



# Distribution and genetic variability of young-of-the-year greater amberjack (*Seriola dumerili*) in the East China Sea

Takamasa Hasegawa · Ching-Ping Lu · Sheng-Tai Hsiao · Tsubasa Uchino · Hsin-Ming Yeh · Wei-Chuan Chiang · June-Ru Chen · Chiyuki Sassa · Kazuyoshi Komeyama · Ryo Kawabe · Takashi Sakamoto · Satoshi Masumi · Jun Uchida · Takashi Aoshima · Yoshitaka Sakakura

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**Abstract** We examined the distribution and genetic variability of the greater amberjack *Seriola dumerili* in the East China Sea (ECS) from the mitochondrial DNA (mtDNA) control region of young-of-the-year (YOY) individuals, which may reflect the genetic characteristics of the spawning population. In the years 2016 and 2017, a total of 165 YOY *S. dumerili* were collected from two different locations in the ECS: the southern part of the ECS, and western Japanese coast. The

spawning period was estimated using otolith daily increments from a total of 67 larvae and juveniles collected in the ECS. Results from size and age distribution indicated that *S. dumerili* spawned near the shelf break region in the southern ECS from January to April. Phylogenetic analysis based on mtDNA sequence data showed no significant genetic differentiation among samples collected from different locations, implying *S. dumerili* in the ECS is mainly composed of one

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T. Hasegawa · Y. Sakakura (✉)  
Graduate School of Fisheries and Environmental Sciences,  
Organization for Marine Science and Technology, Nagasaki  
University, 1-14 Bunkyo-machi, Nagasaki 852-8521, Japan  
e-mail: sakakura@nagasaki-u.ac.jp

T. Hasegawa  
Nagasaki Prefectural Institute of Fisheries, 1551-4 Taira-machi,  
Nagasaki 851-2213, Japan

C.-P. Lu  
National Taiwan Ocean University, No.2 Peining Road,  
Zhongjheng District, 20224 Keelung City, Taiwan

S.-T. Hsiao · H.-M. Yeh · W.-C. Chiang · J.-R. Chen  
Council of Agriculture, Fisheries Research Institute, 199 Hou-Ih  
Road, Keelung 20246, Taiwan

T. Uchino · T. Sakamoto  
School of Marine life Science, Tokyo University of Marine  
Science and Technology, 4-5-7 Konan, Minato-ku,  
108-8477 Tokyo, Japan

T. Uchino  
Japan Fisheries Research and Education Agency, National  
Research Institute of Aquaculture, 224-1 Hiruta, Watarai-gun,  
Tamaki, Mei 519-0423, Japan

C. Sassa  
Japan Fisheries Research and Education Agency, Seikai National  
Fisheries Research Institute, 1551-8 Taira-machi,  
Nagasaki 851-2213, Japan

K. Komeyama  
Graduate School of Fisheries Sciences, Hokkaido University,  
3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan

R. Kawabe  
Institute for East China Sea Research, Organization for Marine  
Science and Technology, Nagasaki University, 1551-7  
Taira-machi, Nagasaki 851-2213, Japan

S. Masumi · J. Uchida · T. Aoshima  
Faculty of Fisheries, Nagasaki University, 1-14 Bunkyo-machi,  
Nagasaki 852-8521, Japan

population. *S. dumerili* around the Japanese coast may be originated from the southern ECS.

**Keywords** Mitochondrial DNA · Otolith · Genetic variation · Population structure · Early life history

## Introduction

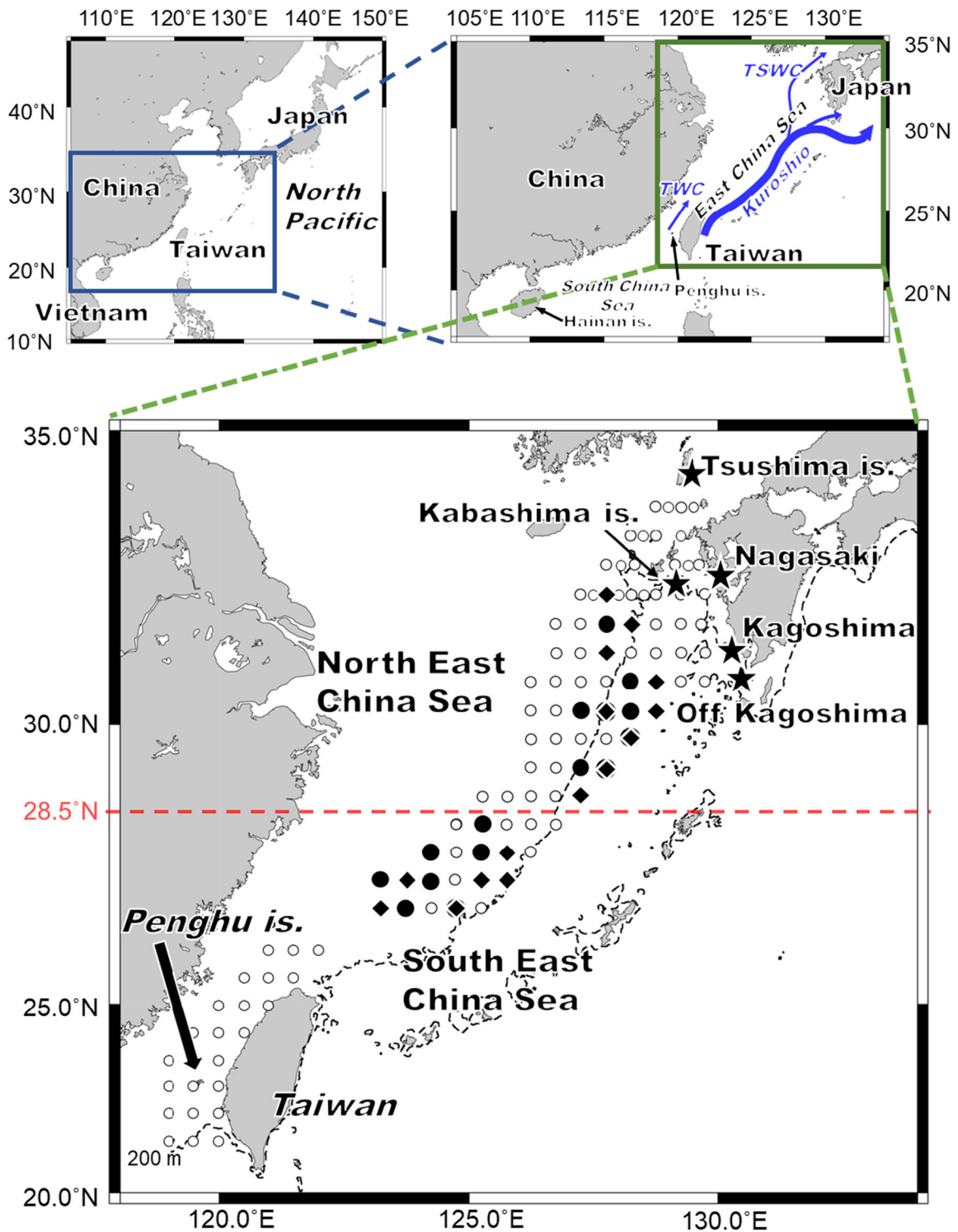
The greater amberjack *Seriola dumerili* (family Carangidae) is a marine pelagic species with circumglobal distribution from temperate to tropical waters (Taki et al. 2005). This species is valuable for commercial and recreational fisheries (Gold and Richardson 1998) and aquaculture (Nakada 2002, 2008). Juveniles of *S. dumerili* of 1.7–29.7 cm in standard length (SL) associate with floating objects such as drifting seaweeds (Badalamenti et al. 1995; Yamasaki et al. 2014; Hasegawa et al. 2017a). The young fish then leave the drifting seaweeds and shift their habitat to the middle or bottom layer as they grow (Uchida et al. 1958), frequently concentrating around reefs, rock outcrops and wrecks (Manooch and Potts 1997). Off the Atlantic coast in the southeastern U.S., females become mature at 1–5 years of age (51.4–82.6 cm in fork length) with 1.3 years being the mean age at which 50% of females are mature (25–47 million oocytes per female), indicating that they grow quickly, mature early, and exhibit high fecundity (Harris et al. 2007). Since this species distributes all over the world, several different populations are recognized, two in the U.S. coast and two in the eastern Asia. A tagging survey (over 1400 recaptures from approximately 14,000 releases) revealed the existence of two stocks or subpopulations of *S. dumerili* in the western Atlantic from the U.S. coast to the Gulf of Mexico (Cummings and McClellan 1996). The results of Gold and Richardson (1998) supported the existence of these two subpopulations of *S. dumerili* in U.S. waters based on variations in the restriction sites of mitochondrial (mt) DNA.

Nugroho et al. (2000) examined genetic variations of *S. dumerili* for aquaculture seedlings in Japan which were captured from Vietnam and coastal waters of Japan, respectively, using polymorphism of the mtDNA D-loop and microsatellite DNA markers. They revealed that at least two genetically different subpopulations existed, which originated from Vietnam and Japan, respectively. Araki et al. (2018) also discriminated two subpopulations of *S. dumerili* captured off the Hainan

Islands, China (in the South China Sea: SCS) and Kochi, Japan (Pacific coast) by structural variations of resequenced genome data. From these evidences, there may be two subpopulations of *S. dumerili* in Asia: the population in the East China Sea (ECS) and that in the SCS.

Hasegawa et al. (2017b) collected larval and early-juvenile *S. dumerili* (11–51 days after hatching) near the Penghu islands, Taiwan (Fig. 1) and posited that the open water area off the Penghu islands is one of the spawning grounds of *S. dumerili*. Larvae and early-juvenile of *S. dumerili* are not common around the Japanese coastal area (Uchida et al. 1958), while the relatively large size of the juveniles associated with drifting seaweed occurs on the western Japanese coast of the ECS from July (Fujita and Mori 1982). The Kuroshio Current and the Tsushima Warm Current (TSWC) affect the transportation of fish eggs, larvae and juveniles (e.g., see Fukutaki 1960; Sassa et al. 2008; Sassa and Tsukamoto 2010; Fig. 1). As for the congeneric yellowtail (*S. quinqueradiata*), the major spawning has been shown to occur from January to June at around the edge of the continental shelf in the ECS, and juveniles of *S. quinqueradiata* hatched in the ECS are transported to the coastal area of Japan with drifting seaweeds by the Kuroshio Current and/or TSWC (Yamamoto et al. 2007). Similar to *S. quinqueradiata*, *S. dumerili* hatched in the southern part of the ECS near Taiwan are transported to the Japanese coast with drifting seaweeds. Therefore, we hypothesized that young-of-the-year (YOY) *S. dumerili* in the ECS from Taiwan to the Japanese coast are composed of one population.

Highly migratory marine teleosts occur throughout large portions of the world's oceans due to their cosmopolitan distributions, and thus analysis of the population structure of these circumglobal fishes is complicated by their ubiquity (Carlsson et al. 2004). In the ECS, information on the migration of adult *S. dumerili* is lacking, and because these fish have the potential to migrate over extensive distances, determination of their genetic population structure would be very difficult. It is likely that YOY fish better reflect the genetic composition of the spawning population compared to older fish with greater migratory capacity (Graves et al. 1996; Carlsson et al. 2004). Thus, we speculated that we could identify the spawning population of *S. dumerili* in the ECS by targeting YOY fish.



**Fig. 1** Geographical location of sampling sites in the East China Sea in the years 2016 and 2017. Circles are the sampling stations by research vessels in this study; *S. dumerili* were collected at the stations with filled circles in 2016 and with filled diamonds in

2017. Stars represent stations where *S. dumerili* were collected by angling, or with a fixed net (see Table 1 for details). The 200 m isobath is shown with dashed thin lines. TWC and TSWC are the Taiwan Warm Current and Tsushima Warm Current, respectively

In the present study, we first examined the distribution and ages (days after hatching) of YOY *S. dumerili* using daily increments in otoliths. We also estimated the spawning period and spawning ground from their ages and the ocean currents, because we considered that information on the spawning period and spawning ground could facilitate our understanding of the genetic variability of *S. dumerili*. Secondly, we examined the genetic variability of YOY *S. dumerili* from the ECS by mtDNA sequencing. Finally, we discussed the early life history of *S. dumerili* in the ECS based on aging and genetic variability, and the importance of fishery management for this species in the ECS.

## Materials and methods

### Sample collection

We conducted sampling at three geographic locations in the ECS: around Taiwan, around the edge of the continental shelf in the ECS and along the western Japanese coast (Fig. 1). Larvae and juveniles (under 10 cm in total length: TL) were collected in the shelf-break region of the ECS during the cruise of the RV “Yoko-Maru” (Seikai National Fisheries Research Institute, Fisheries Research and Education Agency) between 11 and 28 April 2016 and between 11 and 29 April 2017, respectively (Fig. 1). A neuston net (mouth size 1.3 × 0.75 m, mesh size 1.0 mm; Oozeki et al. 2001) was towed for

10 min with a towing speed of 3.5 knots at the upper 0.75 m layer in 77 stations in 2016 and 90 stations in 2017. Specimens were fixed in 10% buffered formalin seawater for 6 h, formalin was rinsed out with freshwater, and then the specimens were transferred into 90% ethanol solution for preservation. Along the southwestern to northwestern part of Taiwan, larvae and juveniles were collected during the cruise of the R/V “Fishery Researcher 1” (Taiwan Fishery Research Institute, Council of Agriculture) between 22 and 25 April 2017 (Fig. 1). Surface tows of an ORI net (mouth size  $\Phi$ 1.6 m, mesh size 0.33 mm) during daytime (0600–1830 h National Standard Time) in 17 stations and oblique tows of an ORI net from the surface down to 50 m depth during night time (19:00–05:30 h National Standard Time) in seven stations were conducted. The ORI net was towed for 10 min with a towing speed of 2 knots. Specimens were preserved in 95% ethanol solution for 6 h, and then transferred into fresh 95% ethanol solution. From collected larvae and juveniles, *S. dumerili* was identified according to Okiyama (1988, 2014).

Along the western Japanese coast in the ECS, young fish (over 10 cm in TL) were collected by angling from the T/V “Kakuyo-Maru” (Nagasaki University), and from private set nets in Nagasaki and Kagoshima Prefecture, Japan (Fig. 1) between 6 July and 6 September 2016 and between 26 August and 28 September 2017, respectively (Table 1). Specimens were kept frozen until measurement. All the individuals were grouped by geographic regions: Tsushima island (n = 28), Kabashima

**Table 1** Collection date, area and body size of young-of-year (YOY) *S. dumerili* collected in the present study. ECS means the East China Sea

Year	Collection					Total length (cm)			
	Area*	Date	Long. (°E)	Lat. (°N)	Method	n	Mean ± S.D.	Min.	Max.
2016	North part of the ECS	13–18 Apr	127°45–128°15	29°25–30°25	Neuston net	13	1.7 ± 1.0	0.7	3.9
	South part of the ECS	23–25 Apr	123°15–125°15	26°75–28°25	Neuston net	11	1.6 ± 1.0	0.6	4.1
	Kagoshima, Japan	24 Aug	130°08	31°25	Fixed net	34	26.7 ± 2.2	20.0	29.5
	Nagasaki coast, Japan	6 Jul–6 Sep	129°45–129°49	32°43	Angling	5	26.1 ± 5.3	16.9	29.8
2017	North part of the ECS	13–27 Apr	127°15–128°45	28°75–32°24	Neuston net	26	2.8 ± 1.9	0.5	7.2
	South part of the ECS	19–24 Apr	123°15–125°45	26°75–27°75	Neuston net	17	2.1 ± 1.1	0.4	4.6
	Off Kagoshima, Japan	26 Jul	130°10	31°11	Angling	7	18.7 ± 2.2	15.1	21.2
	Nagasaki coast, Japan	27 Jul–28 Sep	129°26–130°05	32°34–33°00	Angling	8	23.1 ± 6.1	11.6	29.6
	Kabashima Is., Japan	20 Jul–26 Sep	128°59–129°00	32°44–32°46	Angling	15	22.6 ± 4.9	11.7	29.6
	Tsushima Is., Japan	11–16 Aug	129°17–129°19	34°32–34°33	Fixed net	29	26.6 ± 1.7	22.5	29.3

\* Area is shown in Fig. 1 in detail

island (n = 15), Nagasaki coast (n = 13), Off Kagoshima (n = 41), Northern part of the ECS (n = 34), or Southern part of the ECS (n = 25). Then, the collecting year was prefixed to the geographic region to create four groups for further molecular analyses: 16ECS (n = 24), 16Japan (n = 39), 17ECS (n = 43) and 17Japan (n = 59) (Table 1).

The total lengths (TL cm) of *S. dumerili* were measured using a digital microscope (Keyence, VH6300) or digital caliper. Since many of the specimens collected from the ECS in 2016 were damaged due to sampling, making it difficult to measure the total length, TL was estimated from SL using the following equation: ( $R^2 = 0.99$ ). This equation was calculated from *S. dumerili* collected in the ECS (0.4–7.2 cm in TL, n=43) and along the western Japanese coast (11.6–40.3 cm in TL, n=79) in 2017 (Fig. 1). After measurement, a piece of a fin or the whole body (in the case of fish under 10 cm in TL) was individually preserved in 95% ethanol solution or RNA later (Qiagen, Valencia, ca.) for DNA extraction.

#### Age determination of YOY *S. dumerili* from the ECS

Larval and juvenile *S. dumerili* deposit otolith increments on a daily basis (Hasegawa et al. 2017b). Pairs of sagittal otoliths were extracted under a dissecting microscope. The otoliths were laid on a glass slide and embedded in epoxy resin. Then, the otoliths were observed after grinding using lapping film (9  $\mu\text{m}$  and 3  $\mu\text{m}$ ). Otolith increments were counted under a light microscope at a magnification of 1000 using an oil immersion lens. Since the daily increments in the otoliths of large fish (over 10 cm in TL) were not clear in our study, we defined YOY *S. dumerili* as individuals under 30 cm in TL (24.7 cm in SL, calculated from the above equation), according to the growth rate on the U.S. Atlantic coast, where YOY *S. dumerili* grow approximately 25 cm in SL (30.4 cm in TL, calculated using the above equation) in 6 months (Wells and Rooker 2004) and where one-year-old fish exceed 40 cm in fork length (Harris et al. 2007).

To compare the distribution and spawning period of *S. dumerili* between geographic regions, we divided our study area into the following two subareas: the northern part of the ECS between 33.0° N and 28.5° N, and the southern part of the ECS between 28.5° N and 26.5° N (Fig. 1), since latitudinally discriminated distributions of *S. dumerili* in the ECS were observed both in 2016 and 2017 (Fig. 1).

#### Sequencing of the mitochondrial DNA control region

DNA was extracted by a standard phenol-chloroform method or by using the DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's instructions. The *S. dumerili* mtDNA genome sequence was obtained from the European Nucleotide Archive database (accession No. AB517558.1) and the specific primers for amplifying the control region (CR) of the mtDNA of *S. dumerili* (GA-F: 5'-TGC TCA GAG AAA GGG GAC TT-3'; GA-R: 5'-GGA CCA AAC CTT TGT GCT TG-3') were designed using the Primer 3 program (Untergasser et al. 2012). PCR amplifications were performed in a 9  $\mu\text{l}$  reaction volume containing 10x Ex Taq Buffer (Takara Bio, Shiga, Japan), 2.5 mM dNTP mixture (Takara Bio), 0.025  $\mu\text{M}$  each of forward and reverse primers, and 0.05  $\mu\text{l}$  of 5U/ $\mu\text{l}$  Ex Taq (Takara Bio), and 1.0  $\mu\text{l}$  of template DNA containing approximately 30–100 ng/ml of DNA. The PCR amplifications were programmed as an initial denaturation at 95 °C for 3 min; one cycle of 94 °C for 30 s, 62 °C for 30 s and 72 °C for 1 min; one cycle of 94 °C for 30 s, 60 °C for 30 s and 72 °C for 1 min; one cycle of 94 °C for 30 s, 58 °C for 30 s and 72 °C for 1 min; one cycle of 94 °C for 30 s, 56 °C for 30 s and 72 °C for 1 min; 28 cycles of 94 °C for 30 s, 55 °C for 30 s and 72 °C for 1 min; followed by a final extension at 72 °C for 5 min. Each PCR product was evaluated in 2% agarose gel electrophoresis with a standard size marker (TaKaRa Bio). PCR products were purified with illustra ExoProStar (GE Healthcare, Milwaukee, WI) and ExoSAP-IT Express PCR Product Cleanup (Affymetrix, Santa Clara, ca.). The mtDNA CR was sequenced in both directions with the PCR forward and reverse primers. The reactions of DNA sequencing were performed by the FASMAG Co. (Kanagawa, Japan), and Eurofin Genomics (Tokyo), except in the case of 16 s. For 16 s, sequencing PCR with forward and reverse primers was performed using a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). After purification with BigDye XTerminator (Applied Biosystems), the DNA sequencing reaction products were run on an Applied Biosystems 3130xl DNA Analyzer (ThermoFisher Scientific).

#### Molecular diversity index and genetic differentiation

The alignments of multiple sequences were performed with CLUSTALW (Thompson et al. 1994) in MEGA X

(Kumar et al. 2018) using default settings. The number of mitochondrial haplotypes, polymorphic sites, haplotype diversity ( $Hd$ ), and nucleotide diversity ( $\pi$ ) were estimated in DnaSP v6 (Rozas et al. 2017). Nucleotide sequence data for the haplotypes used in this paper were deposited in GenBank under accession numbers MT027362–MT027489. The mtDNA CR sequences were analyzed to estimate the index of genetic differentiation ( $F_{ST}$ ) and gene flow ( $Nm$ ) between sampling localities pairs, and by the analysis of molecular variance (AMOVA) (Excoffier et al. 1992) under alternative hierarchical arrangements to analyze the population differentiation in Arlequin v3.5 (Excoffier and Lischer 2010). The minimum spanning network cladogram was estimated by TCS v 1.21 (Posada and Crandall 2001) using the parsimony method.

## Results

### Fish collection

From various geographic locations in the ECS, 63 specimens were collected in 2016 and 106 specimens were collected in 2017. Around the edge of the continental shelf in the ECS, a total of 24 and 43 specimens were collected from 15 stations in 2016 and 2017, respectively (Fig. 1; Table 1). The TLs of *S. dumerili* from the ECS ranged between 0.6 and 4.1 cm in 2016 and between 0.4 and 7.2 cm in 2017 (Fig. 2; Table 1). There were significant difference in TLs between 2016 and 2017 of the ECS, but not between northern and southern part of the ECS (Two-way ANOVA, year:  $df=1$ ,  $F=5.531$ ,  $p<0.05$ , location:  $df=1$ ,  $F=2.150$ ,  $p=0.148$ , year  $\times$  location:  $df=1$ ,  $F=0.928$ ,  $p=0.339$ ). Along the western Japanese coast in the ECS, a total of 39 (16.9–29.8 cm in TL) and 59 (11.6–29.6 cm in TL) *S. dumerili* were collected in 2016 and 2017, respectively (Table 1). From the southwestern to northern part of Taiwan, *S. dumerili* was not collected by surface towing of an ORI net in 2017.

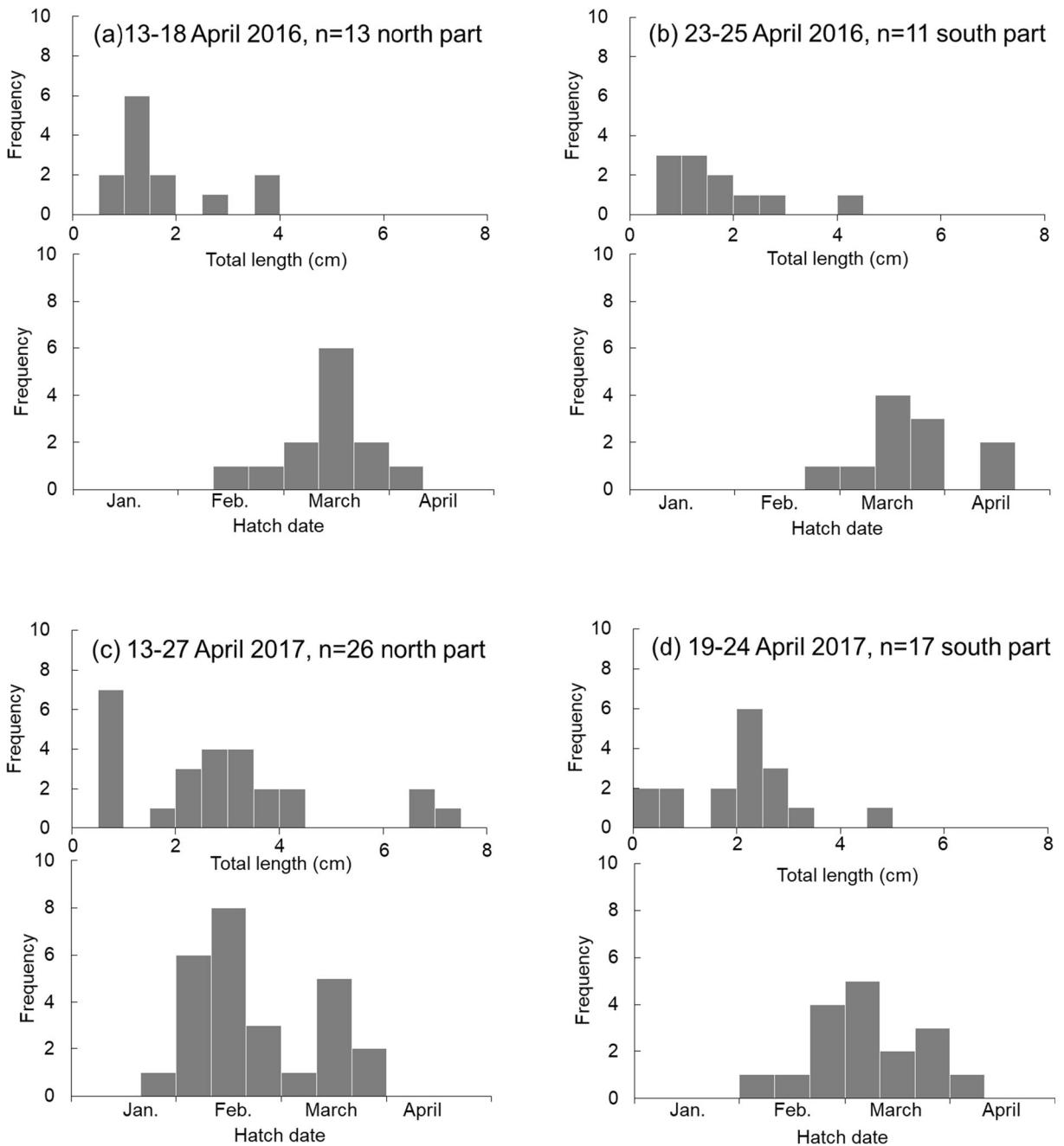
### Age determination

We determined the age of all the specimens both in the year 2016 and the year 2017 from the ECS. The age (days after hatching) of specimens from the ECS ranged between 9 and 62 in 2016 and between 9 and 82 in 2017, respectively (Figs. 2 and 3). We then estimated their

spawning periods from February to April in 2016 and January to April in 2017 (Fig. 2). Larvae collected in 2017 hatched at earlier month than those in 2016, and fish from northern part of the ECS hatched earlier than those of southern part of the ECS (Two-way ANOVA, year:  $df=1$ ,  $F=5.060$ ,  $p<0.05$ , location:  $df=1$ ,  $F=8.520$ ,  $p<0.01$ , year  $\times$  location:  $df=1$ ,  $F=0.376$ ,  $p=0.542$ ). The growth curves between age ( $x_{day}$ , days after hatching) and TL ( $y_{TL}$ , cm) were described by the following equations: ( $n=24$ ,  $r=0.96$ ) for 2016 and ( $n=43$ ,  $r=0.96$ ) for 2017 (Fig. 3). Individuals with different body size and age were dispersedly distributed in the southern and northern part of the ECS, and there was no discernible trend in the distribution of large size and early hatched fish in the northern part of the ECS (Fig. 2).

### Molecular diversity indices

A total 683 bp of mtDNA CR sequences (Supplementary Table 1) were used to characterize the genetic diversity of the western Japanese coast and ECS *S. dumerili* populations. There was no significant difference among sampling years (2016, 2017) or hierarchical geographical locations in the analysis of molecular variance (AMOVA) test (Table 2). Both Slatkin's linearized  $F_{ST}$  and pairwise  $F_{ST}$  calculated from mtDNA CR data revealed values near zero and negative values (data not shown,  $p>0.05$ , ns). The results showed that there was no difference among the four groups in the ECS. With the AMOVA results, in the one-group AMOVA test, the majority of the variation in *S. dumerili* was observed among individuals within populations ( $\Phi_{ST}=-0.00737$ ,  $p>0.001$ , ns). With multiple alternative grouping, there was no significant difference between the ECS and western Japanese coast ( $\Phi_{CT}=0.00098$ ,  $p>0.001$ , ns), and no significant difference between 2016 and 2017 ( $\Phi_{CT}=-0.00066$ ,  $p>0.001$ , ns). Thus we combined the year 2016 and 2017 samples and retained the hierarchical geographical locations for molecular analyses. Genetic variation among the Western Japanese coast and ECS populations revealed very high numbers of haplotypes and high levels of haplotype diversity (Table 2). A total of 128 haplotypes were identified within 156 specimens with an average haplotype diversity of  $0.997 \pm 0.001$ . Haplotype diversity ranged from 0.993 to 1 among populations. The populations of Tsushima Island, Kabashima

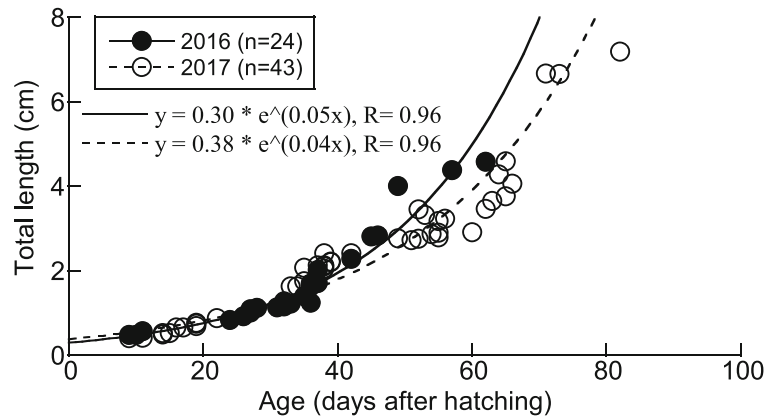


**Fig. 2** Size and hatch dates distribution of *S. dumerili* collected in the northern and southern parts of the East China Sea in 2016 and 2017. Collection dates, locations and sample size are indicated in each histogram

Island, the Nagasaki coast and the North East China Sea had the highest haplotype diversity value ( $Hd = 1$ ), while the South East China Sea displayed the lowest haplotype diversity ( $Hd = 0.993 \pm 0.013$ ), although even that was a relatively high value

(Table 3). These results showed that the mtDNA CR of the *S. dumerili* exhibited high diversity and was less conserved. The average number of nucleotide differences ( $k$ ) and average value of nucleotide diversity were 12.068 and  $0.0177 \pm 0.00069$ , ranging

**Fig. 3** Growth of young-of-year (YOY) *S. dumerili* collected in the East China Sea in 2016 and 2017



from 10.936 to 13.68 and  $0.01602 \pm 0.00105$  to  $0.02006 \pm 0.00126$ , respectively. The southern ECS displayed the highest value of nucleotide diversity ( $\pi = 0.01917$ ) and the Off Kagoshima region had the lowest nucleotide diversity value ( $0.01602 \pm 0.00105$ ). Neutrality indices calculated by Fu's  $F_s$  test were negative in all populations and showed significant differences ( $p < 0.01$ ). These results, like those for haplotype diversity, showed an excess number of alleles, as would be expected from the recent population expansions of YOY *Seriola dumerili* in the Western Japanese coast and ECS, or the genetic hitchhiking effect impacting the YOY *S. dumerili* mtDNA CR region. The minimum spanning network cladogram shows that the alleles

were rarely shared among populations (Fig. 4). Most haplotypes were detected only once and showed a large number of connections between populations.

#### Pairwise genetic difference analysis

For the pairwise comparisons of population genetic differentiation ( $F_{st}$ ), we found there was low genetic differentiation between the ECS and western Japanese coast (Table 4). There was no differentiation between the ECS and most of the western Japanese coast except off Kagoshima. Also, the same results were found that there was no differentiation among Tsushima Island and others except off Kagoshima. Thus, the gene flow between the

**Table 2** Analyses of molecular variance (AMOVA) to detect population differentiation by year and localities grouping test

Source	d.f.	Sum of squares	Variance components	Significance tests (P-value)
Among groups (year 2017 vs. 2016)	1	4.137	-0.04	$0.425 \pm 0.016$
Among populations within group	2	20.5	0.294	$0.275 \pm 0.015$
Within populations	152	912.587	6.044	$0.425 \pm 0.017$
Total	155	937.224	6.033	
Among groups (Japan coast vs. ECS)	1	4.633	-0.029	$0.49 \pm 0.015$
Among populations within group	2	20.004	0.022	$0.339 \pm 0.014$
Within populations	152	912.587	6.044	$0.387 \pm 0.012$
Total	155	937.224	6.037	
Among groups (island vs. coast vs. ECS)	2	0.95	-0.0005	$0.697 \pm 0.013$
Among populations within group	3	1.5	0.00007	$0.446 \pm 0.015$
Within populations	150	74.836	0.498	$0.706 \pm 0.016$
Total	155	77.288	0.498	

There were no significant differences by any of the three different groupings. Statistical significance test:  $P < 0.05$



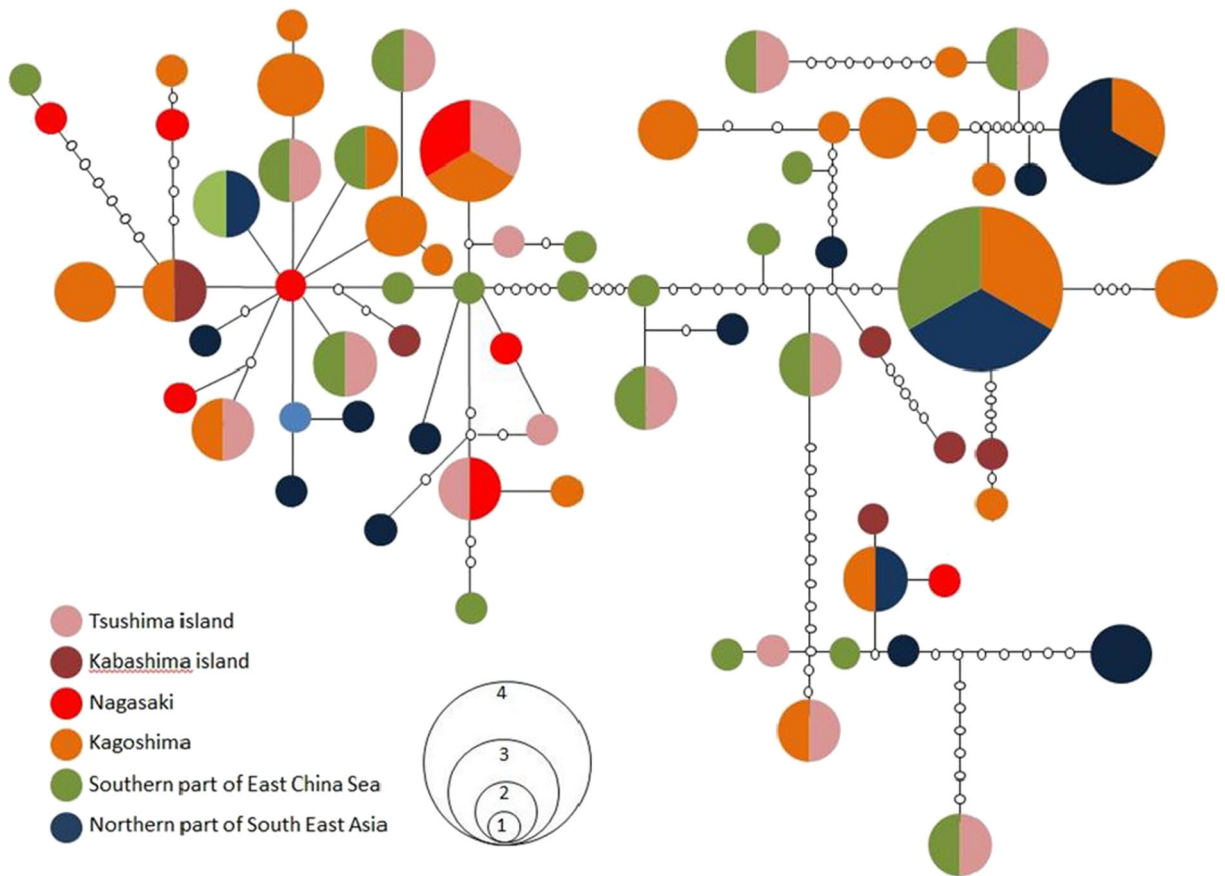
**Table 3** Diversity and neutrality indices of young-of-year (YOY) *Seriola dumerili* in the populations of the Western Japanese coast and East China Sea revealed by mitochondrial DNA control region (D-Loop) sequences

Site	n	h	S	k	Haplotype diversity ± S.D	Nucleotide diversity ± S.D	Fu's Fs test
Tsushima Island	28	28	66	13.114	1 ± 0.010	0.01920 ± 0.00118	-18.404**
Kabashima Island	15	15	50	11.410	1 ± 0.024	0.01671 ± 0.00172	-6.740**
Nagasaki coast	13	13	40	12.321	1 ± 0.030	0.01804 ± 0.00236	-4.868**
Off Kagoshima	41	36	60	10.936	0.994 ± 0.007	0.01602 ± 0.00105	-22.590**
Western Japanese coast	97	84	87	11.758	0.997 ± 0.002	0.01721 ± 0.00069	-89.749**
North East China Sea	34	34	66	11.708	1 ± 0.007	0.01717 ± 0.00108	-27.569**
South East China Sea	25	23	60	13.680	0.993 ± 0.013	0.02006 ± 0.00126	-9.157**
East China Sea	59	56	80	12.629	0.998 ± 0.004	0.01855 ± 0.00091	-51.573**
Total	156	128	98	12.068	0.997 ± 0.001	0.0177 ± 0.00055	-163.216**

A total 683 bp of mtDNA CR sequences were used in the molecular analysis. n: number of sequences; h: number of haplotypes, S: number of polymorphic sites; k: average number of nucleotide differences. Fu's Fs test for statistical significance: \*\* P < 0.01

ECS and western Japanese coast was highly connective. According to the results of the analyses using mtDNA CR sequences, there was no

significant population differentiation and high connectivity among *S. dumerili* samples between the ECS and western Japanese coast.



**Fig. 4** The minimum spanning network cladogram revealed by mtDNA CR haplotype

**Table 4** Pairwise genetic difference ( $F_{st}$  in lower diagonal) and gene flow (Nm in upper diagonal) of *Seriola dumerili* of Western Japanese coast and East China Sea populations from mitochondrial DNA control region

$F_{st} \setminus Nm$	Tsushima island	Kabashima island	Nagasaki coast	Off Kagoshima	NECS	SECS
Tsushima island		$\infty$	$\infty$	513.2	$\infty$	$\infty$
Kabashima island	0		$\infty$	320.3	268.5	$\infty$
Nagasaki coast	-0.00831	0		372.5	265.7	$\infty$
Off Kagoshima	-0.00040	0.00156	0.00134		$\infty$	513.2
NECS	-0.00616	-0.00191	-0.00220	0.00097		$\infty$
SECS	0.00180	0.00186	0.00188	-0.00020	-0.00059	

NECS represented North East China Sea, SECS represented South East China Sea, Nm represented numbers of migrants,  $\infty$  represented highly connectivity. There were no significance differences of p value ( $\alpha = 0.05$ ) among populations differentiation

## Discussion

### Spawning period and ground

In the present study, the spawning period of *S. dumerili* from the ECS was from January to April. Previous studies in other waters also reported that the majority of spawning of *S. dumerili* occurs between winter and summer: from February to April by hatching date analysis off Galveston, Texas in the U.S. (Wells and Rooker 2004), from January to June with peak spawning in April and May in the South Atlantic (Sedberry et al. 2006) and off the Atlantic coast in the Southeastern U.S. (Harris et al. 2007), in winter in the western Atlantic (Fahay 1975) and in June and July in the Mediterranean Sea (Raya and Sabatés 2015). Hasegawa et al. (2017b) showed that spawning of *S. dumerili* around Taiwan occurs from April to June.

In our study, early larvae (<9 days after hatching) were collected, and their distribution and hatch dates postulated that *S. dumerili* larvae hatched around the edge of the continental shelf in the southern ECS and were transported northward in the ECS. Thus, we postulate that one of the spawning grounds of *S. dumerili* is around the edge of the continental shelf in the southern ECS. In the southern U.S., the spawning ground of *S. dumerili* is estimated to be around the shelf-edge reef sites of 50–100 m depth (Sedberry et al. 2006). Sassa et al. (2016) suggested that the spawning ground of Japanese jack mackerel *Trachurus japonicus* was formed in a rather confined area in the southern ECS, because the centers of distribution of the larval *T. japonicus* in the southern ECS did not differ among the 12 years surveyed. However, *S. dumerili* individuals with different body size and age were dispersedly

distributed in the southern and northern parts of the ECS, indicating that the spawning ground of *S. dumerili* is widely formed along the edge of the continental shelf of 50–100 m depth in the southern ECS. In addition, *S. dumerili* was not collected from the southwestern to northwestern part of Taiwan in 2017. There are three possible reasons for this result. One is that the majority of spawning grounds of *S. dumerili* are distributed in the shelf break region of northern Taiwan in the southern ECS. The second is that the dearth of *S. dumerili* was due to a gear bias or an inadequate net-towing speed, which could have disturbed the capture of larvae and juvenile *S. dumerili*. Third, the spawning of *S. dumerili* had finished around Taiwan in April 2017, and the larvae and juveniles were transported northward by current (e.g., the Taiwan Warm Current and Kuroshio Current; Fig. 1). Previous studies reported that larval and juvenile *S. dumerili* were collected around Taiwan (Liu 2001; Chen et al. 2012), and thus *S. dumerili* may also have spawned around Taiwan in 2017.

In the present study, we could not determine the age of the YOY individuals with LTs greater than 10 cm collected on the western Japanese coast. Assuming that *S. dumerili* in the ECS show the same growth rate as those on the western Atlantic coast (Wells and Rooker 2004), *S. dumerili* will grow to 25 cm in SL within about 160 days after hatching. Accordingly, it is estimated that the YOY fish collected from July to September on the western Japanese coast were born in February to April. Thus, the spawning period of *S. dumerili* in the southern ECS and western Japanese coast may be overlapped, indicating transportation of larval and juvenile *S. dumerili* from the southern ECS to western Japanese coast. Synthesizing these results, we conclude that

*S. dumerili* in the ECS is expected to spawn from late winter to early summer and to be transported to the Japanese coast from the southern ECS.

### Genetic variability

By restricting analyses to YOY *S. dumerili*, it is likely that our samples reflected the genetic composition of the spawning population better than using older fish with greater migratory capacity (Graves et al. 1996; Carlsson et al. 2004). The high levels of variation in haplotypes of the mtDNA CR in *S. dumerili* supports our hypothesis that *S. dumerili* in the ECS is one population. This is because the minimum spanning network cladogram tree represented mixed distribution and there was no significant difference among the 4 groups with different geographical locations and years—i.e., the southern ECS and the western Japanese coast along the ECS in 2016 and 2017. In the present study, however, high haplotype diversities were observed and individuals from different locations shared several haplotypes with higher frequency, while the otolith analyses suggested that the spawning ground of *S. dumerili* in the ECS may be dispersedly formed. From these results, there are two interpretations regarding the variations of the mtDNA CR of *S. dumerili* in the ECS.

First, *S. dumerili* in the ECS is one population and variations of the mtDNA CR may result from significant levels of gene flow and/or transportation of individuals. In marine organisms, a pelagic larval stage increases the opportunities for long-distance dispersal and is often associated with little genetic differentiation over large geographical distances (Riginos and Victor 2001). For instance, marine fish species which have no or short pelagic larval phases show distinct regional genetic differentiation (Riginos and Victor 2001; Bernardi and Vagelli 2004). Based on our estimation, the larval phase of *S. dumerili* may be at least 30 days in the wild (Fig. 3), because *S. dumerili* reaches the juvenile stage at 1.1 cm in SL under rearing conditions (Tachihara et al. 1993). In addition, juveniles of *S. dumerili* of 1.7–29.7 cm in SL associate with floating objects such as drifting seaweeds (Badalamenti et al. 1995; Yamasaki et al. 2014; Hasegawa et al. 2017a). Since drifting seaweeds are passively transported by surface current (Komatsu et al. 2014), *S. dumerili* may also be passively dispersed even in the juvenile stage. Such a long passive dispersal period would enable *S. dumerili* to disperse over a geographically wide range, resulting in gene flow

among geographically distant areas. Larval transportation by ocean currents is a key factor in the gene flow between geographically distant areas. For example, it has been confirmed that the Notothenioidei fish in the southern Scotia Arc, Antarctica showed low-population differentiation and high gene flow from microsatellites and mtDNA analyses (Damerou et al. 2012). As for the Japanese eel *Anguilla japonica*, no significant genetic differentiations were observed between specimens collected in East Asia by microsatellite DNA analysis (Han et al. 2010). In the ECS, the Kuroshio Current is assumed to be strongly related to the dispersal and genetic variability of *S. dumerili* (Fig. 1), since the Kuroshio Current affects the transportation of fish eggs, larvae and juveniles to the Japanese coast (e.g., Sassa et al. 2008; Sassa and Tsukamoto 2010). Larvae and juveniles of *S. dumerili* hatched in the southern ECS may also be transported to the Japanese coast by the Kuroshio Current (Fig. 1), as presumed from the results of otolith analysis in the present study. Additionally, rearing experiments have revealed that the triggering factors for spawning of *S. quinqueradiata* (Mushiake et al. 1998) and *S. dumerili* (Hamada and Soyano 2009) are an increase in water temperature and the occurrence of a long photoperiod. Since the spawning ground of *S. quinqueradiata* may shift northward during the spawning season in the ECS (Yamamoto et al. 2007), similar shifts of spawning ground are expected in the congeneric species *S. dumerili*. Thus, adults of *S. dumerili* in the ECS may spawn in order with the northward shifting of optimum water temperature in the southern ECS. And larvae and juveniles would be mixed during transportation by the Kuroshio Current and the Tsushima Warm Current. This transportation system and long passive dispersal period of larvae may enhance the gene flow of *S. dumerili*, resulting in high haplotype diversity and no geographical genetic variability in the ECS.

Second, variations of the mtDNA CR of *S. dumerili* may result from multiple subpopulations in several regions in the ECS, because *S. dumerili* frequently concentrate around reefs, rock outcrops and wrecks (Manooch and Potts 1997). Therefore, *S. dumerili* is not assumed to migrate a greater distance compared to congeneric *S. quinqueradiata*, which shows extensive spawning migration (Yamamoto et al. 2007). If this is the case, high haplotype diversities occurred due to the difference of spawning timing and dispersal during the transportation. However, the ocean current system in the

ECS may prevent the formation of subpopulations in the different locations in the ECS, while there is little information on the migration pattern of adult *S. dumerili* in the ECS. Further, previous studies suggested the existence of two subpopulations of *S. dumerili* in the SCS and Japanese coast (Nugroho et al. 2000; Araki et al. 2018). Therefore, it is likely that variations of the mtDNA CR result from significant levels of gene flow and/or transportation of individuals.

#### Perspectives and management of *S. dumerili* in the ECS

In 2014, the most produced aquaculture *Seriola* sp. in Japan was *S. quinqueradiata* at 107,059 tons, followed by *S. dumerili* at 38,770 tons (Sicuro and Luzzana 2016), and the production of *S. dumerili* continues to increase. The aquaculture seedlings of *S. dumerili* are mainly wild-caught juveniles from Japan and from the SCS (Nakada 2008), and *S. dumerili* in these two waters are recognized as genetically different populations (Nugroho et al. 2000; Araki et al. 2018). Our results indicate that the *S. dumerili* in Japanese waters are originated from the ECS, and that they may be spawned around Taiwanese waters, southern ECS. The catch of juvenile *S. quinqueradiata* as aquaculture seedlings is strictly managed by the Japanese government both in terms of the period and amount of the catch, and this fishery management successfully led to a high production of aquaculture and stable catch of wild yellowtail (Nakada 2008). However, there are no strict fishery regulations for *S. dumerili* juveniles either in Japan or Taiwan. Considering the increasing demand for *S. dumerili* seedlings in Japan, it is recommended that stock assessment and fishing regulations be developed as for yellowtail. Since the main spawning ground of *S. dumerili* in the ECS is assumed to be around Taiwanese waters, it will be important to promote international cooperation between Japan and Taiwan, who share the resource of *S. dumerili*, for the fishery management of this species, and for sustainable fisheries and aquaculture in general.

In conclusion, our results imply that *S. dumerili* in the ECS is composed of one population, probably due to physical dispersion and ecological features in the early life history of *S. dumerili*: spawning in an unconfined area around the shelf break region in the southern ECS from late winter to early summer, followed by transport of the larvae and juveniles to the Japanese coast by the Kuroshio Current. Since our study only examined

differences in mtDNA with small sample size, it is necessary to investigate the genetic variation of *S. dumerili* using more DNA markers with higher variability (such as microsatellite DNAs) than the mtDNA CR over wider geographic scales and with larger sample sizes. Further, there is little information on the spawning ecology and migration pattern of *S. dumerili* in the ECS. Biologging of spawning adults together with examinations of gonadal development should be conducted in order to reveal the spawning ecology and migration pattern of *S. dumerili* in the ECS. This information may facilitate understanding of the genetic population structure of *S. dumerili* in the ECS.

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