . F_{ST} comes from foundational work by Sewall Wright looking at hierarchical partitioning of genetic variation among groups (Wright 1943, Wright 1951, Wright 1965). Φ_{ST} is an analogue of F_{ST}

Table 2. Molecular diversity indices for the mitochondrial control region for focal species: *Auxis thazard*, *Euthymus affinis*, *Katsuwonus pelamis*, *Rastrelliger kanagurta*, and *Scomberomorus commerson*. Sample location, number of specimens (n), haplotype diversity (h), number of haplotypes (n_h), nucleotide diversity (π).

Sample location	<i>Auxis thazard</i>			<i>Euthymus affinis</i>			<i>Katsuwonus pelamis</i>			<i>Rastrelliger kanagurta</i>			<i>Scomberomorus commerson</i>		
	n	h	π	n	h	π	n	h	π	n	h	π	n	h	π
1. Aceh	13	1.00	0.031	22	1.00	0.063	22	1.00	0.063	19	0.96	0.012	23	0.99	0.056
2. Medan	10	1.00	0.029	22	1.00	0.008	15	1.00	0.064	19	0.96	0.012	23	0.99	0.056
3. Nias				3	1.00	0.011	3	1.00	0.039				20	0.98	0.052
4. Padang													3	1.00	0.012
5. Anyer				3	1.00	0.002				5	1.00	0.008	23	1.00	0.048
6. Karimunjawa										3	0.00	0.000	20	0.96	0.030
7. Lombok	5	1.00	0.031												
8. Flores															
9. Selayar	14	1.00	0.028	19	1.00	0.028				23	0.95	0.010	9	0.89	0.005
10. Makassar	10	0.98	0.039	16	1.00	0.009	12	1.00	0.067	23	0.95	0.010	9	0.89	0.005
11. Manado	5	1.00	0.043				17	1.00	0.071	19	0.96	0.010			
12. Bitung				15	1.00	0.008	5	1.00	0.041						
13. Halmahera	27	1.00	0.032	18	1.00	0.009	20	1.00	0.064	20	0.94	0.011	13	1.00	0.052
14. Raja Ampat	15	1.00	0.042	16	1.00	0.031	19	1.00	0.059	19	0.95	0.010	10	1.00	0.035
15. Manokwari	15	0.99	0.035	18	1.00	0.058	20	1.00	0.065	19	0.90	0.016			
16. Biak	16	0.95	0.037	19	1.00	0.099	17	1.00	0.060	15	0.94	0.012			
17. Yapen	5	1.00	0.037	19	1.00	0.098	11	1.00	0.067	17	0.92	0.022	6	0.93	0.034
18. Jayapura				20	1.00	0.023	16	1.00	0.055	19	0.81	0.011			

that incorporates genetic distances between sequences to assess allelic correlations among groups (Excoffier et al. 1992). Φ_{ST} is particularly informative in instances where F_{ST} is low as it is less likely to underestimate population structure when allelic diversity is high (Hedrick 1999, Hedrick 2005, Bird et al. 2011). Statistical significance of pairwise estimates was assessed after Bonferroni correction (using a family-wise alpha rate of 0.05). We also assessed population structure of pelagics by calculating the standardized statistic G''_{ST} , using unbiased estimates of heterozygosity within subpopulations (H_S) and total heterozygosity (H_T) generated in Arlequin (Meirmans and Hedrick 2011).

We then evaluated genetic differentiation across a previously reported region of vicariance in the archipelago, grouping sampling localities to reflect the separation of eastern and western Indonesia during Pleistocene low sea levels. Sampling localities were grouped into western (localities 1–8) and eastern Indonesia (sampling localities 9–18) (Fig. 1). We performed an Analysis of Molecular Variance (AMOVA) in Arlequin (Excoffier et al. 2005). Significance of AMOVAs was estimated using a permutation test with 10,000 replicates. Chi-squared analyses were performed concurrently using DnaSP v5.10 (Librado and Rozas 2009).

To determine the location of barriers to larval dispersal throughout region, we used the software Barrier (Manni et al. 2004). Barrier uses a computational geometry approach involving Delaunay triangulation and Voronoi tessellation to visualize patterns of genetic variation. Geographic distances are overlaid with genetic distances among sampling localities to detect the presence of barriers. We tested the significance of barriers by comparing geographic distance matrices against genetic distance matrices comprised of pairwise F_{ST} and Φ_{ST} values estimated in Arlequin, performing 10 replicate analyses for each species. We will use the terms “strong” and “weak” barriers to indicate the relative frequency with which a given barrier appeared in the Barrier analyses. Strong barriers were confirmed by both F_{ST} and Φ_{ST} pairwise estimates, while weak barriers were only seen for one fixation index or the other. We will use strength of barriers (depicted by their widths in Fig. 2) as a proxy for permeability of barriers and to identify potential phylogeographic breaks.

We empirically tested the role of Pleistocene vicariance events by generating coalescent genealogies. We calibrated a Bayesian skyline plot using a lognormal relaxed clock in BEAST v1.7.5 (Drummond et al. 2012). We allowed mutation rates to vary between 1% and 7% per million years (e.g., McCune and Lovejoy 1998) to generate lineage divergence dates. We used literature-derived mutation rates because fossils and calibration points were unavailable for our focal species. We used jModelTest 0.1.1 (Posada 2008) to select the nucleotide substitution model that best fit the control region data using Akaike information criterion. Analysis of sequences indicated that the GTR +I +G model best fit the data for *E. affinis*, *R. kanagurta*, and *S. commerson*, the GTR +G model best fit the data for *A. thazard* and the HKY +I +G model best fit the data for *K. pelamis*. To evaluate convergence of MCMC chains we ran each dataset three times for 50 million steps in BEAST. Effective sample size values of >200 suggested convergence as well as proper length and mixing of MCMC chains.

Finally, to test an alternative hypothesis to Pleistocene vicariance, we investigated whether isolation by distance could explain patterns of genetic subdivision in pelagic fishes. Limited dispersal across the archipelago (approximately 5000 km across) may result in a positive correlation between genetic distance and geographic distance. Pairwise Φ_{ST} values were generated in Arlequin and pairwise geographic distances

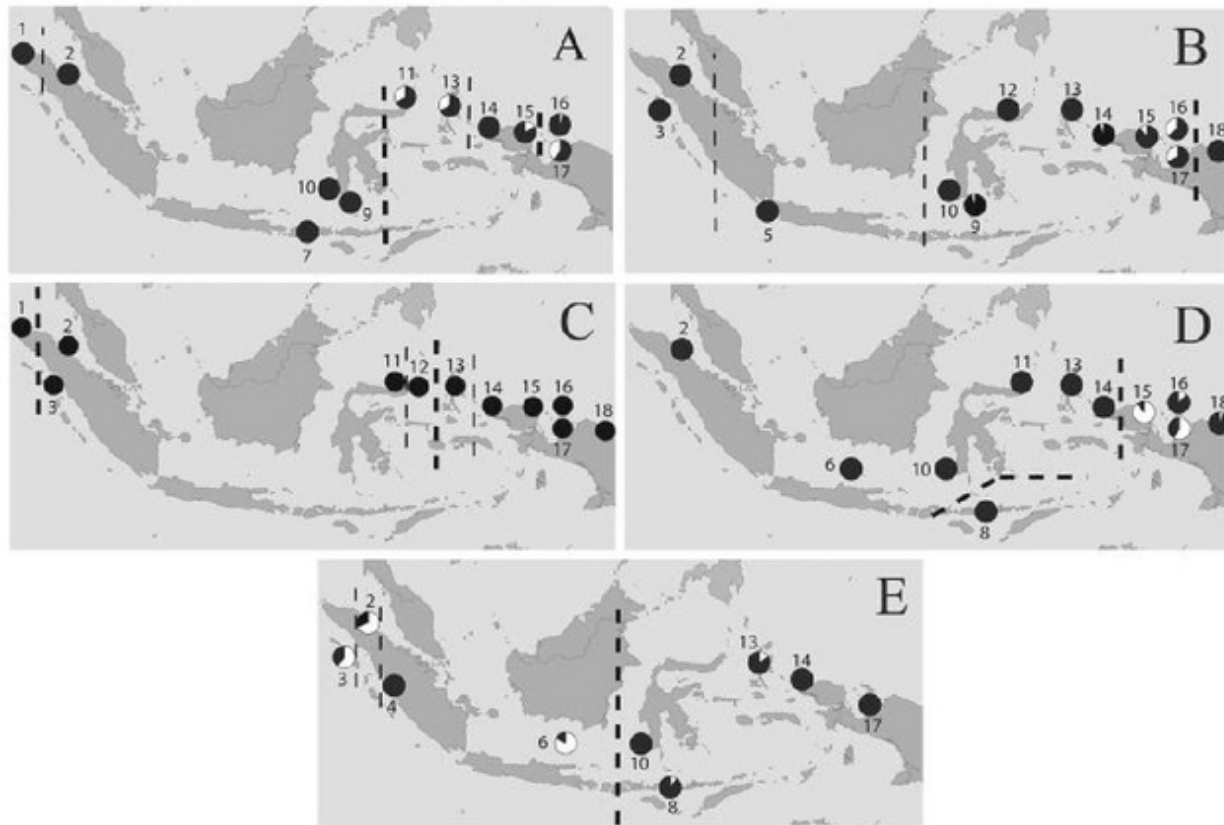


Figure 2. Pie diagrams for (A) *Auxis thazard*, (B) *Euthymus affinis*, (C) *Katsuwonus pelamis*, (D) *Rastrelliger kanagartha*, and (E) *Scomberomorus commerson*. Each pie chart illustrates the relative frequency of each clade among samples within a sampling locality. Dashed lines represent barriers to dispersal highlighted in BARRIER. Thick lines depict potential barriers that are supported by both F_{ST} and Φ_{ST} , while thin lines depict barriers that are only supported by significant values of one of these statistics.

between all sampling localities were estimated using a Geographic Distance Matrix Generator (Ersts 2013). Some geographic distances calculated in this way may include over land distances; however, this is not a major concern for this study as there are numerous potential pathways to measure distances between sampling sites on islands. Thus, such over land estimates may essentially average the difference between potential measured distances. We used Mantel and partial Mantel tests, implemented using the vegan package v2.0-9 in R (Oksanen et al. 2013), to test the significance of isolation by distance. Partial Mantel tests assess the correlation between geographic distance matrices and genetic distance matrices while also controlling for the effect of hierarchical population structure. Hierarchical population structure can introduce bias to isolation by distance analyses (Meirmans 2012). Matrices for hierarchical population structure were coded with 0s and 1s to reflect whether pairs of populations were or were not in the same regional cluster. Partial Mantel tests were only performed in instances when we detected statistically significant hierarchical population structure in the AMOVA.

RESULTS

We sequenced approximately 400 base pairs of control region for 805 tissue samples. Haplotype diversity was high across sampling localities for all five species, ranging from 0.81 to 1.00 (Table 2). For *A. thazard*, 100 sites were polymorphic, yielding 129 unique haplotypes from a total of 135 samples. For *E. affinis*, 143 sites were

polymorphic, yielding 109 unique haplotypes from a total of 188 samples. For *K. pelamis*, 165 sites were polymorphic, yielding 172 unique haplotypes from a total of 177 samples. For *R. kanagurta*, 36 sites were polymorphic, yielding 83 unique haplotypes from a total of 178 samples. For *S. commerson*, 103 sites were polymorphic, yielding 113 unique haplotypes from a total of 127 samples. Nucleotide diversity ranged from 0.002 to 0.099 between sampling localities for all five species (Table 2).

Significant departures from neutrality were observed in all five pelagics (Table 3). Tajima's *D* was negative and statistically significant for seven of 12 *E. affinis* sampling localities but was non-significant in the remaining four species. *D** was also negative and statistically significant in five of 12 sampling localities of *E. affinis*. For the remaining four species, *D** values were non-significant. In contrast, negative Fu's *F*_s values were statistically significant in all five species. Negative *F*_s and *D** values indicate a departure from neutrality due to an excess of recent mutations (number of segregating sites greater than pairwise nucleotide diversity) from a potential population expansion or following a selective sweep. Although significantly positive values could result from sampling multiple distinct gene pools, for example as a result of an influx of divergent haplotypes from unsampled populations, our neutrality tests are uniformly negative. Given that samples for each locality were taken within the same 20 to 30 km region, they likely represent a single gene pool.

Neighbor-joining trees revealed one to two well-supported clades for each species, with no evidence found to suggest cryptic speciation (Online Fig. 1A–E). All samples for *K. pelamis* were considered a single clade due to low bootstrap support (<40%) for identified clades. *Auxis thazard* samples formed two clades, with 98% bootstrap support or higher, and 4.12% average sequence divergence between clades. *Euthynnus affinis* samples formed two clades, with 96% bootstrap support or higher, and 6.37% average sequence divergence between clades. *Rastrelliger kanagurta* formed two clades, with 79% bootstrap support or higher, and 2.15% average sequence divergence between clades. *Scomberomorus commerson* samples formed two clades, with 82% bootstrap support or higher, and 2.80% average sequence divergence averaged between clades. Visually, pie charts suggest regional trends in the distribution of clades among demes of *A. thazard*, *E. affinis*, *R. kanagurta*, and *S. commerson* within the Indonesian Archipelago. Multiple data sets confirm the presence of clades unique to eastern Indonesia [white clades for *A. thazard* (Fig. 2A), *E. affinis* (Fig. 2B), and *R. kanagurta* (Fig. 2D)]. In *S. commerson*, there is a decline in the abundance of the white clade from west to east across the archipelago (Fig. 2E). Pairwise Φ_{ST} values reaffirmed these geographic trends (Online Tables 1A–E).

All five pelagics exhibited varying degrees of population structure across the Indonesian Archipelago (Table 4). We used previous categories defined by Wright (1965) to describe the magnitude of population structure observed in our focal species. Based on global Φ_{ST} values, we observed strong population structure in *R. kanagurta* ($\Phi_{ST} = 0.3728$, $P < 0.0001$) and *S. commerson* ($\Phi_{ST} = 0.3253$, $P < 0.0001$), moderate population structure in *A. thazard* ($\Phi_{ST} = 0.0953$, $P < 0.0001$) and *E. affinis* ($\Phi_{ST} = 0.1073$, $P = 0.0001$) and weak population structure in *K. pelamis* ($\Phi_{ST} = 0.0113$, $P = 0.0315$). Based on *F*_{ST} values, we observed weak population structure in *A. thazard* ($F_{ST} = 0.0069$, $P = 0.0001$), *E. affinis* ($F_{ST} = 0.0074$, $P < 0.0001$), *K. pelamis* ($F_{ST} = 0.0313$, $P = 0.0421$), and *S. commerson* ($F_{ST} = 0.0225$, $P < 0.0001$), and moderate population structure in *R. kanagurta* ($F_{ST} = 0.0773$, $P < 0.0001$). *G*'_{ST} values further supported genetic differentiation of populations for all five focal species. For *K.*

Table 3. Neutrality test statistics for the mitochondrial control region **23** focal species: *Auxis thazard*, *Euthynnus affinis*, *Katsuwonus pelamis*, *Rastrelliger kanagurta* and *Scomberomorus commerson*. Sample location, number **48** specimens (*n*), Tajima's *D*, Fu and Li's *D** and Fu's *F*_s, as reported by Arlequin 3.11 and DnaSP v5.10. * denotes statistical significance of *P* < 0.05 for Tajima's *D* and Fu's *F*_s and *P* < 0.02 for Fu and Li's *D**.

Sample location	28 <i>A. thazard</i>				<i>Euthynnus affinis</i>				<i>Katsuwonus pelamis</i>				<i>Rastrelliger kanagurta</i>				<i>Scomberomorus commerson</i>			
	<i>n</i>	<i>D</i>	<i>D</i> *	<i>F</i> _s	<i>n</i>	<i>D</i>	<i>D</i> *	<i>F</i> _s	<i>n</i>	<i>D</i>	<i>D</i> *	<i>F</i> _s	<i>n</i>	<i>D</i>	<i>D</i> *	<i>F</i> _s	<i>n</i>	<i>D</i>	<i>D</i> *	<i>F</i> _s
1. Aceh	13	-1.02	-1.41	-5.55*	22	0.07	-0.26	-3.66	22	0.07	-0.26	-3.66	23	-0.23	-0.15	-6.18*	23	-0.23	-0.15	-4.66*
2. Medan	10	-0.63	-1.42	-3.53*	22	-1.67*	2.48*	-9.97*	15	-0.21	-0.20	-3.61*	19	0.10	-0.15	-6.18*	20	1.49	0.12	-3.42
3. Nias					3	0.00	—	0.13	3	0.00	—	1.54					3	0.00	—	0.31
4. Padang																				
5. Anyer					3	0.00	—	0.20					5	-0.49	-0.19	-2.12*	23	-0.07	-0.12	-7.62*
6. Karimunjawa																				
7. Lombok	5	-0.39	-0.53	-3.76																
8. Flores																				
9. Selayar	14	-1.46	-1.54	-6.72*	19	-2.28*	-3.64*	-3.02*					3	0.00	—	0.00	20	-0.93	0.02	-2.29
10. Makassar	10	-0.43	-0.22	-1.01	16	-1.48	-2.19	-6.13	12	-0.03	-0.23	-2.18	23	0.03	-0.01	-8.53*	9	0.11	0.69	-2.33*
11. Manado	5	-0.01	-0.21	0.15	17	-0.27	-0.87	-4.20*	19	-0.27	-0.87	-4.20*	19	-0.02	-0.78	-9.24*				
12. Bitung					15	-1.67*	-1.65	-7.92*	5	-0.18	-0.18	0.21								
13. Halmahera	27	-1.20	-1.56	-9.59*	18	-1.58*	-2.01	-7.10*	20	-0.54	-0.58	-6.26*	20	-0.49	-0.29	-7.55*	13	0.00	0.22	-3.27*
14. Raja Ampat	15	-0.96	-1.27	-5.67*	16	-2.24*	-3.10*	-0.10	19	-0.20	-0.30	-6.10*	19	-0.13	-0.63	-5.70*	10	-0.64	-0.70	-2.70
15. Manokwari	15	-0.96	-1.08	-4.24*	18	-1.74*	-2.08*	0.93	20	-0.10	0.00	-6.26*	19	-0.30	0.28	-1.09				
16. Biak	16	-0.33	-0.52	-1.73	19	1.49	0.64	0.18	17	-0.37	-0.50	-2.87	15	-0.70	0.06	-3.46*				
17. Yapen	5	-0.37	-0.34	-0.04	19	-0.07	-0.68	2.14	11	-0.56	-0.79	-1.76	17	1.37	1.04	-1.57	6	-0.05	-0.31	1.28
18. Jayapura					20	-2.29*	-3.42*	0.27	16	-0.16	-0.08	-1.35	19	-1.21	-1.53	-0.61				

Table 4. Global estimates of Φ_{ST} and F_{ST} for focal species: *Auxis thazard*, *Euthymnus affinis*, *Katsuwonus pelamis*, *Rastrelliger kanagurta*, and *Scomberomorus commerson*. * denotes statistical significance of $P < 0.05$ and ** of $P < 0.001$. P values were not provided for G''_{ST} since estimates were calculated manually.

Species	Φ_{ST}	F_{ST}	G''_{ST}
<i>Auxis thazard</i>	0.0980**	0.0069**	0.5843
<i>Euthymnus affinis</i>	0.1073**	0.0074**	0.1276
<i>Katsuwonus pelamis</i>	0.0113*	0.0313*	0.9995
<i>Rastrelliger kanagurta</i>	0.3728**	0.0773**	0.5356
<i>Scomberomorus commerson</i>	0.3253**	0.0225**	0.4599

pelamis, G''_{ST} approached a maximum value of one (Table 4). Results for *K. pelamis* in conjunction with the haplotype network suggest high levels of genetic differentiation are due to a lack of shared alleles among populations, with nearly every sequence representing a unique haplotype (Fig. 47C). G''_{ST} values for *A. thazard*, *E. affinis*, *R. kanagurta*, and *S. commerson* ranged between 0.1276 and 0.5843 (Table 4). Lower G''_{ST} values observed in the aforementioned species reflect both high haplotypic diversity and a higher proportion of shared alleles among demes (Fig. 3A,B,D,E).

Barriers to larval dispersal identified using Barrier are consistent with regional subdivision of groups of pelagic fishes (Fig. 2). Two strong barriers were identified in *A. thazard* separating western demes (Aceh, Nias, Lombok, Makassar, and Selayar) from two groups of eastern demes (Manado, Halmahera, Raja Ampat, and Manokwari; and Biak and Yapen). Weaker breaks were also observed between Aceh and Nias and between Halmahera and Raja Ampat. One strong barrier was observed in *E. affinis* separating Jayapura in Papua from the rest of the localities in the archipelago. Additional weaker barriers subdivided the archipelago into three groupings (Nias and Medan; Padang; and Makassar, Selayar, Bitung, Halmahera, Raja Ampat, Manokwari, Biak, and Yapen). Two strong barriers were observed in *K. pelamis* separating Aceh from a group of central (Nias, Medan, Bitung, and Manado) and eastern demes (Halmahera, Raja Ampat, Manokwari, Biak, Yapen, and Jayapura). Additional weaker barriers separated Bitung from Manado and Halmahera from Raja Ampat. Two strong barriers were observed in *R. kanagurta* subdividing the archipelago into three regional groups [western and central (Nias, Karimunjawa, Makassar, Manado, Halmahera, and Raja Ampat), southern (Flores), and eastern (Manokwari, Biak, Yapen, and Jayapura) Indonesia]. One strong barrier was observed in *S. commerson*, confirming the divide between western and eastern Indonesia observed in the AMOVA and chi-squared analysis. Additional weaker breaks were observed dividing Nias, Medan and Padang from one another.

We tested two potential hypotheses for regional subdivision of pelagic fishes: historical vicariance and isolation by distance. We found strong evidence to support the role of Pleistocene vicariance in structuring demes of pelagics. AMOVAs supported partitioning of genetic variation between eastern and western Indonesia in *S. commerson* ($\Phi_{CT} = 0.113$, $P = 0.0445$), with 11.31% of variation between regions, 16.62% within regions, and 72.07% within populations (Table 5). A chi-squared analysis further supported this trend ($\chi^2 = 123.257$, $P = 0.0177$, $df = 105$). Coalescent analyses revealed that all individuals sampled for each species coalesced to a most recent common ancestor that dated within the Pleistocene epoch (approximately 2,500,000 to 11,800 years ago) (Fig. 4). Results are inconsistent with the notion that observed patterns of genetic subdivision of pelagic demes reflect an ancestral divergence of 5–20

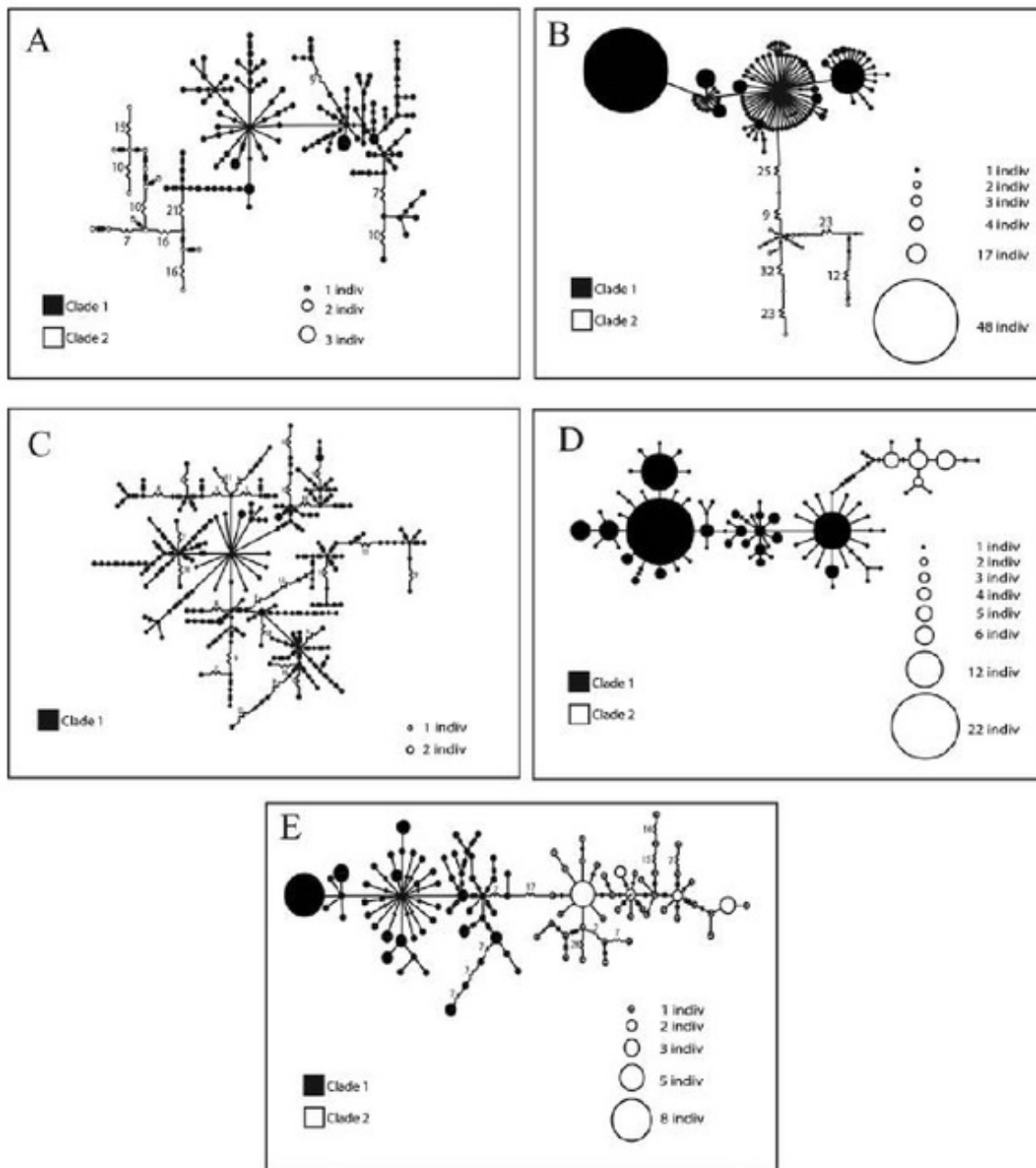


Figure 3. Haplotype networks for (A) *Auxis thazard*, (B) *Euthynnus affinis*, (C) *Katsuwonus pelamis*, (D) *Rastrelliger kanagurta*, and (E) *Scomberomorus commerson*. Circles are sized proportionally to the number of individuals that possess each haplotype. All haplotypes are separated by one mutation step unless denoted with hatch marks or a number. Haplotypes are color-coded based on associated clades in neighbor-joining trees.

Table 5. AMOVA results for focal species, *A. thazard*, *Euthynnus affinis*, *Katsuwonus pelamis*, *Rastrelliger kanagurta*, and *Scomberomorus commerson*, showing degrees of freedom (df), variance components (var), percent variation (% var) and *F* statistics to test regional hypothesis for vicariance between western and eastern Indonesia. * denotes statistical significance of $P < 0.05$. Φ_{CT} represents the correlation of random haplotypes within a group of populations region relative to that of random pairs drawn from the entire species. Φ_{SC} represents the correlation of random haplotypes within populations relative to random pairs of haplotypes drawn from the region. Φ_{ST} represents the correlation of random haplotypes within populations relative to random pairs of haplotypes in the entire species.

Species	Among regions				Among populations within regions				Within populations			
	df	var	% var	Φ_{CT}	df	var	% var	Φ_{SC}	df	var	% var	Φ_{ST}
<i>A. thazard</i>	1	0.02	0.28	0.003	9	0.59	9.50	0.095*	134	5.64	90.22	0.098*
<i>E. affinis</i>	1	-1.70	-0.14	-0.017	10	0.99	12.43	0.122*	176	7.11	89.27	0.107*
<i>K. pelamis</i>	1	-0.01	-0.08	-0.001	10	0.15	1.21	0.012*	165	11.86	98.87	0.011*
<i>R. kanagurta</i>	1	-0.15	-3.93	-0.039	9	1.57	41.22	0.397*	167	2.39	62.72	0.373*
<i>S. commerson</i>	1	1.75	14.66	0.147*	7	2.14	17.86	0.209*	118	8.07	67.47	0.325*

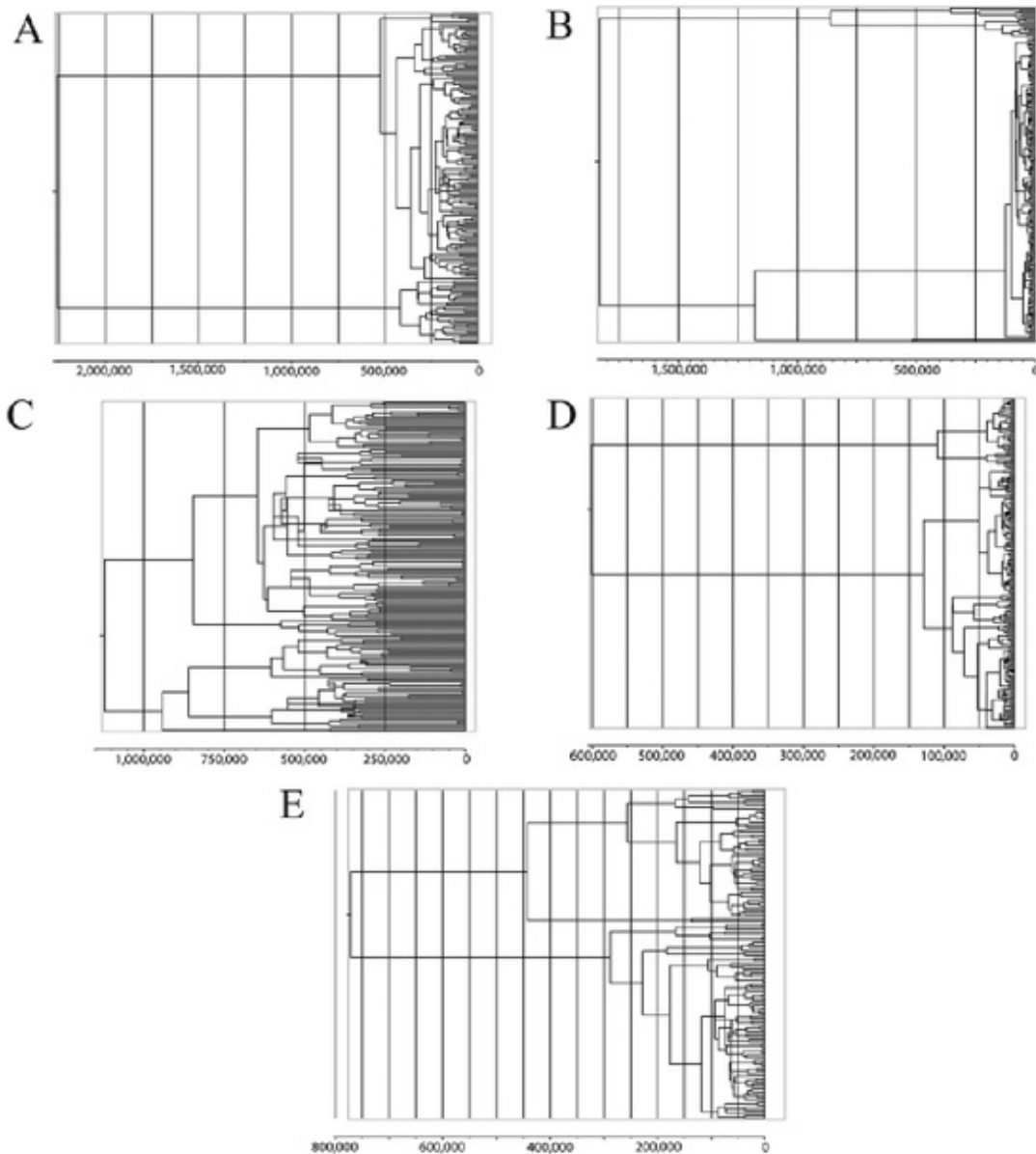


Figure 4. Coalescent genealogies generated in BEAST showing divergence dates for (A) *Auxis thazard*, (B) *Euthynnus affinis*, (C) *Katsuwonus pelamis*, (D) *Rastrelliger kanagurta*, and (E) *Scomberomorus commerson*. Divergence dates are listed in years.

Myrs. Within clades, the majority of individuals began to diverge between 326,000 and 64,000 years ago; 68,000 and 15,000 years ago for *E. affinis*; 470,000 and 400,000 years ago for *K. pelamis*; 54,000 and 19,000 years ago for *R. kanagurta*; and 120,000 and 41,000 years ago for *S. commerson*. *Euthynnus affinis* and *R. kanagurta* explicitly show some lineages that have diverged since the last glacial maximum (26,000 to 19,000 years ago). In contrast, we found no support for isolation by distance. All Mantel tests had non-significant correlation coefficients for *A. thazard* ($r = -0.1355$, $P = 0.7683$), *E. affinis* ($r = -0.1065$, $P = 0.7588$), *K. pelamis* ($r = 0.0070$, $P = 0.4111$), *R. kanagurta* ($r = -0.0251$, $P = 0.4402$), and *S. commerson* ($r = 0.1050$, $P = 0.2309$). We performed a single partial Mantel test due to an instance of hierarchical population structure in *S. commerson*. The partial Mantel test also yielded non-significant correlation coefficients after controlling for both geographic distance ($r = 0.0966$, $P = 0.2720$) and hierarchical population structure ($r = 0.0773$, $P = 0.2697$).

DISCUSSION

26 Pelagic fishes are expected to exhibit weak genetic differentiation over large geographic distances due to their large effective population sizes and potential for long distance dispersal (Ward et al. 1994, McQuinn 1995, Nesbo et al. 2000). Numerous empirical studies have shown an absence of genetic structure in pelagic fishes (Graves et al. 1984, Ely et al. 2005, Santos et al. 2010, Kumar et al. 2012). In instances where strong genetic subdivision was observed it was seen between demes in separate ocean basins (Chow and Ushiyama 1995, Bremer et al. 2005, Lu et al. 2006, Diaz-Jaimes et al. 2010). Limited studies of pelagics within the Indonesian Archipelago have been unable to find evidence of genetic structure in nearshore or epipelagic fish species (e.g., Arnaud et al. 1999, Santos et al. 2010). In contrast, our study of five pelagic fishes shows strong evidence of regional genetic differentiation across the Indonesian Archipelago. Genetic structure ranged from a minimum of $\Phi_{ST} = 0.011$ ($F_{ST} = 0.0313$) in *K. pelamis* up to $\Phi_{ST} = 0.373$ ($F_{ST} = 0.0773$) in *R. kanagurta*, showing high variation among haplotypes and strong regional differences in haplotype frequencies. Both historical and contemporary processes have likely limited genetic exchange within Indonesia, subdividing demes of pelagics throughout the archipelago.

EVIDENCE OF BARRIERS TO DISPERSAL IN INDONESIAN PELAGIC FISHES

Numerous phylogeographic breaks observed in marine taxa in the Coral Triangle have been attributed to genetic divergence driven by Pleistocene sea level fluctuations (McMillan and Palumbi 1995, Williams and Benzie 1998, Benzie 1999, Barber et al. 2000, Carpenter et al. 2011). Barriers to larval dispersal observed in our datasets are similar to those seen in both invertebrate and fish species within the Indonesian Archipelago. Concordance of some barriers suggest similar responses of marine organisms to past vicariance events. Variation observed in the exact placement of some barriers may indicate the presence of tension zones, which shift in space based on the balance between spatially variant selection and dispersal (Barton and Hewitt 1985). Despite these minor variations in placement, the majority of phylogeographic barriers observed could be categorized in the following ways: barriers isolating western Indonesian localities near Sumatra, barriers isolating localities in Papua and broad scale regional barriers isolating eastern and western Indonesia.

Divergence in Western Indonesia.—The first major category of barriers were observed in *A. thazard*, *K. pelamis*, *R. kanagurta*, and *S. commerson*. Similar phylogeographic breaks have been observed in both sessile and motile invertebrates (Barber et al. 2002, 2006, DeBoer et al. 2008, Kochzius and Nuryanto 2008, Vogler et al. 2008), as well as in damselfish, syngnathids, and caesionids (Lourie et al. 2005, Timm et al. 2008, Drew and Barber 2009, Leray et al. 2010, Ackiss et al. 2013). Divergence of western Indonesian demes including Medan, Nias, and Aceh has likely resulted from reduced pelagic marine habitats, exposure of the Sunda Shelf during Pleistocene low sea stands, as well as the cooling of surface water temperatures facilitated by upwelling (Fleminger 1986, Springer and Williams 1990). Combined, these processes may have led to the extirpation of marine populations across much of the archipelago and drastically reduced adult and larval dispersal. Additionally, since Sumatra represents one of the westernmost boundaries of the Indo-Pacific barrier, we might predict evidence of increased intraspecific isolation among demes in this region.

Divergence in Eastern Indonesia.—A second major category of barriers were observed in *A. thazard*, *E. affinis*, *K. pelamis*, and *R. kanagurta*. Demes in eastern Indonesia were genetically divergent, particularly those in Teluk Cenderawasih such as Manokwari, Biak, and Yapen. These findings contribute to a growing body of literature indicating genetic divergence in this region for multiple reef-dwelling invertebrates and some fishes (Barber et al. 2006, 2011, Crandall et al. 2008b, DeBoer et al. 2008, Timm et al. 2008, Nuryanto and Kochzius 2009). The large number of recently described endemic reef fishes (e.g., Allen and Adrim 2000, Allen and Erdmann 2006, Allen 2008, Gill and Allen 2011) further support the patterns of geographic isolation observed in marine species in eastern Indonesia.

Genetic divergence in eastern Indonesia could be driven by three mechanisms. Barber et al. (2002, 2011) suggested that the Halmahera Eddy may facilitate divergence. The Halmahera Eddy is an anticyclonic gyre that forms south of the North Equatorial Countercurrent (Wyrтки 1961, Arruda and Nof 2003). The eddy may be responsible for larval retention within Teluk Cenderawasih (includes Biak, Manokwari and Yapen), with water masses moving in a closed loop at speeds of up to 50 cm s⁻¹ (Lukas et al. 1991) potentially limiting east to west larval transport between demes of pelagic fishes. The Mindanao Eddy may also drive genetic divergence among groups depending on the monsoon season (Schiller et al. 2008). The presence of a sill at 10–200 m in depth (Hall 2002) across Teluk Cenderawasih is a second mechanism that may facilitate genetic divergence in eastern Indonesia. During Pleistocene low sea levels stands, the exposure of this sill could have constricted water flow and larval dispersal in and out of Teluk Cenderawasih, promoting vicariance and genetic divergence in the region. Finally, it has been hypothesized that a combination of tectonic activity and changing sea levels has resulted in numerous isolations of Teluk Cenderawasih over the past 5 Myrs (Allen and Erdmann 2006).

Divergence Near the Makassar Strait.—The final major category of barriers are observed in the vicinity of Sulawesi at the Makassar strait in *S. commerson* and *E. affinis*, and the Maluku Sea in *A. thazard* and *K. pelamis*. These barriers roughly divide the archipelago into eastern and western Indonesia. An observed barrier at the Maluku Sea mirrors a historical biogeographic break known as Weber's Line (van den Bergh et al. 2001). Phylogeographic breaks at Weber's Line have been seen in mantis shrimp, nautilus, and syngnathids (Wray et al. 1995, Lourie et al. 2005, Barber et al. 2011). A break at the Makassar Strait has been seen in a few reef-dwelling and pelagic fish species (Perrin and Borsa 2001, Lourie et al. 2005). The Makassar Strait represents the primary passageway of the Indonesian Throughflow, which dominates the oceanography of the Indonesian Archipelago, and represents a dispersal pathway bringing water from the Pacific Ocean to the Indian Ocean (Godfrey 1996, Gordon and Fine 1996). The presence of a barrier to larval dispersal for pelagic fishes at the Makassar strait may reflect inter-decadal variability in water pathways due to El Niño Southern Oscillations (Valsala et al. 2011), thereby restricting regional connectivity and reinforcing historical genetic divergence among demes.

DEMOGRAPHIC HISTORY

Our genetic data sets provide strong evidence to support a shared demographic history among pelagic fishes in the Indonesian Archipelago. Statistically significant Fu's F_s values in all five species, in conjunction with star polytomies observed in haplotype networks and coalescent analyses, indicate populations of pelagic fishes have

either recovered from a selective sweep or undergone a recent population expansion. Potential signals of population expansion are likely a signature of rising sea levels after the Pleistocene. Species once occupying the Sunda and Sahul shelves would have experienced a series of local extinctions, followed by recolonization events as sea levels rose. Inter-specific differences were, however, observed in Fu and Li's D^* . Statistically significant values were only observed in one of the tuna species, *E. affinis*. Values indicate that strong population structure observed in *E. affinis* may partly result from background selection.

RELEVANCE TO CONSERVATION AND FISHERIES MANAGEMENT

Genetic analyses are potentially invaluable to management of commercial species (Utter 1991, Carvalho and Hauser 1994). Failure to properly delineate and manage distinct fish stocks can result in local overfishing, species declines and a lack of recovery in exploited stocks (Cook et al. 1997, Hutchings 2000). Indonesia has significant economic incentives for protecting its marine resources given that marine fishing activity employs about 3.3 million people and annual exports of *K. pelamis* and other tunas approximate \$68 million USD (FAO 2004, Hutagalung 2012). Results from our study reinforce management unit boundaries proposed within the archipelago in Carpenter et al. (2011), with geographic isolation observed in demes in Sumatra and Teluk Cenderawasih. Additionally, the recent shift towards more local scale management of marine resources in Indonesia is favorable given evidence of regional subdivision of pelagic species. Localized fisheries management plans focus on implementation of community-based management initiatives (Christie 2005, Ablan 2006) and more spatially explicit strategies (Planes et al. 2009).

Our findings also allow us to make inferences about which regions in the archipelago may require more immediate management and conservation action. Regional genetic subdivision of demes in western and eastern Indonesia aligns with regional differences in fishing pressure. 45 rts with the highest annual landings are found in western Indonesia (FAO 2004, Ministry of Marine Affairs and Fisheries 2011), with the majority of all fishers operating from the islands of Sumatra and Java (Dwipongoo 1987, Cardinale et al. 2009). While evidence suggests that stocks in eastern Indonesia are less exploited, in recent years this region has experienced the greatest increase in landings (FAO 2004, Ministry of Marine Affairs and Fisheries 2011). Given observed genetic divergence of demes off western Sumatra and high levels of exploitation, commercial species surrounding Sumatra may require more immediate management attention.

LIMITATIONS OF SINGLE LOCUS STUDY

Finally, we would like to briefly address potential limitations of inferences made from our results given the use of a single mitochondrial 37 marker. Analysis of a single molecular marker may only reveal a small portion of the evolutionary history of a species and in some instances provide unreliable assessments of genome-wide heterozygosity. Despite the limitations, our study provides evidence of multiple species displaying similar responses to evolutionary processes and biogeographic events. The Coral Triangle represents 36 well-studied region in which a number of concordant phylogeographic patterns have been observed across a wide variety of marine taxa. A large portion of the seminal work in 17 region was based on analysis of single locus or mitochondrial DNA data sets (i.e., McMillan and Palumbi 1995, Lavery et al. 1996, Palumbi et al. 1997), with analysis of additional markers often times reconfirming

phylogeographic patterns. Our study provides an excellent starting point for understanding population dynamics of this under-studied group of fishes across the Indonesian Archipelago. ¹

In conclusion, using the mitochondrial control region, we investigated population structure and phylogeography of five pelagic fishes in the Indonesian Archipelago. Our study revealed population structure in all five species and evidence of divergent populations across multiple taxa in both western Sumatra and Papua. Regional patterns of genetic subdivision in pelagic fishes are highly consistent with the timing of Pleistocene vicariance events, as seen for numerous other marine species in the Indonesian Archipelago. Future work could involve simulation studies to explicitly test whether lineage diversification can be directly linked to the presence of observed phylogeographic barriers. Nonetheless, our improved knowledge of regional subdivision of tuna and mackerel species provides crucial information to enhance management of commercial pelagic fishes in the Indonesian Archipelago.

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