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Population Structure and Historical Demography of the Spotted Mackerel (*Scomber australasicus*) off Taiwan Inferred from Mitochondrial Control Region Sequencing

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Tzong-Der Tzeng (2007) Population structure and historical demography of the spotted mackerel (*Scomber australasicus*) off Taiwan inferred from mitochondrial control region sequencing. *Zoological Studies* **46**(6): 656-663. The strong debate as to whether or not the spotted mackerel (*Scomber australasicus*) off Taiwan is genetically structured continues. Sequence analyses of the complete mitochondrial DNA control region (886 bp in length) were conducted to elucidate the population structure and historical demography of spotted mackerel off Taiwan. In total, 157 individuals were separately collected from the East China Sea (ECS), waters off Ilan (ILAN, northeastern Taiwan), Taitung (TT, southeastern Taiwan), and Linyan (LY, southern Taiwan), and the South China Sea (SCS), and 132 haplotypes were obtained. The haplotype diversity (*h*) was high for all samples (99.6%), with values from 99.1% (ECS) to 99.8% (SCS). Nucleotide diversity (π) was low for all samples (0.70%), with values from 0.61% (LY) to 0.75% (ILAN). A median-joining network of 132 haplotypes revealed no significant phylogeographic structure. Analysis of molecular variance (AMOVA) and spatial analysis of molecular variance (SAMOVA) indicated no significant heterogeneity. F_{ST} values indicated no significant difference in each pairwise combination of these 5 sampled areas except the one between the ECS and SCS samples. These results suggest that spotted mackerel off Taiwan belong to the single gene pool. Both mismatched distribution analysis and neutrality tests suggested that spotted mackerel in these waters have experienced population expansion since the late Pleistocene (approximately between 46,399 and 8,980 yr ago).
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Key words: Mitochondrial control region, *Scomber australasicus*, Population structure, Population expansion.

Information on the population structure is important for the management of commercial marine fishes (Utter 1991). Marine organisms frequently reveal low levels of genetic differentiation over large geographic scales (Grant and Bowen 1998, Avise 2000). Higher dispersal potentials during planktonic egg, larval, or adult history stages coupled with the lack of physical barriers to movement seem to greatly facilitate extensive gene flow among populations of marine organisms (Hewitt 2000). However, there is growing evidence that widespread marine organisms are more genetically structured than expected (Palumbi 1997, Benzie 1999, Briggs 1999). Thus, there may be limits to the actual dispersal of marine organisms with high dispersal potential (Benzie and Williams 1997). These limits vary widely with species, habitats, local ocean conditions, or historical events, and they may produce sufficient chances for genetic distinction (Palumbi 1994) such as that seen in coral (Benzie et al. 1995, Yu et al. 1999), sea urchins (Palumbi et al. 1997), and false clownfish (Nelson et al. 2000).

The present population genetic structure of a species may be fully interpreted if one considers the influence of historical events and the complex interactions of biology, geography, and climatic shifts (Hewitt 2000). Climatic shifts can create great changes in species' geographical distributions and abundances, which can be expected to

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have genetic consequences. DNA technology provides suitable markers to examine the genetic effects of such changes (Avise 2000, Hewitt 2000). It is known that during late Quaternary glacial cycles, there were drastic changes in the areal extents and configurations of marginal seas of the western Pacific (Wang 1999). For example, during the Last Glacial Maximum (about 20,000 yr ago), when the sea level was at its lowest at about 130 m below the present sea level, an extensive area of the continental shelf of the East China Sea (ECS) was exposed.

Spotted mackerel (*Scomber australasicus*) is a pelagic fish that is restricted to the Pacific Ocean, southeastern Indian Ocean, and Red Sea. In the western Pacific Ocean, this species is distributed mainly along the continental shelf of the ECS, extending northward to the Pacific coast of Japan and southward to the South China Sea (SCS), Australia, and New Zealand, but has been seldom found in the Taiwan Strait (Tsujita and Kondo 1957, Tzeng 1988). Spotted mackerel populations from the Southwest Pacific (Australian and New Zealand) are genetically distinct from Northwest Pacific populations (around Japan) (Scoles et al. 1998). Tagging experiment indicated that the spotted mackerel in the ECS and the Pacific coast of Japan belong to the same population (Chang and Wu 1977a). However, the debate as to whether or not this species off Taiwan is genetically structured continues. Various data have been used to examine the population structure of spotted mackerel off Taiwan, but the debate has still not been resolved. Analyses of morphological characters (Chang and Chen 1976, Tzeng and Yeh 2002, Tzeng 2004), catch data (Chang and Wu 1977b), and life parameters (Ku and Tzeng 1985) indicated there are 2 different stocks, but catch data (Tzeng 1988) and isoenzymes (Lin 1998) showed that all spotted mackerels off Taiwan are of the same stock.

Mitochondrial (mt)DNA has many attributes that make it particularly suitable for population genetic studies, including its rapid rate of evolution, lack of recombination, and maternal inheritance (Hoelzel et al. 1991). Since different regions of mtDNA evolve at different rates, certain regions of mtDNA have been targeted for different types of studies. Since its control region has been shown to be the most variable region in both vertebrates and invertebrates, this region is an ideal marker for characterizing geographical patterns of genetic variation within and between populations (Simon 1991). Mitochondrial control region sequence data have proven to possess adequate levels of variation in mackerels of the genus *Scomber* (Scoles et al. 1998, Nesbo et al. 2000, Zardoya et al. 2004). The objective of this paper was to examine variations in mtDNA control region sequences to elucidate the population structure and historical demography of spotted mackerel off Taiwan.

MATERIALS AND METHODS

Sampling

In total,157 individuals were collected from the ECS, waters off ILAN, TT, and LY, and the SCS during Feb. and May 2003 (Fig. 1, Table 1). Specimens were iced or frozen immediately after capture and later kept at -75°C until DNA extraction.

DNA extraction, amplification, and sequencing

Total DNA was extracted from muscle tissue using a standard DNA proteinase *K* digestion/phenol-chloroform extraction procedure. The complete control region was amplified using the

Table 1. Sample code, sampling locality, sample size, gene diversity (*h*), and nucleotide diversity (π) with their standard deviation (S.D.) in 5 spotted mackerel samples off Taiwan

Sample code	Locality	Sample size	*h* ± S.D.	π ± S.D.
ECS	East China Sea	33	99.1% ± 1.1%	0.73% ± 0.05%
ILAN	Ilan, northeastern Taiwan	31	99.4% ± 1.1%	0.75% ± 0.05%
TT	Taitung, southeastern Taiwan	31	99.4% ± 1.1%	0.68% ± 0.06%
LY	Linyan, southern Taiwan	31	99.6% ± 0.9%	0.61% ± 0.06%
SCS	South China Sea	31	99.8% ± 0.9%	0.69% ± 0.06%
Total		157	99.6% ± 0.2%	0.70% ± 0.03%

primers L-pro (5'-TACCCCAAACTCCCAAAGCTA-3') and H-12Sr (5'-GCGGATACTTGCATGTGTA-3'), which bind to the $tRNA^{pro}$ and 12Sr RNA genes, respectively. Polymerase chain reaction (PCR) was conducted according to a standard protocol (Kocher et al. 1989). Thermal cycling was performed in a GeneAmp 2400 thermal cycler (Perkin-Elmer, Norwalk, CT, USA) and PCR conditions consisted of 39 cycles of denaturation at 95°C for 50 s, annealing at 50°C for 1 min, and extension at 72°C for 1.5 min. An initial denaturation step at 95°C for 5 min and a final extension holding at 72°C for 10 min were included in the first and last cycles, respectively. Amplified DNA was separated through electrophoresis on 1.5% agarose gels and purified with the Gene Clean II kit (BIO101, Vista, CA, USA). The sequencing reactions of the PCR products were analyzed using an Applied Biosystems Prism 377 automated sequencer (Applied Biosystems, Inc.; Foster City, CA, USA).

Sequence analyses

DNA sequences were aligned with the sequence of *Scomber scombrus* (GenBank accession no.: AB120717) using the PILEUP program in GCG (Genetics Computer Group, vers. 7.0;

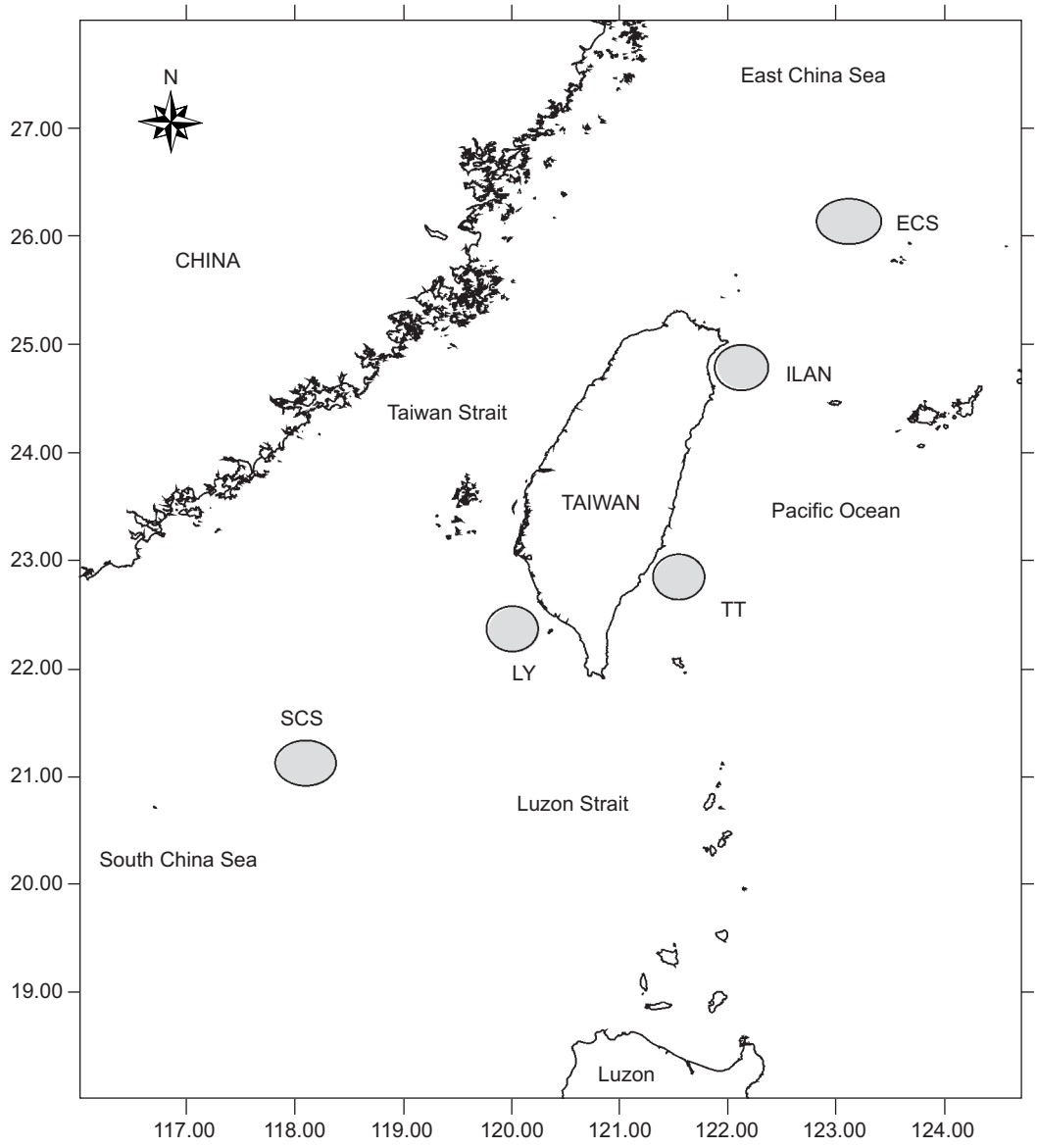

Fig. 1. Sampling localities of spotted mackerel off Taiwan.

Devereux et al. 1991). The nucleotide composition and numbers of variable sites were assessed with MEGA3 (Kumar et al. 2004). The gene diversity (*h*) and the nucleotide diversity (π) (Nei 1987) in each sample were calculated using DnaSP vers. 4.10 (Rozas et al. 2003). A haplotype network was constructed using the median-joining method in Network vers. 4.2.0.1(Bandelt et al. 1999).

To examine whether two of the sampling areas genetically differed from each other, the pairwise F_{ST} statistic (Wright 1965) between the 5 sampled areas was determined using the program ProSeq (Filatov 2002). The statistical significance of the estimate was tested through 10,000 permutations.

It was previously (Chang and Chen 1976, Chang and Wu 1977b, Ku and Tzeng 1985, Tzeng and Yeh 2002, Tzeng 2004) suggested that spotted mackerel off Taiwan are divided into 2 separate groups. To determine the validity of this conclusion, possible combinations of 2 groups among these 5 sampled areas were examined by analysis of molecular variance (AMOVA) as implemented in ARLEQUIN vers. 3.01 (Excoffier et al. 2005), with 1023 permutations of sequences among samples for evaluation of Φ statistics.

To investigate the spatial structure of spotted mackerel, the program SAMOVA vers. 1.0 (spatial analysis of molecular variance; Dupanloup et al. 2002) was also used. This maximizes the proportion of the total genetic variation between groups of populations, without pre-defining the populations.

To check for deviations from neutrality, Tajima's *D* statistical test (Tajima 1989) and Fu and Li's *D* statistical test (Fu and Li 1993) were carried out using DnaSP. Historical demographic expansion was investigated by examining the frequency distributions of pair-wise differences between overall sequences (mismatched distribution) with ARLEQUIN. Rough dates of population expansion were estimated with the formula $T = \tau / 2\mu$ (Rogers and Harpending 1992), where *T* is the time since expansion, τ is the expansion time, and 2μ is μ (the mutation rate) x generation time x number of bases sequenced.

RESULTS

The 866 bp of the mtDNA control region was used for analyses. As with the control region of other fish, the relative frequencies of the 5 nucleotides differed; adenine was the most prevalent (33.68%), followed by thymine (28.62%), cytosine (22.66%), and guanine (15.03%). In total, 93 variable sites, including 45 singletons and 48 parsimoniously informative sites, were observed. In total, 72 transitions and 30 transversions were scored. The haplotype diversity (*h*) was high for all samples (99.6% ± 0.2%), with values from 99.1% ± 1.1% (ECS) to 99.8% ± 0.9 % (SCS). Nucleotide diversity (π) was low for all samples (0.70% ± 0.03 %), with values from 0.61% ± 0.06 % (LY) to 0.75% ± 0.05 % (ILAN) (Table 1).

Among the 157 specimens studied, 132 haplotypes were found and 117 were unique. The median-joining network for the 132 haplotypes appeared star-like and showed no notable haplotype clustering (Fig. 2). This suggests that spotted mackerel probably underwent a recent population expansion.

F_{ST} values are shown in table 2. The range of F_{ST} values was from 0.0185 (ECS-SCS) to 0.0000. F_{ST} values indicated no significant difference ($p > 0.05$) in each pairwise combination of these 5 sampled areas except the one between the ECS and SCS.

Results of AMOVA are shown in table 3. AMOVA of the 5 sampled areas yielded a Φ_{ST} value of 0.0051, indicating no significant heterogeneity between any pairwise combination of these 5 sampled areas ($p > 0.05$). The hypothesis of 2 spotted mackerel populations was also tested

Table 2. F_{ST} values between 5 spotted mackerel samples off Taiwan. Abbreviations for sampling locations are defined in table 1

	ECS	ILAN	TT	LY	SCS
ILAN	0 ns				
TT	0.0132 ns	0 ns			
LY	0.0126 ns	0.0063 ns	0 ns		
SCS	0.0185*	0.0004 ns	0.0048 ns	0.0007 ns	

*Significant at $p < 0.05$; ns, not significant.

by AMOVA, revealing that no Φ_{CT} values in any groupings were significant.

Results of SAMOVA are shown in table 4. The SAMOVA analyses which assumed different numbers of groups (2, 3, and 4 groups) of populations showed no genetic differentiation among groups.

Tajima's *D* and Fu and Li's *D* statistical tests were performed to determine departures from neutrality. Significant negative values were obtained for both of these tests (Tajima's $D = -2.1098$, $p < 0.05$; Fu and Li's $D = -4.8363$, $p < 0.02$). Therefore, the hypothesis of selective neutrality was rejected.

The mismatch analysis (with a mean of 6.025 and variance of 6.212) produced a unimodal distribution of pairwise differences (Fig. 3) consistent with a sudden population expansion model. τ, the estimated time since population expansion, was 5.786 /2 μ generations (95% confidence interval (CI), 4.309-6.853). There are very large discrepancies in estimations of divergence rates for the control region of teleosts. In the absence of a specific calibrated mutation rate for the control region of spotted mackerel, 2 very distinct rates were assumed: 3.6% (Domingues et al. 2005) and 18.6% (Donaldson and Wilson 1999) divergence per site per million yr. As female and male spotted mackerel mature at different sizes and ages (around 3 and 5 yr, respectively, Tzeng 1988) a generation time of 4 yr was used. In waters adjacent to Taiwan, the spotted mackerel population expansion was estimated to have taken place approximately 46,399 (95% CI, 34,554-54,954) to 8980 (95% CI, 6687-10,636) yr ago.

DISCUSSION

The mitochondrial control region sequences revealed a high level of haplotypic diversity (0.996) and a low level of nucleotide diversity (0.007) that were similar to those found in Australia ($h = 0.86$, $\pi = 0.007$) and New Zealand ($h = 0.85$, $\pi = 0.007$), and which were higher than those found in the Red Sea ($h = 0.95$, $\pi = 0.004$), Japan ($h = 0.81$, $\pi = 0.003$), and Mexico ($h = 0.59$, $\pi = 0.001$) (Scoles et al. 1998). It has been proposed

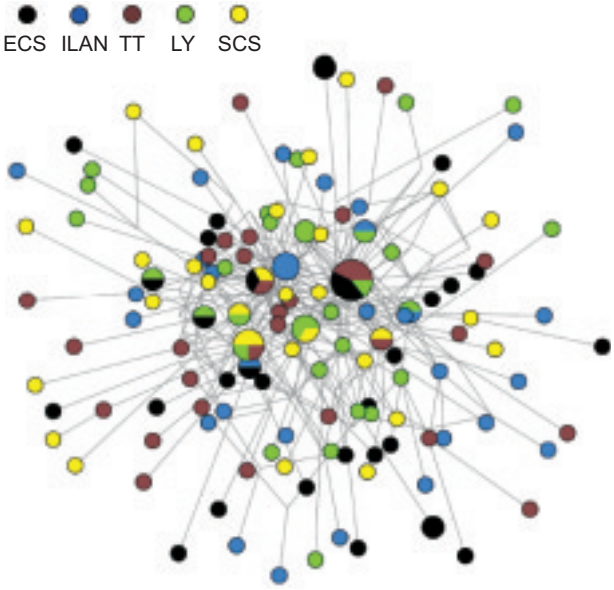

Fig. 2. Haplotype network of spotted mackerel off Taiwan. Different symbols represent different sampling areas. Small symbols indicate 1 individual, while large ones indicate more than 1 individual.

Table 3. Results of AMOVA. Abbreviations for sampling locations are defined in table 1

Groupings	Variance (%)	Φ-statistics	*p* value
One group	Among sampling locations		
1 Group 1{ECS, ILAN, TT, LY, SCS}	0.0153	$\Phi_{ST} = 0.0051$	> 0.05
	Among groups		
Two groups			
1 Group 1 {ECS, ILAN, TT, LY}	0.0090	$\Phi_{CT} = 0.0029$	> 0.05
Group 2 {SCS}			
2 Group 1 {ECS, ILAN, TT}	0.0137	$\Phi_{CT} = 0.0045$	> 0.05
Group 2 {SCS, LY}			
3 Group 1 {ECS, ILAN}	0.0245	$\Phi_{CT} = 0.0081$	> 0.05
Group 2 {SCS, LY, TT}			
4 Group 1 {ECS}	0.0339	$\Phi_{CT} = 0.0112$	> 0.05
Group 2 {SCS, LY, TT, ILAN}			

that marine fishes can be classified into 4 categories based on different combinations of small and large values for haplotype diversity (*h*) and nucleotide diversity (π) of the mtDNA sequences for interpreting different scenarios of their population history (Grant and Bowen 1998). They indicated that fish with high *h* and low π probably underwent population expansion after a period of low effective population size. In contrast, the high haplotype diversity (0.996) and lower nucleotide diversity (0.007) suggest that spotted mackerel in the studied waters underwent population expansion. The expansion of spotted mackerel was also supported by significant negative values of Tajima's *D* and Fu and Li's *D*, the median-joining network of haplotypes (Fig. 2), and the mismatch analysis (Fig. 3).

Past geological and climatic events have undoubtedly played a major role in the population expansion of spotted mackerel off Taiwan. Sea levels were 130-150 m lower than the present level in the ECS and 100-120 m lower in the SCS during the Last Glacial Maximum. Consequently, the entire Yellow Sea and Taiwan Strait were exposed, and the ECS was reduced to an elongated trough (Wang and Sun 1994). The disappearance of habitat restricted marine species to relatively limited areas and caused mixing among populations, thus reducing the genetic variation among populations (Benzie and Williams 1997). Estimates of the time since population expansion of spotted mackerel in the study areas (6687-10,636 to 34,545-54,954 yr before the present) suggest consistency with a sea level rise since the late Pleistocene (1,600,000-10,000 yr ago).

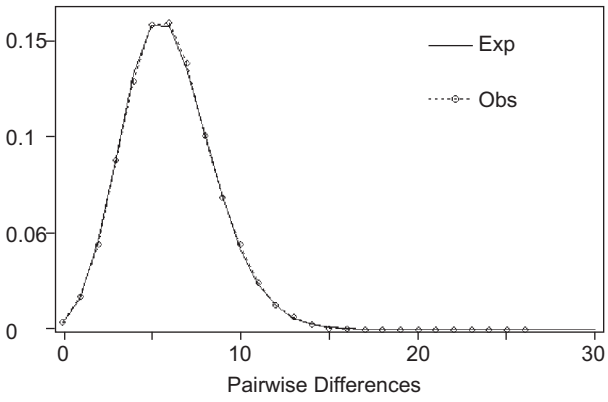

Fig. 3. Mismatched distribution constructed using pairwise differences among complete control region sequences of spotted mackerel off Taiwan.

Although the F_{ST} value between the ECS and SCS samples indicated a significant genetic difference, analyses of the other pairwise combinations of these 5 sampled locations were not significant (Table 2). Moreover, results of the AMOVA and SAMOVA detected no significant differences at all hierarchical levels (Tables 3, 4), indicating that no significant population genetic structure exists in the study areas. Although most spotted mackerel had different mtDNA haplotypes, the same mtDNA haplotypes were observed in the different sampled areas (Fig. 2), and this also provides no support for the existence of spatial genetic heterogeneity in spotted mackerel off Taiwan. The age composition of this species in the northern SCS was 3-5 yr old, but that in the ECS was 1-4 yr old, and no dominant year class was found (Tzeng 1988). Therefore, the genetic difference between ECS and SCS samples may have been derived from spawning aggregations.

Table 4. Results of SAMOVA. Abbreviations for sampling locations are defined in table 1

Number of *p* value groups (*k*)	Structure tested	Variance among groups (%)	Φ-statistics	*p* value
2	Group 1 {ECS} Group 2 {SCS, LY, TT, ILAN}	0.0339	Φ_{CT} = 0.0112	> 0.05
3	Group 1 {LY, SCS} Group 2 {ECS} Group 3 {ILAN, TT}	0.0277	Φ_{CT} = 0.0092	> 0.05
4	Group 1 {ECS} Group 2 {SCS} Group 3 {TT, LY} Group 4 {ILAN}	0.0371	Φ_{CT} = 0.0123	> 0.05

The most likely groupings of populations are presented assuming the presence of 2, 3, or 4 groups.

As the warm and highly saline Kuroshio Current reaches the steep east-west continental shelf break of the ECS, it turns eastwards and then northeastwards, and a minor part of the Kuroshio runs over the shelf of the ECS (Hsueh et al. 1992). The cold and low-saline China Coastal Current flows from north to south and spreads to the north of Taiwan (Wu 1982). These 2 currents cause spotted mackerel migrating southward from the ECS to never enter the Taiwan Strait but concentrate in waters northeast of Taiwan. However, the path of the Kuroshio from east of Taiwan to the southern part of the ECS moves seaward in the spring and summer, and shoreward in the fall and winter (Sun 1987). This seasonal shift in the Kuroshio may enable some individuals of spotted mackerel to migrate southward along the east coast of Taiwan to southern Taiwan and the northern SCS. This local current condition supplies some evidence to explain why spotted mackerel in the East China Sea, in the coastal waters of Taiwan, and the northern South China Sea are of the same stock.

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