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Genetic diversity, population genetic structure, and demographic history of *Auxis thazard* (Perciformes), *Selar crumenophthalmus* (Perciformes), *Rastrelliger kanagurta* (Perciformes) and *Sardinella lemuru* (Clupeiformes) in Sulu-Celebes Sea inferred by mitochondrial DNA sequences

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ABSTRACT

Aside from having an important ecological role in the ocean food web, small pelagic fishes have become the major food source in the Sulu-Celebes Sea (SCS) which is bordered by Indonesia, Malaysia and the Philippines. Conservation and management of these fishes are of prime importance because the people living around the SCS are highly dependent on these resources. Nevertheless, basic biological information, especially relating to genetic diversity, population genetic structure, and demographic patterns, are often deficient. In this study, population genetic methods were used to investigate the genetic structure and diversity as well as historical demography of four ecologically and economically important small pelagic fishes in the SCS: *Auxis thazard* (Lacepède, 1800); Bali sardine, *Sardinella lemuru* (Bleeker, 1853); Indian mackerel, *Rastrelliger kanagurta* (Cuvier, 1816); and bigeye scad, *Selar crumenophthalmus* (Bloch, 1793). Fish samples were collected from 5 geographic locations: (Philippines: Zamboanga, Tawi-Tawi and Palawan; Indonesia: Manado; and Malaysia: Kudat) around the SCS and muscle tissues were sequenced for the mitochondrial DNA (D-loop) control region (n = 150, 231, 169 and 224 for AT, SL, RK, and SC, respectively). Low overall F_{ST} values, high haplotype diversity but low genetic differentiation among haplotypes, and highly mixed clusters from BAPS analysis indicate no distinct genetic population structuring among the samples. Furthermore, neutrality tests, mismatch analysis and Bayesian skyline plots suggest population expansion for all species. Generally, these results indicate that the four marine pelagic species are very resilient over evolutionary time scales; yet, proper management is very necessary, especially because overexploitation of small pelagic fishes has already been reported in the SCS region.

1. Introduction

The Sulu-Celebes (Sulawesi) Sea is bounded by East Malaysia, Indonesia and southern Philippine Islands (Ablan et al., 2002). It is a highly productive fishery area (deVantier et al., 2004; Heileman, 2008) lying at the epicenter of global marine diversity – the Coral Triangle (Carpenter and Springer, 2005; Allen, 2008; Gaither et al., 2011). The marine waters of Sulu and Celebes seas form a large marine ecosystem (LME), a management unit identified by its unique hydrogeographic regime, topography, biochemical characteristics and trophically linked populations (Sherman and Duda, 1999; Watson et al., 2003). Fish landings in the Sulu-Celebes Sea (SCS) are composed mainly of pelagic fishes captured by different gears (deVantier et al., 2004). However, due to the improved efficiency of these fishing gears and the significant increase in the number of fishing boats (Kahn and Fauzi, 2001; Myers and Worm, 2003), overexploitation of small pelagic species has been reported in the SCS (Mullon et al., 2005; Worm et al., 2009; Pinsky et al., 2011; Munpholsri et al., 2013).

Conservation of these fish resources is very important since the pelagic fishery is the principal contributor to the total fish landings in the SCS (deVantier et al., 2004). However, spatial management is challenged by the mobility and dispersal capabilities of marine pelagic fishes and the dynamic nature of the pelagic environment

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(Rohfritsch and Borsa, 2005; Game et al., 2009; Trebilco et al., 2011). Moreover, offshore fishery resources, particularly transboundary populations (Andrady, 2011), are threatened by the competitive fishing practices of countries sharing common resources, not taking into account cooperative measures for management (Kang, 2006). Consequently, sufficient knowledge of the scale and direction of genetic connectivity and phylogeographic structure of different resources (Waples and Gaggiotti, 2006; Palsbøll et al., 2007) is pertinent to effective marine conservation (Carvalho and Hauser, 1995; Begg and Waldman, 1999; Almany et al., 2009; McCook et al., 2009; Kininmonth et al., 2011; Beger et al., 2010; Olds et al., 2012) and fisheries management (Leis et al., 2011).

Different approaches like life history characteristics and growth rate assessment (Beamish and McFarlane, 1983; Berkeley et al., 2004), morphometrics and meristics (Wiens, 2004), and otolith microchemistry (Campana et al., 1994; Campana and Thorrold, 2001; Elsdon et al., 2008) were used to determine and classify structure of populations. Tagging experiments (Hurst et al., 1999; Hay and McKinnell, 2002; Block et al., 2005) were also useful in tracking movements of fishes, but were found to be difficult in the case of small pelagic fishes due to their size (Fréon et al., 2005). Henceforth, genetic data is widely utilized in conservation biology (Schwartz et al., 2007), systematics (Ward et al., 2005; Dasmahapatra and Mallet, 2006; Pedrosa-Gerasmio et al., 2012), and population genetic studies (Pearse and Crandall, 2004; Lemer et al., 2007; Crandall et al., 2000; Allendorf et al., 2012; Palumbi, 2003; Reiss et al., 2009; Santos et al., 2010; Jackson et al., 2014) as it could provide direct measurement and examination of genetic diversity, migration, effective population size and population demographic history (Emerson et al., 2001; Hare et al., 2011; Pearse and Crandall, 2004).

To date, genetic assessment studies that include some samples from the SCS region are from broad-scale phylogeography and phylogenetic studies across the Indo-Pacific and the Coral Triangle (Reece et al., 2010; Ely et al., 2005; Horne et al., 2008) and therefore could not detect breaks within the SCS region alone. Also, the majority of these studies has focused on reef-associated fish populations (Timm et al., 2008; Drew and Barber, 2009; Leray et al., 2010) and only a few researchers have investigated genetic connectivity and dispersal barriers among pelagic fish populations (Jackson et al., 2014). Pelagic marine fishes are known to exhibit little genetic divergence over large spatial scales because of their high dispersal potential at egg and larval stages, high mobility and seasonal migration of adults, and large effective population sizes (Borsa, 2003; Ely et al., 2005; Theisen et al., 2008). Little to no apparent phylogeographic structure were previously identified in some pelagic fishes, e.g., Atlantic and Pacific samples of *Thunnus albacares* and *Katsuwonus pelamis* (Ely et al., 2005) and *Euthynnus affinis* sampled in Southeast Asia (Santos et al., 2010) and the Indian coast (Kumar et al., 2012a). A number of studies, however, provide some evidence of genetic subdivision among demes of pelagic fishes in the Coral Triangle and the Indo-Pacific region (Perrin and Borsa, 2001; Rohfritsch and Borsa, 2005; Sulaiman and Ovenden, 2009; Lu et al., 2006; Thomas et al., 2014).

The objective of the present paper is to investigate genetic diversity, population genetic structure, and demographic patterns among natural populations of four ecologically and economically important small pelagic fishes, namely: frigate tuna, *Auxis thazard* (Lacepède, 1800); Bali sardine, *Sardinella lemuru* (Bleeker, 1853); Indian mackerel, *Rastrelliger kanagurta* (Cuvier, 1816); and bigeye scad, *Selar crumenophthalmus* (Bloch, 1793) which are all abundant in the SCS region. Fish samples were collected from landing sites or local markets of five pre-identified locations surrounding the SCS. Sequence data from the hypervariable region of the mitochondrial DNA (D-loop or control region) were utilized to determine genetic diversity indices, genetic variation, and female effective population sizes among the four pelagic fishes. The mtDNA D-loop marker is highly polymorphic (Niwa et al., 2003) and is considered sensitive at identifying population genetic structure of many marine fish resources (Borsa, 2002, 2003; Marko et al., 2007; Yan et al., 2008; Xia et al., 2008; Santos et al., 2010). These favorable characteristics of the mtDNA D-loop marker and the different analytical approaches employed in this study should aid in elucidating the roles of historical and contemporary processes in generating patterns of genetic variations among the four abundant pelagic populations in the SCS region. Knowledge of phylogeography and population structure is useful for the management and conservation of these commercially important pelagic fishes in the Sulu and Celebes Seas.

2. Materials and methods

2.1. Sampling and sequencing

A total of 150 individuals of *Auxis thazard* (AT), 231 individuals of *Sardinella lemuru* (SL), 169 individuals of *Rastrelliger kanagurta* (RK) and 224 individuals of *Selar crumenophthalmus* (SC) were collected from five geographic locations during 2011–2012. Sampling locations were: (1) Zamboanga, Philippines; (2) Tawi-Tawi, Philippines; (3) Palawan, Philippines; (4) Manado, Indonesia; and (5) Kudat, Malaysia. All the fish samples were either gathered from landing sites or collected from the local wet markets, although some samples were not completed for all sites due to species seasonality. Approximately 1 g of muscle tissues obtained from the dorsal portion of each fish were preserved in 95% ethanol placed in individual 1.5 mL Eppendorf tubes prior to extraction. Total DNA was extracted using the Cetyl trimethylammonium bromide (CTAB) extraction method (Doyle and Doyle, 1987) pretreated with Proteinase K (Hilz et al., 1975).

The hypervariable site of the mtDNA control region (D-loop) for the four species was amplified using the primers CB3R420 and 12Sar430 (Diamed Enterprise). The primer sequences used were CB3R420, 5′-CCCCCTAACTCCCAAAGCTAGG-3′ (forward) and 12Sar430, 5′-GCCTGCGGGGCTTTCTAGGGCC-3′ (reverse). A polymerase chain reaction (PCR) for amplifying DNA was carried out in a total volume of 25 μL containing 13.38 μL milliQ H_2O, 2.5 μL 10× PCR Buffer, 2.5 μL 2 mM dNTPs, 2.0 μL 25 mM MgCl2, 1.0 μL BSA, 1.25 μL 10 μM Primer 1, 1.25 μL 10 μM Primer 2, 0.125 μL *Taq* DNA Polymerase and 1 μL of DNA template. PCR was carried out using a thermal cycler (Labnet International, Inc.) under the following conditions: initial denaturation set at 94 °C for 10 min; 39 times of the main amplification cycle: 30 s of denaturation at 94 °C, 30 s of annealing at 45 °C, and 45 s of extension at 72 °C); and 10 min of final elongation at 72 °C. After amplification, the PCR products were evaluated for quality and quantity using 1% agarose gels stained with ethidium bromide. The PCR amplicons were then sent to Macrogen Korea for purification and sequencing. Sequencing was done using 3730/3730xl DNA Analyzer.

2.2. Data analysis

2.2.1. Genetic diversity and population structure

Consensus sequences were created using Geneious v5.4 (Drummond et al., 2011) and were further aligned and edited using MEGA v5 (Tamura et al., 2011). The number of haplotypes and polymorphic sites were determined using DnaSP v5 (Librado and Roxas, 2009). Haplotype or gene diversity (H) and nucleotide diversity (π), and their corresponding variances were obtained using ARLEQUIN v3.1 (Excoffier et al., 2005). Moreover, analysis of molecular variance (AMOVA), which also runs in ARLEQUIN v3.1 (Excoffier et al., 2005), was used to obtain genetic differentiation indices (F_{ST})

and genetic variation partitioning within and among populations. Furthermore, pairwise population comparisons following Tamura and Nei distance method (Tamura and Nei, 1993) were also computed in ARLEQUIN v3.1 (Excoffier et al., 2005).

Using the program NETWORK v4.6.1.0 (copyright 2004–2012, Fluxus Technologies Ltd.; http://www.fluxus-engineering.com), median joining haplotype networks were drawn to visually illustrate haplotype variability. Furthermore, Bayesian assignment tests were done for the four species using the software BAPS v6 (Corander et al., 2008; Corander and Tang, 2007) to identify clusters of individuals without an a priori assumption of population membership. A cluster groups based on genetic similarities under model assumptions of Hardy–Weinberg equilibrium and linkage equilibrium (Corander et al., 2008; Corander and Tang, 2007).

2.2.2. Demographic history

To test for past demographic expansion, Tajima's D (Tajima, 1989) and Fu's F_S (Fu, 1997) tests were implemented in ARLEQUIN v3.1 (Excoffier et al., 2005) and p-values were generated using 1000 simulations. The former (Tajima, 1989) makes use of the frequency of the number of variable positions (segregating or polymorphic nucleotide sites) while the latter (Fu, 1997) uses the distribution of haplotypes or alleles. These neutrality tests can be used to investigate demographic history and detect selection in cases where DNA polymorphism deviates from those predicted by the Wright-Fisher neutral model of evolution (Tajima, 1989; Fu, 1997).

Mismatch distribution analysis was also employed to further test for demographic history and expansion. All the figures illustrating the frequency of pairwise comparison (y-axis) between individuals with corresponding number of pairwise differences (x-axis) were generated using DnaSP v5 (Librado and Roxas, 2009). Expected demographic parameters (τ, θ_0, θ_1,), Harpending's raggedness index (*Hri*) and sum of squared deviation (SSD) were estimated in ARLEQUIN v3.1 (Excoffier et al., 2005) based on the sudden expansion model (Rogers and Harpending, 1992). In addition, the times to the most recent common ancestor (tMRCA) were estimated using Bayesian skyline plot analysis implemented in BEAST v.1.4.6 (Drummond and Rambaut, 2006) with XML files prepared using BEAUti v1.7.5 (Drummond et al., 2012). The software program BEAST uses a standard Markov chain Monte Carlo (MCMC) algorithm to generate a posterior distribution of effective population size through time (Drummond and Rambaut, 2006). The MCMC analysis was run for 4^7 generations (sampled every 4000 iterations) using the HKY nucleotide-substitution model. Rate variations among sites were modeled using a gamma distribution and the mutation rate was set at 3.6% per million years based on the average mutation rate previously employed for the mtDNA control region in teleosts (Donaldson and Wilson, 1999). Convergence of the sampled parameters was visualized using the TRACER v1.5 (Rambaut and Drummond, 2009). Ancestral female effective population sizes are important estimates to understand demographic patterns corresponding to how climate changes affected marine pelagic species in the evolutionary times.

3. Results

3.1. Genetic diversity

A final length of 309, 305, 323, and 364 base pairs (bp) of the hypervariable (Lee et al., 1995) mtDNA D-loop or control region were analyzed for a total of 150, 231, 169 and 224 individuals of *Auxis thazard* (AT), *Sardinella lemuru* (SL), *Rastrelliger kanagurta* (RK) and *Selar crumenophthalmus* (SC), respectively. The proportion of sharing between locations was compared to the total haplotypes of both locations together. Over the whole set of data, 137, 98, 60 and 33 polymorphic (variable) sites were identified for AT, SL, RK and SC, respectively. These variable sites have defined 143 haplotypes for AT, 215 haplotypes for SL, 64 haplotypes for RK and 61 haplotypes for SC (Table 1) resulting in a very high global value of haplotypic diversity ranging from $H = 0.972–1.000$ for AT, $H = 0.998–1.000$ for SL, $H = 0.957–1.000$ for RK and $H = 0.726–0.781$ for SC with a mean H of 0.9994, 0.9993, 0.9614 and 0.7510 for AT, SL, RK and SC respectively. Although haplotype diversity values were high, low nucleotide diversity (π) values (ranging between $\pi = 0.306–0.359$ for AT, $\pi = 0.310–0.398$ for SL, $\pi = 0.012–0.288$ for RK and $\pi = 0.0048–0.055$ for SC) indicate only small genetic differences between haplotypes. This combination of having high haplotype diversity (H) and low nucleotide diversity (π) values suggests shallow mtDNA genealogies among the four species, a recurring feature of marine fishes (Grant and Bowen, 1998).

3.2. Population structure

AMOVA was employed to show overall genetic variation within and among populations of AT, SL, RK and SC. The majority (nearly 100%) of genetic variation was contained within localities rather than among them. This result indicates little (for SL and RK) to no (AT and SC) geographic population structure (Table 2). Furthermore, population divergence was small for all species, and most comparisons were not significant (Tamura and Nei, 1993). However, in the case of RK, while most comparisons were significant, values were still small (Table 3).

Median joining networks (Supplementary Fig. 1) generated for each marine pelagic species illustrate network topology of haplotypes. The sizes of the circle indicate the number of individuals in a certain haplotype; the smallest with one individual. Based on the networks, there were many haplotypes and all were in low frequency, except for SC. The datasets did not partition into any clades, geographic, or otherwise. Generally, all haplotype diversity values were very high for all species which were clearly reflected in their haplotype networks (Supplementary Fig. 1).

Moreover, Bayesian analysis performed in BAPS v6 (Corander et al., 2008; Corander and Tang, 2007) grouped individuals into clusters which resulted in a few clusters with highly mixed membership (Supplementary Fig. 2). There were 4 resulting clusters for AT, SL and RK and 5 clusters for SC. Partitions for all species in all geographic locations were presented in Fig. 1.

3.3. Demographic history

Both Fu's F_S (Fu, 1997) and Tajima's D (Tajima, 1989) tests suggested population growth or expansion for the four pelagic fish populations. Fu's F_S values (Table 4) were significantly negative in all sampling locations for all the four species, but for Tajima's D (Table 4), the results were only significant for AT (Palawan, Zamboanga and Malaysia (Kudat) locations) and SC (Palawan, Malaysia (Kudat), Indonesia (Manado) and Tawi-Tawi). Significant negative values indicate an excess of rare haplotypes and rejection of the null hypothesis of neutral evolution (Fu, 1997; Tajima, 1989).

The parameters of the expansion model (θ_0, θ_1, τ), *Hri* and SSD for the entire mtDNA D-loop region data set are shown in Table 5. All species except for some locations of RK (Palawan and Malaysia) exhibited a unimodal distribution (Fig. 2), which were not significantly different (as measured by the SSD; $p > 0.05$) from that predicted by the growth expansion model (Rogers and Harpending, 1992). Furthermore, the Harpending's raggedness indexes were low for all species, ranging from $Hri = 0.0060$ (SL) to $Hri = 0.0353$ (SC) indicating a significant fit between the observed and expected distributions, and therefore further evidence of population expansion (Harpending, 1994). Estimated tau

Table 1
Sample size (n), number of haplotypes (k), polymorphic sites (PS), Clusters, haplotype (H) and nucleotide diversity (π) ±SD per population.

Population	n	K	Clusters	PS	$H \pm$ SD	$\pi \pm$ SD
AT	150	143	4	309bp		
Palawan	49	49	2,3,4	78	1.0000 ± 0.0041	0.034123 ± 0.017556
Zamboanga	39	37	2,3,4	82	0.972 ± 0.0068	0.030625 ± 0.015967
Malaysia	40	39	2,3	97	0.9987 ± 0.0062	0.032696 ± 0.016961
Indonesia	22	21	1,2,3	66	0.9952 ± 0.0165	0.035913 ± 0.018972
SL	231	215	4	305bp		
Palawan	40	39	1,2,3,4	57	0.9987 ± 0.0060	0.039748 ± 0.020382
Zamboanga	50	48	1,2,3,4	66	0.9984 ± 0.0044	0.037405 ± 0.019145
Malaysia	49	49	1,2,3,4	54	1.0000 ± 0.0041	0.030987 ± 0.016057
Indonesia	48	46	1,2,3,4	56	0.9981 ± 0.0050	0.036779 ± 0.018860
Tawi-Tawi	44	44	1,2,3,4	54	0.9984 ± 0.0044	0.036413 ± 0.018720
RK	169	64	5	323bp		
Palawan	31	25	1,2,3,4,5	44	1.0000 ± 0.0962	0.028797 ± 0.015128
Zamboanga	47	25	1,2,3	17	0.9574 ± 0.0133	0.011691 ± 0.006658
Malaysia	48	27	1,2,3,4	20	0.9628 ± 0.0127	0.018975 ± 0.010195
Tawi-Tawi	43	25	1,2,3,5	29	0.9574 ± 0.0133	0.012735 ± 0.007182
SC	224	63	5	364bp		
Palawan	49	23	1,2,3,4,5	20	0.7432 ± 0.0700	0.005425 ± 0.003463
Zamboanga	38	16	1,2,3,4,5	15	0.7255 ± 0.0804	0.004831 ± 0.003185
Malaysia	50	22	1,2,3,4,5	22	0.7690 ± 0.0641	0.005482 ± 0.003490
Indonesia	50	22	1,2,3,4,5	19	0.7518 ± 0.0675	0.005108 ± 0.003303
Tawi-Tawi	37	14	1,2,3,4,5	17	0.7808 ± 0.0678	0.005318 ± 0.003436

AT = Auxis thazard; SL = Sadinella lemuru; RK = Rastrelliger kanagurta; SC = Selar crumenophthalmus.

(τ) values were generally very similar for all locations, and for all the four species, except for the τ value in Palawan for RK samples. This trend of having very similar τ values indicates that population expansion in all locations may date back to about the same historical period (Harpending, 1994). Similarly, Bayesian skyline plots revealed population expansion in all pelagic fish populations, with time of expansion varying across species. The rapid increase of female effective population size started within the range of 400,000–650,000 years ago in AT; around 1,125,000 years ago for SL; 75,000 years ago for RK; and, around 60,000 years ago for SC assuming a lineage mutation rate of 3.6% per million years based on the average mutation rate previously used for mtDNA control region in teleosts (Donaldson and Wilson, 1999). Long-term coalescent female effective population size (N*ef*) estimated in BEAST were approximately 3.797×10^8 effective females for AT, 2.975×10^8 for SL, 1.1139×10^7 for RK, and 1.8361×10^7 for SC, with the highest N*ef* values for AT, followed by SL. Furthermore, using the mismatch parameters θ_0 and θ_1 (Harpending, 1994) obtained from ARLEQUIN v3.1 (Excoffier et al., 2005), mean female effective population size after expansion (θ_1) were estimated to be about 31,000, 11,000, 20, and 20 times higher than before the expansion (θ_0) for AT, SL, RK and SC, respectively.

3.4. Accession numbers

Haplotype sequences for all populations were deposited in GenBank with the following accession numbers: KF058561 to KF058703 for AT, KF254945 to KF255159 for SL, KF218100 to KF218163 for RK, and KF241890 to KF241950 for SC.

4. Discussion

Pelagic fishes *Auxis thazard* (AT), *Sardinella lemuru* (SL), *Rastrelliger kanagurta* (RK) and *Selar crumenophthalmus* (SC) are pelagic in neritic and oceanic waters (Riede, 2004; Dalzell and Peñaflor, 1989; Collette, 1995). The distribution of AT, a small tuna species occurring in both tropical and subtropical waters, extends from 61° N to 51° S, and 180° W to 180° E (Collette and Nauen, 1983) while SL, a highly abundant sardine species in the SCS region (Willette et al., 2011; Willette and Santos, 2013; Purwaningsih et al., 2011), is distributed in tropical waters extending from 38° N to 33° S and 97° E

Table 2
Analysis of Molecular Variance (AMOVA) results for AT, SL, RK and SC.

	Source of variation	d.f.	Sum of squares	Variance component	Percentage of variation
Population					
AT	Among populations	3	12.807	−0.02353 Va	−0.46
	Within populations	143	731.051	5.11224 Vb	100.46
Fixation index:	−0.00462				
SL	Among populations	4	29.226	0.03896 Va	0.70
	Within populations	226	1245.132	5.50943 Vb	99.30
Fixation index:	0.00702**				
RK	Among populations	3	20.675	0.09843 Va	3.43
	Within populations	165	456.787	2.76841 Vb	96.57
Fixation index:	0.03433*				
SC	Among populations	4	3.253	−0.00318 Va	−0.33
	Within populations	219	209.130	0.95493 Vb	100.33
Fixation index:	−0.00334				

* Statistical significance $P < 0.05$
** Statistical significance $P < 0.01$.

Table 3
AMOVA haplotype F_{ST} results for pairwise population comparisons with corresponding significance indications (Tamura and Nei, 1993).

AT	Malaysia	Indonesia	Zamboanga	Palawan
Malaysia		–		
Indonesia	0.00299	–		
Zamboanga	−0.00593	−0.00114	–	
Palawan	−0.00772	0.00484	−0.00171	–

SL	Zamboanga	Indonesia	Malaysia	Palawan	Tawi-Tawi
Zamboanga	–				
Indonesia	0.00201	–			
Malaysia	0.00302	0.00581	–		
Palawan	0.01387	0.01344*	0.01260	–	
Tawi-Tawi	0.00632	−0.00792	0.01491	0.00874	–

RK	Zamboanga	Palawan	Malaysia	Tawi-Tawi
Zamboanga	–			
Palawan	0.04002*	–		
Malaysia	0.05665*	−0.00274	–	
Tawi-Tawi	−0.00636	0.04464*	0.06516*	–

SC	Zamboanga	Malaysia	Indonesia	Palawan	Tawi-Tawi
Zamboanga	–				
Malaysia	−0.00475	–			
Indonesia	−0.01316	−0.00294	–		
Palawan	−0.01012	−0.00128	−0.00485	–	
Tawi-Tawi	0.00600	−0.00378	0.00198	0.00115	–

* Statistical significance $P < 0.05$.

to 134° E (Froese and Pauly, 2014). Additionally, RK, which is widely distributed in the Indo-West Pacific region can reach from 34° N to 24° S and 30° E to 180° E (Collette and Nauen, 1983; Madhavi and Lakshmi, 2012) and SC, a small pelagic carangid of circumtropical distribution (Smith-Vaniz, 1995), could be seen in waters from 47° N to 24° S, 180° W to 180° E (Froese and Pauly, 2014). According to Lam et al. (2008), sea surface temperature has a strong influence on the temporal distribution of mobile marine pelagic species since temperature is a key factor which affects the physiological needs of these fishes, e.g., reproduction, growth and survival.

While the four pelagic species prefer shallow coastal waters (Maguire et al., 2006; Jayasankar et al., 2004; Pauly et al., 1996; Roos et al., 2007; Gasparini and Floeter, 2001), reproduction happens in open oceans (AT, SL, RK and SC) and deeper waters (SC)

Table 4
Tajima's D and Fu's F_S neutrality tests with P-values.

Population	Tajima's D	P-value	Fu's F_S	P-value
AT				
Palawan	−1.50710	0.04400*	−24.62732	0.00000***
Zamboanga	−1.67308	0.03200*	−24.59605	0.00000***
Malaysia	−1.80749	0.01400*	−24.51626	0.00000***
Indonesia	−1.17382	0.12000	−9.37038	0.00300**
Mean	−1.54037	0.05250	−20.77750	0.00075***
SL				
Palawan	−0.78710	0.24000	−24.60867	0.00000***
Zamboanga	−1.13588	0.12000	−24.63234	0.00000***
Malaysia	−1.05315	0.15100	−24.82279	0.00000***
Indonesia	−0.79651	0.19200	−24.66132	0.00000***
Tawi-Tawi	−0.77575	0.22800	−24.67804	0.00000***
Mean	−0.90968	0.18620	−24.68048	0.00000***
RK				
Palawan	−0.87614	0.21000	−12.17887	0.00000***
Zamboanga	−0.22957	0.46100	−16.31991	0.00000***
Malaysia	0.88245	0.86000	−12.31138	0.00000***
Tawi-Tawi	−1.42594	0.05100	−16.32191	0.00000***
Mean	−0.32811	0.51640	−11.46166	0.00000***
SC				
Palawan	−1.84433	0.00900**	−21.83585	0.00000***
Zamboanga	−1.68939	0.02400*	−11.77634	0.00000***
Malaysia	−1.96328	0.00600**	−19.32557	0.00000***
Indonesia	−1.83025	0.01400*	−20.40399	0.00000***
Tawi-Tawi	−1.78220	0.02000*	−7.78879	0.00000***
Mean	−1.82189	0.01460*	−16.22611	0.00000***

* Statistical significance $P < 0.05$.
** Statistical significance $P < 0.01$.
*** Statistical significance $P < 0.001$.

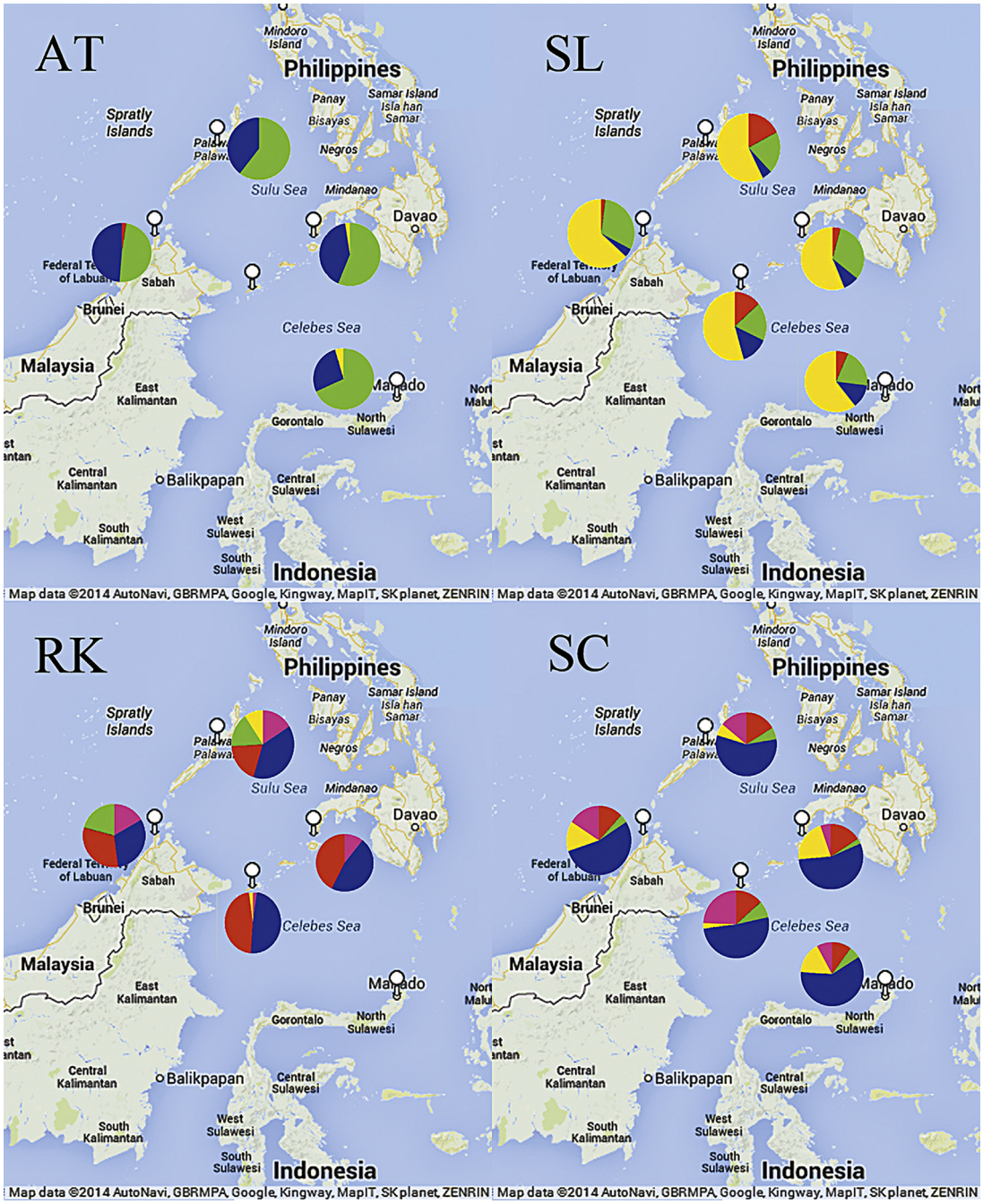

Fig. 1. Distribution of genetic clusters for *Auxis thazard*, *Sardinella lemuru*, *Rastrelliger kanagurta* and *Selar crumenophthalmus* in their respective collection sites. Pie charts are proportional to sample size. SCS map was created using Google Maps.

(Durand et al., 2005; Jayasankar et al., 2004; Collette and Nauen, 1983; Munpholsri et al., 2013) where conditions are optimal or at least suitable for reproductive success (Lam et al., 2008).

Aside from this, migration of these pelagic fishes can be due to their search for food, body mass recovery, survival against predators and movement to areas less accessible to fishermen (Roos et al., 2007; Samonte et al., 2009; Madhavi and Lakshmi, 2012; Collette and Nauen, 1983). The high mobility of these pelagic species together with other biological characteristics like large effective population sizes and high dispersal potential of eggs and larvae (Durand et al., 2005; Jackson et al., 2014) contribute to high gene flow among sampled locations.

4.1. Genetic diversity

The high haplotype diversity (H) of the mtDNA D-loop marker (Table 1) in the present study could be attributed to large effective population sizes of pelagic species, especially in the case of AT and SL (Fig. 3). Populations with larger effective population size will result in a greater number of haplotypes (Table 1) compared to those with smaller effective population size (Ewens, 1972). High haplotype diversity values were similar to those recorded for widely distributed pelagic species such as sardines (Bowen and Grant, 1997) and tuna species (Santos et al., 2010; Ward et al., 1997). On the other hand, nucleotide diversities (π) were low (Table 1) which indicates a high number of closely related haplotypes with

Table 5
Demographic parameters of the four species based on mtDNA D-loop region sequence data: tau (τ), theta at time 0 (θ_0), theta at time 1 (θ_1), Harpending's raggedness index (*Hri*), and sum of squared differences (*SDD*).

Species	Collection Site	τ	$\theta 0$	$\theta 1$	Hri	SSD
AT	Indonesia	9.3359	1.6506	86.9922	0.0113	0.0060
	Zamboanga	7.7559	1.5522	1270.0000	0.0103	0.0028
	Palawan	9.2578	0.0000	99,999.0000	0.0050	0.0035
	Malaysia	10.0918	0.0088	270.3906	0.0068	0.0022
	Mean	9.1103	0.8029	25,406.5957	0.0083	0.0036
	s.d.	0.8471	0.7993	43068.2980	0.0026	0.0015
SL	Indonesia	8.0996	1.7789	206.5625	0.0055	0.0012
	Zamboanga	8.6231	1.8035	107.8125	0.0064	0.0018
	Malaysia	7.9414	0.6416	99,999.0000	0.0069	0.0009
	Palawan	9.7754	1.6539	85.8594	0.0067	0.0036
	Tawi-Tawi	7.3066	3.0848	148.5938	0.0044	0.0012
	Mean	8.3492	1.7925	20,109.5656	0.0060	0.0018
	s.d.	0.8276	0.7764	39,944.7383	0.0009	0.0010
RK	Zamboanga	3.9785	0.0701	22.6611	0.0161	0.0022
	Malaysia	1.7617	5.3578	60.2344	0.0181	0.0140
	Tawi-Tawi	2.3633	1.5961	69.4531	0.0166	0.0024
	Palawan	9.9102	1.9547	14.4629	0.0077	0.0081
	Mean	4.5034	2.2447	41.7029	0.0146	0.0067
	s.d.	3.2251	1.9317	23.5483	0.0041	0.0049
SC	Malaysia	2.3731	0.0000	5.9692	0.1099	0.0284
	Indonesia	2.3008	0.0598	3.9142	0.0164	0.0011
	Palawan	2.9629	0.0207	3.1675	0.0099	0.0001
	Zamboanga	1.7461	0.4887	3.4747	0.0257	0.0034
	Tawi-Tawi	1.8535	0.5643	4.8804	0.0146	0.0010
	Mean	2.2473	0.2267	4.2812	0.0353	0.0068
	s.d.	0.4329	0.2467	1.0231	0.0377	0.0109

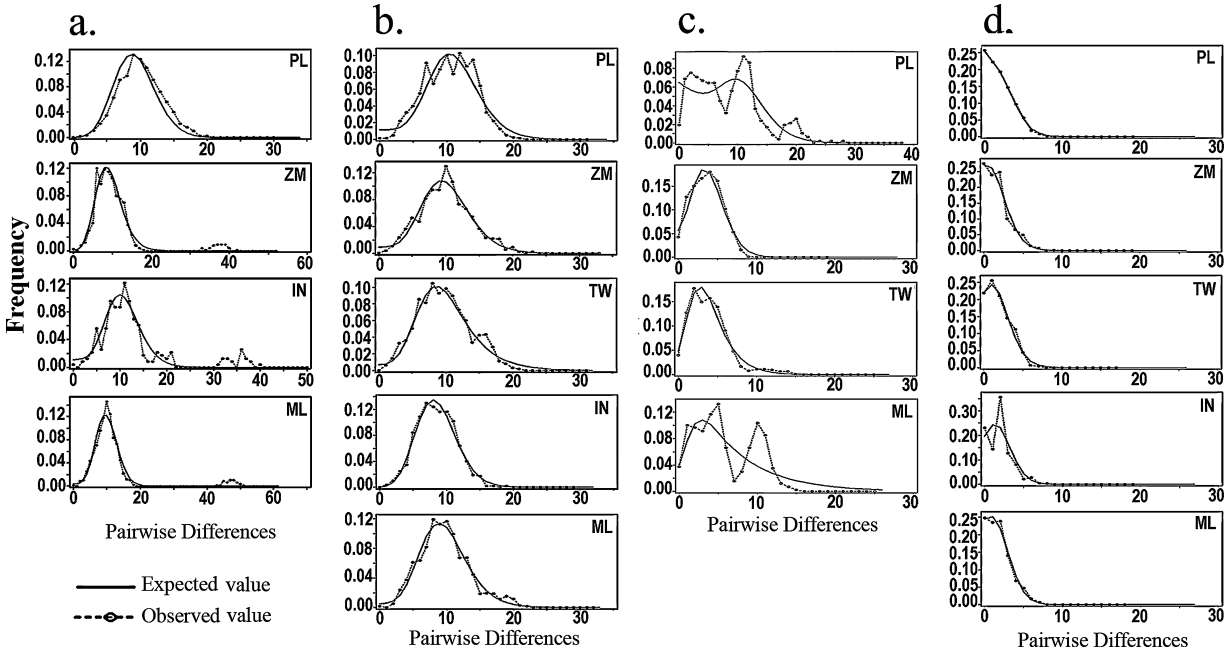

Fig. 2. Mismatch distribution for each of the analyzed populations of: (a) *Auxis thazard*; (b) *Sardinella lemuru*; (c) *Rastrelliger kanagurta*; and *Selar crumenophthalmus* in all locations (IN = Indonesia; ZM = Zamboanga; PL = Palawan; ML = Malaysia; and TW = Tawi-Tawi).

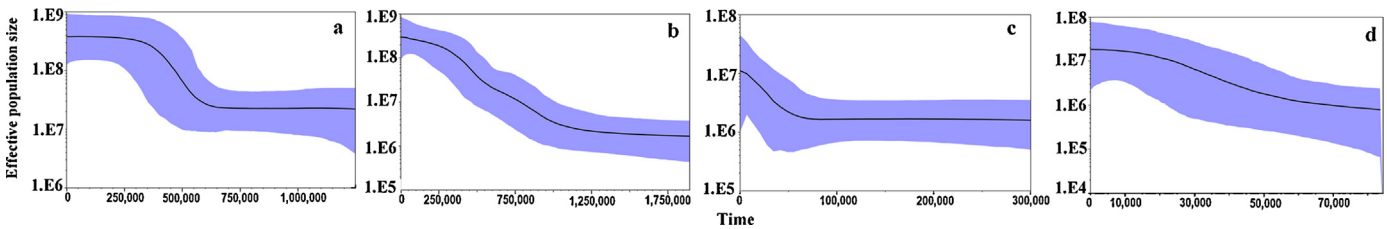

Fig. 3. Bayesian skyline plots of mtDNA control region sequences from: (a) *Auxis thazard*; (b) *Sardinella lemuru*; (c) *Rastrelliger kanagurta*; and *Selar crumenophthalmus* showing female effective population size (N*ef*) through time assuming a lineage mutation rate of 3.6% per million years. The solid line indicates the median estimate while the purple area reflects the s.d. values of the estimated N*ef*.

very minimal differences between each other. Although the numbers of haplotypes identified were large for all species, genetic differences between haplotypes were considerably low. This high haplotype diversity in concurrence with low nucleotide diversity is also similar with many marine taxa inferred using mtDNA sequence data (Grant and Bowen, 1998; Dudgeon et al., 2000; Rocha-Olivares et al., 2000; Muss et al., 2001; Rocha et al., 2002).

4.2. Population genetic structure

Generally, there is no significant population genetic structuring for all species in all sampling locations based on the insignificant F_{ST} values, star-like shape of the haplotype networks (Supplementary Fig. 1), and resultant genetic clusters from BAPS analysis (Supplementary Fig. 2). Though F_{ST} values for SL and RK (Table 2) were significant, these values were relatively low (F_{ST} = 0.00702 in SL and F_{ST} = 0.03433 in RK). In such cases, it is difficult to distinguish whether gene flow is reduced or uninhibited (Palumbi, 2003) implying that any restraint on inter-population gene flow is negligible (Horne et al., 2008). Furthermore, the median-joining networks (Supplementary Fig. 1) indicate little but non-significant haplotype sharing between locations. This means population separation on one hand, but many singular haplotypes in each location on the other, and therefore no distinct structure of a population. In BAPS analysis, 4–5 genetic clusters were suggested for the four species. These clusters were highly mixed with individuals from different sampling locations with inconsistent composition between runs, indicative of panmixia (Hedtke et al., 2007). A few clusters with highly mixed membership indicate high gene flow between sampled locations, which suggests that there is no barrier for genetic homogenization between Sulu and Celebes Seas for all four species.

This weak population genetic structure is expected for pelagic fishes AT, SL, RK and SC because of their common life histories and the assumed homogeneity of the pelagic environment (Fauvelot and Borsa, 2011; Rohfritsch and Borsa, 2005; Game et al., 2009; Trebilco et al., 2011). SL and RK which are both plankton feeders spawn intensively during the monsoon seasons with the abundance of plankton for the survival and growth of their young ones (Yohannan, 1998). In the case of SC and AT, spawning occurs over prolonged periods and peaks during warm months for SC (Roos et al., 2007) and during the monsoon seasons for AT (Kumar et al., 2012a,b). Although SC and AT are not strictly plankton feeders, the abundance of plankton could still influence the availability of their food (e.g., small fishes, crustaceans and larvae of other fishes), being at the first trophic level in the food chain/web. Moreover, these four pelagic fishes, which spawn in open oceans, do not care for the eggs they lay; hence, when eggs are hatched, they should be in an environment with enough food for their survival and growth because planktonic larvae are not yet capable of swimming in search for food (Yohannan, 1998). With the upwelling of waters happening during monsoons, enrichment of the surface waters leads to plankton abundance (Yohannan and Abdurahiman, 1998), making it an appropriate time for the spawning of these pelagic fishes.

Another important factor that is also relevant to the present study is the peculiar ocean current pattern in the SCS. Although the Sulu and Celebes Seas are separated by the Tawi-Tawi ridge, the two marine basins are interconnected by the movement of marine waters (Dumaup et al., 2003) which is strongly due to monsoonal currents (Wyrtki, 1961). The dynamic movement of waters (direction of nutrient and larval transport varies with the monsoons) could also help in the circulation of rich nutrients and the dispersal of the larvae of the four fishes across political boundaries (Wyrtki, 1961; Dumaup et al., 2003; Madhavi and Lakshmi, 2012) and thus low genetic differentiation among samples (Chan et al., 2013). Ocean circulation shifts due to the monsoon cycle also influence seasonal migration of adults (Hardenberg, 1937). Moreover, the tidal shifts and wind-driven surface currents in Sulu and Celebes Seas make ideal conditions for the dispersal of eggs and planktonic larvae (Campos et al., 2008; Dygico et al., 2006) of the four species. Interestingly, in the case of AT, their larvae have a wide range of temperature tolerance (between 21.6 °C and 30.5 °C) – the widest among tuna species (Kumar et al., 2012b). This feature could have a strong influence on the survival of AT larvae after being displaced to more distant sites.

High gene flow and lack of genetic structure also coincides with studies on eastern little tuna in Southeast Asia (Santos et al., 2010); other tunas and swordfishes (Ward et al., 1997; Chow et al., 1997); and round scad mackerel *Decapterus macrosoma* (Carangidae) in the Indo-Malay archipelago (Borsa, 2003). Several pelagic fishes have exhibited little spatial partitioning within and between ocean basins because of the occurrence of continuous, circumtropical pelagic environment and a wide range of suitable spawning grounds (Myers and Worm, 2003; Graves, 1996).

4.3. Demographic history

The results for neutrality tests suggest that the populations of the four species are expanding because of the strongly significant negative values from Fu's F_S indices. Tajima's D, however, only showed significant negative values for AT and SC. Nonetheless, Fu's F_S is more sensitive in the detection of population expansion (Fu, 1997); hence, the results generally suggest population expansion for all four species. Moreover, standard deviations from the mean (τ) were low for AT, SC and SL which suggest a nearly identical distribution per location with the implication that the expansion happened at approximately the same timeline for all locations. This could also be used as supporting evidence for panmixia since it appears that the distributions generated describes one identical population for each of these species. On the other hand, although there seemed to have two divisions in the case of RK, it can still be seen that the 1st mode of the bimodal distribution group overlaps with the mode of the unimodal distribution group (between 0 and 10 pairwise differences), as such, the division is not clear.

Similarly, population expansion revealed in Bayesian skyline plots (Fig. 3) for all four species indicates that the initiation of the sudden population expansion may have occurred during the Pleistocene era (about ~1.8 million until ~10,000 years before present) when repeated glaciations and deglaciations has caused changes in sea levels and temperatures (Graham et al., 2003; Siddall et al., 2003). Since the populations of the four species have expanded within this period of severe environmental fluctuations, it can be assumed with mtDNA D-loop data that these four pelagic fishes are very resilient over evolutionary timescales. Population expansion during the Pleistocene has also been reported in the previous studies for fish populations (Rohfritsch and Borsa, 2005; Ravago-Gotanco and Juinio-Meñez, 2010) and other marine taxa (Casilagan et al., 2013; Crandall et al., 2008).

4.4. Implications for management

Here, the mtDNA D-loop data have not detected a significant genetic structure among sampling locations for the four species in the SCS which means that the samples can be considered panmictic. Currently, it can be assumed that the vulnerability to extinction is low for the four species because of their wide distribution range and low overall F_{ST} values, high haplotype diversity, highly mixed clusters from BAPS and population expansion; yet, proper management of the resources is very important for sustainability, especially because local records have detected overexploitation among small pelagic resources in the SCS region (Mullon et al., 2005; Worm et al., 2009; Pinsky et al., 2011; Munpholsri et al., 2013). Moreover, BEAST estimates of female effective population sizes were also very large

which means that the four species can maintain adaptive genetic variation over longer periods of time.

The lack of genetic differentiation among populations, in part, may be due to post-glacial expansions and a lack of migration-drift equilibrium. While the present data from mtDNA shows no evidence of population decline of the four species, it cannot be ignored that generally, with genetics of high N*ef* marine fishes (Swearer et al., 2002), there can be little or no genetic divergence between sampling locations or 'populations' and yet the populations, in essence, can be demographically separate (i.e., one does not replace harvested individuals in the other). With this, continued unregulated and unscientific fishing remains a serious threat to the depletion of these four marine fishes in the SCS. Furthermore, BEAST estimates of female effective population size provide little in the way of conservation-relevant insights because they are integrated over the coalescent history of the genetic sample and have little to say about the present size of the sampled localities (E. Crandall, pers. comm). Because of the coalescent-based estimation of female effective population size, it is possible that mtDNA data in the study have not detected relatively young processes that might show a different story, e.g., population decline; thus, obtaining genotypes from a number of loci with higher mutation rates, i.e., microsatellites, is recommended.

Indeed, both the number of markers and the number of sampling locations around the SCS should be increased to attain more useful results. Besides, there is also a limitation in the use of mtDNA sequence data in this study since it does not account for paternal inheritance. Nevertheless, the results of this study provide important information on the genetic diversity, population genetic structure and demographic history of four marine pelagic fishes in the SCS. With the initial evidence of the absence of genetic structure among these species, a preventative approach to management can be very helpful in ensuring sustainability and management (McCook et al., 2009) of these fishes in the SCS. Furthermore, integration of the insights from genetic studies with other information can facilitate the development of effective management plans in the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2014.10.006.

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