

Littoral Water in Hong Kong as a Potential Transient Habitat for Juveniles of a Temperate Deepwater Gnomefish, *Scombrops boops* (Acropomatiformes: Scombrotidae)

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A total of 40 juveniles belonging to a temperate deepwater gnomefish species, *Scombrops boops*, were sampled from littoral habitats (2–5 m depth) of eastern Hong Kong waters in April and May 2017 and March 2019. The presence of gnomefish juveniles in subtropical southern China is reported for the first time at a record low latitude of 22°11'–22°21'N. The specimens were identified based on the *COI* gene sequence. The genetic composition between Japan and Hong Kong gnomefish populations were compared by sequencing the mitochondrial *Cytb* gene, which showed no genetic differentiation. The juveniles ranged from 3.5–10.1 cm ($n = 40$) in total length, with 35 individuals caught from *Sargassum* beds and five from rocky reefs. Our findings highlighted that the littoral habitats in Hong Kong waters, in particular the seasonal *Sargassum* beds, are important for small juveniles of *S. boops*.

Key words: Genetic homogeneity, Northwest Pacific, Nursery habitat, *Sargassum* beds, Subtropical.

BACKGROUND

The family Scombrotidae used to belong to the order Perciformes (Nelson et al. 2016), but a recent restructuring moved it to a new order, Acropomatiformes (Ghedotti et al. 2018). *Scombrops* Temminck & Schlegel, 1845 is the only genus in the family, and three members have been reported in the northwestern (NW) Pacific (Oyama et al. 2019), including *Scombrops boops* (Houttuyn, 1782), *Scombrops gilberti* (Jordan &

Snyder, 1901) and an undescribed species *Scombrops* sp. (Mochizuki et al. 2017).

Scombrops boops is generally a temperate benthopelagic species distributed from the coastal area of Hokkaido (Japan) to the East China Sea (China) at which the southernmost existing record was located (22°49'N, as shown in Fig. 1a) (Shao 1987; Hayashi 2002; GBIF 2020; Froese and Pauly 2020). A couple of studies have also reported that *S. gilberti* and *Scombrops* sp. are closely related to *S. boops* genetically, and are

found in the deep water off the Izu Peninsula to the Izu Islands and around the Ryukyu Islands in Japan, respectively (Itoi et al. 2010 2018; Oyama et al. 2019).

As a commercially important species in Japan, the distribution, ecology and population genetics of *S. boops* have been extensively studied (Itoi et al. 2010). The species produces pelagic eggs in the coastal water

of Japan during its spawning season from October to March (Mochizuki 1977). The eggs hatch after three days under controlled conditions in captivity (Yamada 1995). Juveniles of *S. boops* settle and grow in coastal water habitats of Japan and start migrating to the rocky bottom of the continental shelf break (200–700 m depth) after reaching sexual maturation at ~38 cm

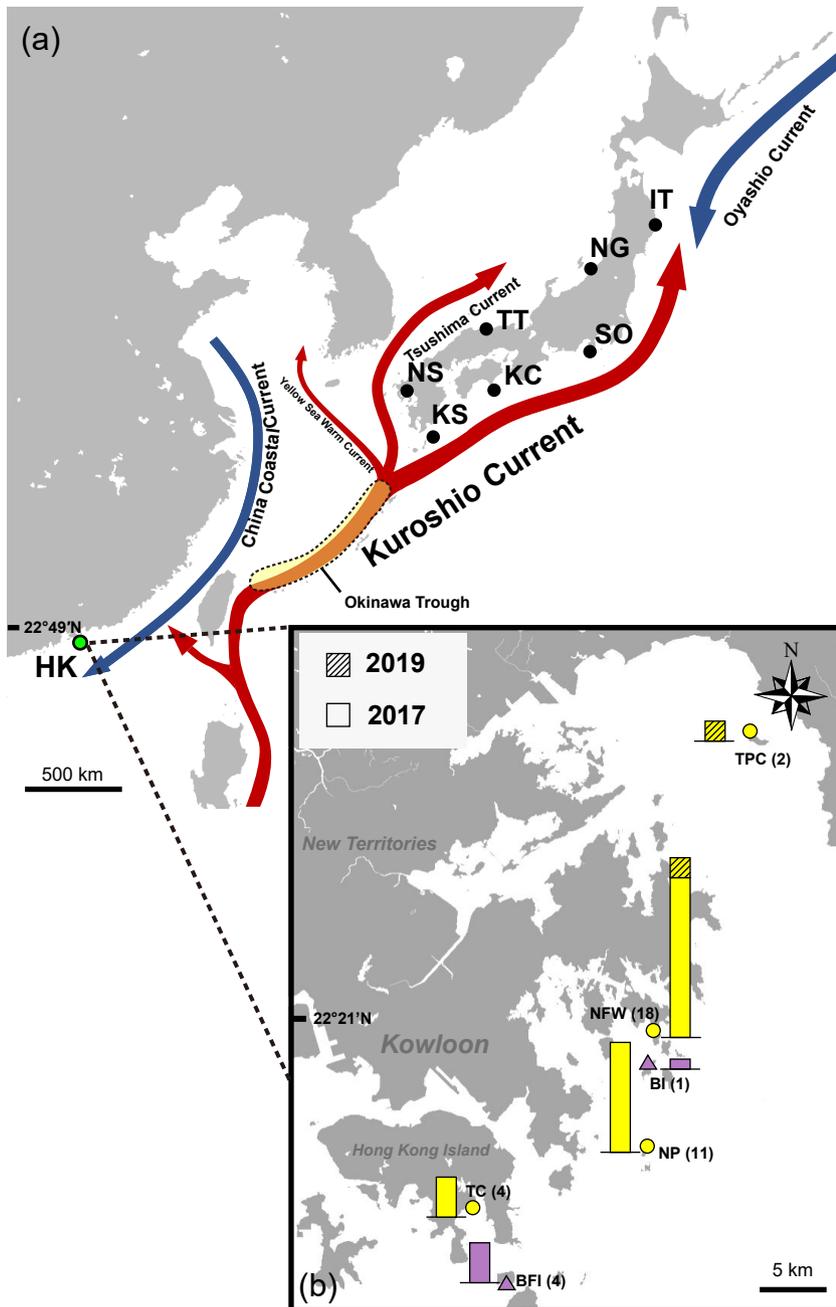


Fig. 1. (a) A map indicating winter ocean currents in Northwest Pacific and geographical location of Hong Kong and sampling sites in Noguchi et al. (2012). HK: Hong Kong; IT: Iwate; KC: Kochi; KS: Kagoshima; NG: Niigata; NS: Nagasaki; SO: Shizuoka; TT: Tottori. (b) The six sampling sites in Hong Kong waters and number of *Scombrops boops* specimens from each site. BFI: Beaufort Island (22°11'N, 114°15'E); BI: Bluff Island (22°19'N, 114°21'E); NFW: Nam Fung Wan (22°21'N, 114°21'E); NP: Ninepins North (22°16'N, 114°21'E); TC: Turtle Cove (22°14'N, 114°13'E); TPC: Tung Ping Chau (22°33'N, 114°25'N). Sites with *Sargassum* habitat indicated by yellow circle, and with rocky reef indicated by purple triangle.

in total length (TL) (Mochizuki 1977 1997; Hayashi 2002; Takai et al. 2014). *Scombrops boops* around the Japanese Archipelago may constitute a single population based on a genetic study. The two dominant northward coastal currents, *i.e.*, Kuroshio Current and the Tsushima Current, may transport the planktonic larvae from the south and facilitate the mixing of geographic populations around the Japanese Archipelago (Noguchi et al. 2012).

The occurrence of *S. boops* juveniles beyond Japanese waters is however largely unknown. This study presents the first records of *S. boops* in Hong Kong waters, which is also the new southernmost occurrence of this species in the NW Pacific region, with only juvenile specimens. This is also the first report of juvenile *S. boops* occurring in the littoral habitats of the South China Sea region. The potential nursery role of the coastal habitats, particularly the seasonal *Sargassum* beds, to this deepwater species was also discussed.

MATERIALS AND METHODS

Sampling and measurement

A total of 40 specimens, initially morphologically identified as *Scombrops* species, were received during the dry-wet transitional season, *i.e.*, April and May 2017 and March 2019, in the eastern waters of Hong Kong based on seasonal surveys. Thirty-six specimens were obtained from five locations in 2017; 31 (~86%) were collected from *Sargassum* beds (*i.e.*, TC, NP and NFW) and five (~14%) were collected from rocky habitat without any *Sargassum* spp. (*i.e.*, BI and BFI) (Fig. 1b). Four specimens were collected in 2019 from two *Sargassum* locations (*i.e.*, NFW and TPC) (Fig. 1b). The fishing gear used was in-shore purse seining (4–6 mm mesh size; top length: 15 m, bottom length: 9.8 m × net depth: 2.5 m) operated by a chartered P4 fishing boat within littoral habitats. The specimens were kept at -20°C in the State Key Laboratory of Marine Pollution (SKLMP) for measurement and genetic analysis. Measurements of fish body length (TL; standard length, SL) and body weight were taken to the nearest 0.1 cm and 0.1 g, respectively.

DNA extraction and polymerase chain reaction (PCR)

Genomic DNA of the skeletal muscle from each specimen was extracted using Chelex® 100 Resin following the manual's instruction (Bio-Rad Laboratories, Inc., United States). Polymerase chain reaction (PCR) was conducted in a total volume of

25 µl, containing 20 ng DNA template, 1 unit of Ex Taq DNA polymerase (Takara), 0.5 µM reverse and forward primers, 0.2 mM mixed dNTPs, 1.5 mM MgCl₂, and 1 × PCR buffer (pH 8.4, 200 mM Tris-HCl and 500 mM KCl). Partial sequences of cytochrome *c* oxidase subunit I (*COI*) gene were amplified using Fish F1 (forward 5'-TCAACCAACCACAAAGA CATTGGCAC-3') and Fish R1 (reverse: 5'-TAGA CTTCTGGGTGGCCAAAGAATCA-3') (Ward et al. 2005). Amplifications of cytochrome *b* (*Cytb*) sequences were performed with L14369tuna-Glu (forward: 5'-ACCACCGTTGTTATTCAACTA-3') and R-DloopY2 (reverse: 5'-CATTAACTTATGCAAGCGT C-3') (Noguchi et al. 2012). PCR cycling conditions for *Cytb* and *COI* are as follow: 95°C for 2 min; 39 cycles of 95°C for 30 s, 51°C for 30 s, and 72°C for 45 s; 72°C for 2 min. PCR product was purified and sequenced by Tech Dragon Ltd. (Hong Kong) with the Sanger sequencing method using an ABI PRISM® 3730xl DNA Analyzer. For each PCR product, sequencings were performed using the same corresponding forward and reverse primers used for PCR reactions.

Genetic analyses

Raw sequences (sequenced from both forward and reverse primers) were assembled using Geneious v9.0.2 (Biomatters Ltd.). Assembled sequences were aligned with datasets from Japanese studies (*COI*, Oyama et al. 2019; *Cytb*, Noguchi et al. 2012) using the MAFFT v7.388 (Kato and Stanley 2013) plugin of the Geneious program with default settings. Both ends of the aligned sequences for each DNA region were trimmed to obtain a uniform length for subsequent analyses (*i.e.*, 607 bp for *COI* and 1114 bp for *Cytb*). Haplotypes of *Cytb* were identified using DnaSP v6 (Rozas et al. 2017). Unique haplotypes from Hong Kong have been deposited in the National Center for Biotechnology Information (NCBI) Genbank database. Fasta files of *COI* sequences and *Cytb* haplotypes are accessible in DataSet S1. Information on *Cytb* haplotypes was summarized in DataSet S2.

HKY+G (Hasegawa et al. 1985) and K80 (Kimura 1980) were selected as the best fit model for *COI* and *Cytb* using jModelTest v2.1.10 (Darriba et al. 2012) based on Bayesian Information Criterion (Schwarz 1978). To identify the collected specimens, a Bayesian inference (BI) tree and a maximum likelihood (ML) tree were reconstructed in MrBayes v3.2 (Ronquist et al. 2012) and MEGA7 (Kumar et al. 2016), respectively, using *COI* sequences of all Hong Kong specimens and scombropid species data from Oyama et al. (2019). Closely related outgroups for BI and ML tree reconstructions were selected based on Oyama

et al. (2019) (i.e., *Epigonus telescopus*, accession number: KJ09756; *Epigonus denticulatus*, JF493426 and AP017435; *Epigonus pandionis*, KT883637). The tree is rooted by *Doederleinia berycoides* (accession number: AP009181) selected from Mochizuki et al. (2017). For the BI tree, two independent Markov chain Monte Carlo runs were performed with four chains for 500,000 generations, sampling every 100 generations and discarding the first 25% samples as burn-in. Sufficient convergence of the runs was estimated by summary statistics implemented in MrBayes v3.2 (Effective sampling size > 200, potential scale reduction factors → 1). For the ML tree, bootstrap values of nodes were estimated by 1000 bootstrap replicates in MEGA7. The genealogy of the of *Cytb* haplotypes was reconstructed using Popart v1.7 (<http://popart.otago.ac.nz>) with the TCS algorithm (Clement et al. 2002). Genetic differentiations between the Japanese and Hong Kong populations were estimated using pairwise F_{ST}

values calculated using the best fit model available in Arlequin v3.5 with 1,000 permutations (Excoffier and Lischer 2010).

RESULTS

Identification and life stage of the collected specimens

The external morphology of the specimens was examined. Pored lateral line scales ranged from 51–58, upper transverse scales 7–9, lower transverse scales 11–12, outer upper gill rakers 5–7, and outer lower gill rakers 13–15 ($n = 12$). Body was dorsally golden brown and ventrally silvery white. The second dorsal and caudal fins were yellow with white to brown edge (Fig. 2). The mean body lengths were 4.3 ± 1.0 cm SL (mean \pm SD) and 5.2 ± 1.2 cm TL, and the mean body weight



Fig. 2. Photographs of juveniles of *Scombrops boops* of different sizes. The upper and middle specimens were 4.6 cm and 7.3 cm total length (TL) collected from the *Sargassum* beds; the lower specimen was 10.1 cm TL collected from a rocky reef.

was 1.7 ± 2.0 g ($n = 40$) (Table 1). The numbers of lower transverse scales and outer lower gill rakers were within the ranges for *S. boops* juveniles of 8.1–10.3 cm SL (Itoi et al. 2008).

The *COI* sequence dataset for the BI and ML tree reconstructions was 607 bp long, including 149 variable sites and 89 parsimony informative sites. *COI* sequences obtained in this study are available on GenBank (accession numbers: MK987135–MK987174). *COI* sequences of specimens from Hong Kong were 99.5–100% identical to *S. boops*, 98.4–98.7% to *S. gilberti*, 98.0–98.5% to an undescribed *Scombrops* sp., and 95.6–96.0% to *S. cf. dubius* (African *Scombrops* specimens previously misidentified as *Scombrops boops*, Oyama et al. 2019). The BI tree indicated four clades within the Scombroptidae (Fig. 3), i.e., *S. boops*, *S. gilberti*, the undescribed *Scombrops* sp. and *S. cf. dubius*. All Hong Kong specimens were nested within the *S. boops* clade supported by a posterior probability of 0.80 and a bootstrap value of 69 (Fig. 3). Based on the morphological and molecular assessments, the 40 specimens sampled were therefore identified as *S. boops* juveniles. Similar molecular identification approach has been used to identify fish at early life stages successfully into species (Chu et al. 2019).

Genetic comparison between populations from Hong Kong and Japan

A trimmed *Cytb* dataset (1,114 bp) for TCS network was generated from a combined sequence data from this study and Noguchi et al. (2012); it contains a total of 115 haplotypes with 74 variable sites, 48 of which were parsimony informative. Since Sb72 and Sb73 from Kochi (Japan) (Noguchi et al. 2012) were identical after trimming for the combined dataset, the two sequences were regarded as one single haplotype and re-named *Cytb72* in our analyses (a specimen from Hong Kong was also identified as *Cytb72*). Among the 115 haplotypes identified, 15 (i.e., *Cytb101*–*Cytb115*) were unique to Hong Kong, 25 were shared by Hong Kong and Japan, and the remaining 75 were

unique to Japan (DataSet S2). Unique haplotypes from Hong Kong were deposited to GenBank under accession numbers MK987120–MK987134. The most common haplotype, *Cytb2*, was observed in eight specimens from Hong Kong and 31 specimens from Japan, which constitutes 20% and 17% of the Hong Kong and Japanese specimens, respectively. Neither haplotypes from Hong Kong nor Japan formed a single monophyletic clade in the TCS network (Fig. 4). Pairwise F_{ST} values of the sampling site pairs ranged from -0.02413 to 0.04120. Pairwise F_{ST} values between most of the site pairs were non-significant ($P > 0.05$), while significant values were only reported in pairs between Kochi and Niigata (Japan), and Kochi and Hong Kong (Table 2).

DISCUSSION

Habitat use of the collected juvenile *Scombrops boops*

Based on the sexual maturation size (~38 cm TL) reported in *S. boops* (Mochizuki 1977 1997; Hayashi 2002), all specimens collected in this study are at their early juvenile stage.

Macroalgal habitats are believed to be important nursery ground for *S. boops*. A relatively high proportion of the specimens was sampled from *Sargassum* beds (canopy-forming species) (Fig. 1b). At NFW, juveniles of *S. boops* were sampled in the same location of the *Sargassum* bed that occurred in both 2017 and 2019 surveys. Juveniles of *S. boops* with 3–12 cm TL were reported to use kelp forest as a seasonal residence in Japan from February to June (Kono et al. 2018). Juveniles of large predatory species, e.g., billfishes, tunas, swordfishes and dolphinfishes, were commonly found in association with *Sargassum* beds (Hoffmayer et al. 2005). A recent review suggested that tropical macroalgal habitats, including *Sargassum* habitat, could provide a key middle step in the triphasic life cycle of certain commercially important predatory fishes such as

Table 1. Body length and body weight of *Scombrops boops* juveniles ($n = 40$) collected in Hong Kong waters. All the data are presented as Mean \pm SD (Range)

	Number of specimens	Total length (cm)	Standard length (cm)	Body weight (g)
<i>Sargassum</i> bed	35	5.0 \pm 0.9 (3.5–7.3)	4.1 \pm 0.8 (2.9–6.1)	1.3 \pm 0.8 (0.6–3.6)
Rocky reef	5	6.6 \pm 2.0 (5.0–10.1)	5.5 \pm 1.6 (4.6–8.3)	4.2 \pm 5.1 (1.6–13.3)
Total	40	5.2 \pm 1.2 (3.5–10.1)	4.3 \pm 1.0 (2.9–8.3)	1.7 \pm 2.0 (0.6–13.3)

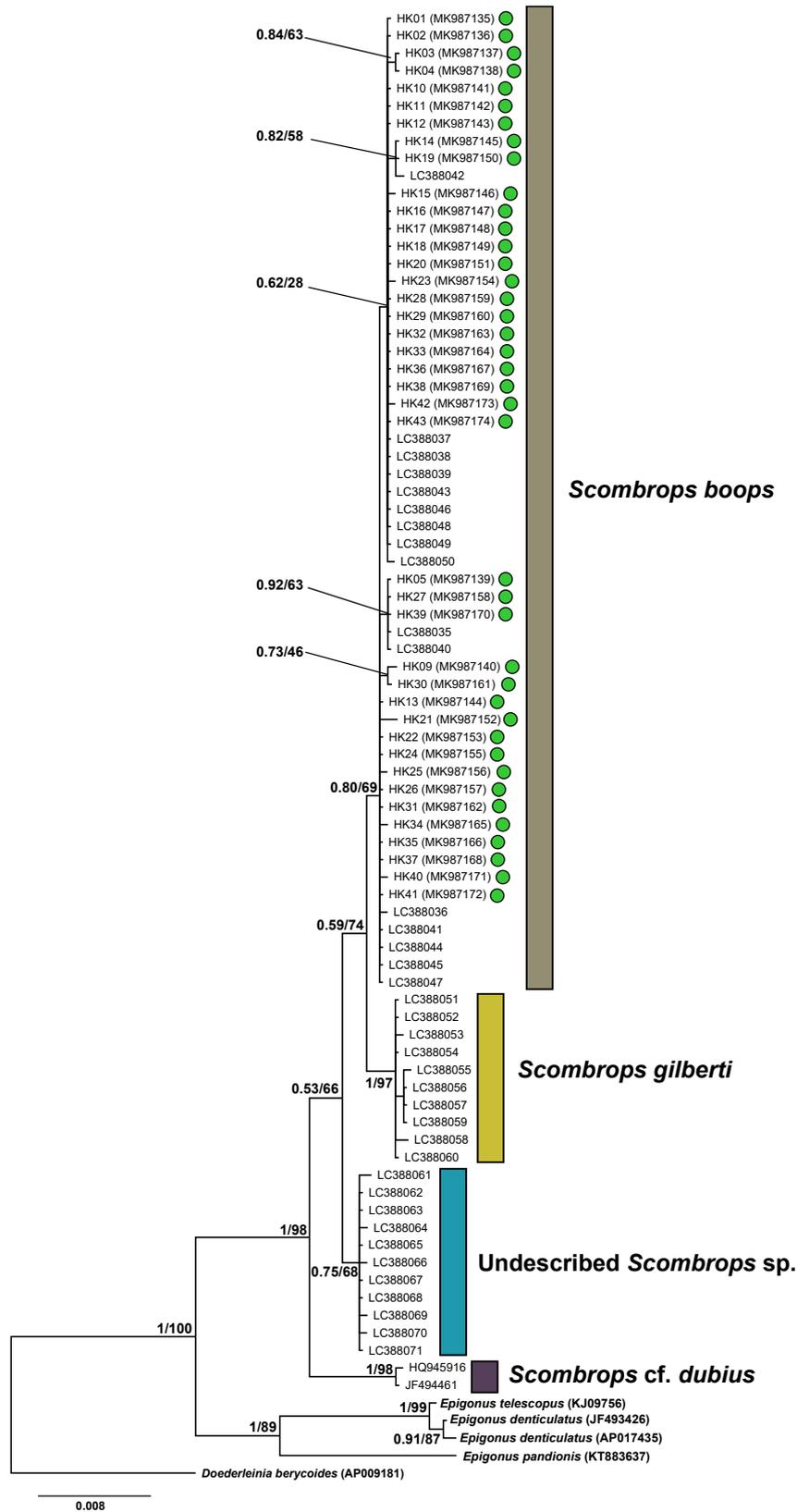


Fig. 3. A COI Bayesian inference tree indicating the identify of the juvenile *S. boops* specimens from Hong Kong. Individuals from Hong Kong are annotated with green circles. Species of each clade are annotated based on Oyama et al. (2019). Posterior probability and bootstrap value of each clade are shown on the nodes.

species from *Cephalopholis* Bloch & Schneider, 1801 and *Epinephelus* Bloch, 1793 (Serranidae), *Lethrinus* Cuvier, 1829 (Lethrinidae) and *Lutjanus* Bloch, 1790 (Lutjanidae) (Fulton et al. 2020).

Sargassum spp. have been designated as an essential fish habitat (EFH) due to its importance as fish and invertebrate nursery habitats (NOAA 1996). The majority (80%) of seaweed-associated fishes are at their

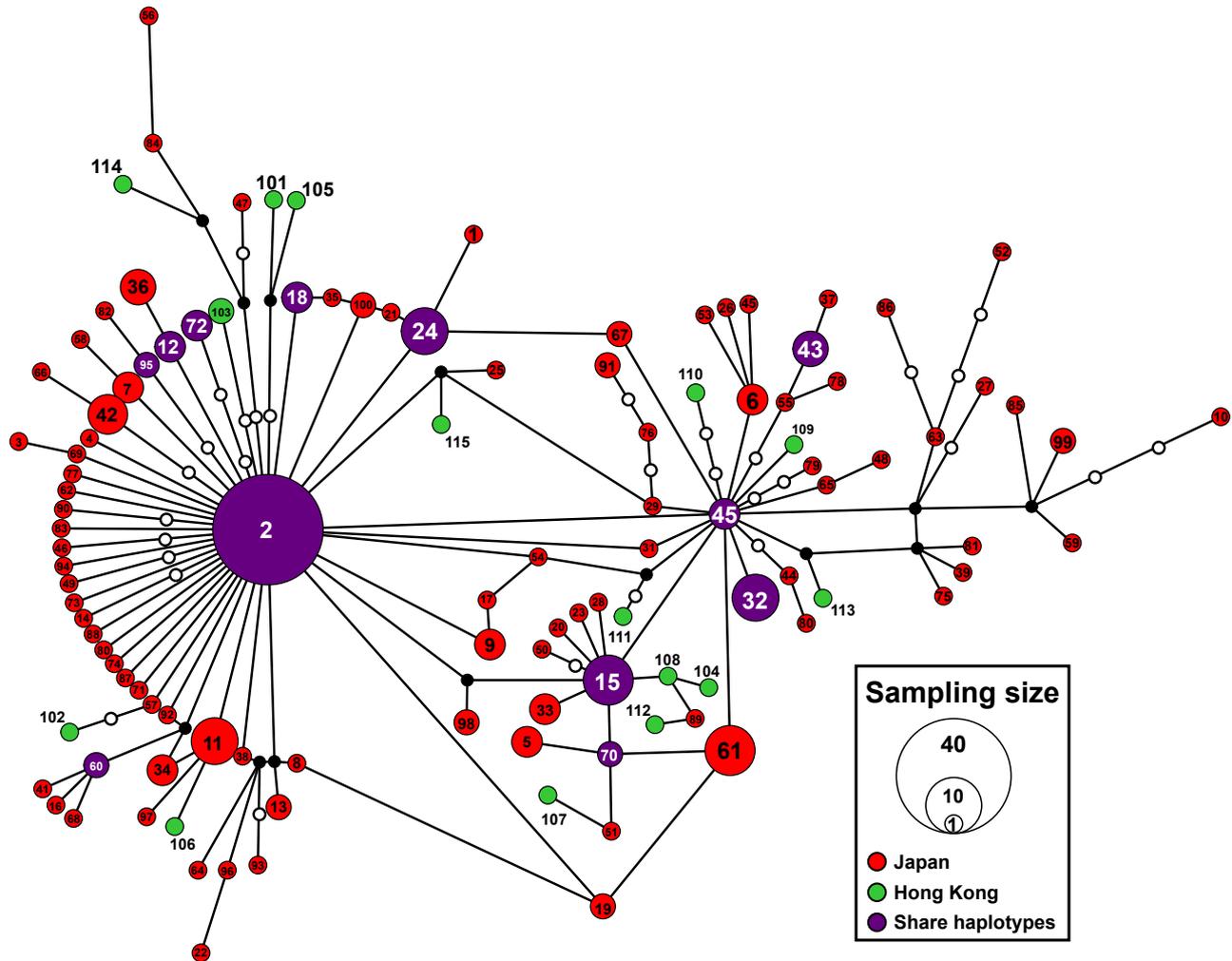


Fig. 4. A haplotype network based on *Cytb* gene sequences showing the relationships among haplotypes identified in *Scombrops boops* specimens from Hong Kong (i.e., this study) and Japan (i.e., Noguchi et al. 2012). Green circles refer to haplotypes unique to Hong Kong, red circles refer to haplotypes unique to Japan, and purple circles refer to haplotypes shared by Hong Kong and Japan.

Table 2. Estimated pairwise F_{ST} (below the diagonal) and p value (above the diagonal) of eight locations: seven from Japan (Noguchi et al. 2012) and one from Hong Kong (this study). Significant ($p < 0.05$) F_{ST} values are indicated by *

	NG	TT	NS	KS	KC	SO	IT	HK
Niigata (NG)	-	0.47656	0.76855	0.92383	0.04590	0.80371	0.62500	0.29785
Tottori (TT)	-0.00174	-	0.92773	0.58496	0.16406	0.63672	0.54199	0.53516
Nagasaki (NS)	-0.00887	-0.01130	-	0.96680	0.18945	0.99121	0.29199	0.61133
Kagoshima (KS)	-0.01603	-0.00379	-0.01412	-	0.06250	0.96387	0.11035	0.16406
Kochi (KC)	0.03516*	0.01339	0.01086	0.02074	-	0.05176	0.11133	0.01465
Shizuoka (SO)	-0.00935	-0.00448	-0.01528	-0.01274	0.02200	-	0.44043	0.14355
Iwate (IT)	-0.00578	-0.00302	0.00395	0.01185	0.01951	-0.00025	-	0.19922
Hong Kong (HK)	0.00382	-0.00287	-0.00327	0.00827	0.02859*	0.00865	0.00716	-

juvenile stages, benefiting from the availability of food sources and shelter provided by the complex canopy structures (Castro et al. 2002). *Sargassum* fronds can in fact act as a habitat for various epifaunal crustaceans such as copepods and amphipods (Mukai 1971; Tararam and Wakabara 1981). Juveniles of *S. boops* less than 4.0 cm SL are known to feed mainly on copepods and decapods (Kimura et al. 1982). Additionally, a previous study reported that the diet of *S. boops* shifted as their size increased, *i.e.*, the smaller juveniles (4.0 to 5.0 cm SL) feed on clupeoid larvae while the larger juveniles (> 5.0 cm SL) on the juveniles and adults of clupeids (Kimura et al. 1982). Clupeoid juveniles, which could be one of the important food sources of *S. boops* juveniles, are also commonly found in the coastal habitats in Hong Kong (PTY Leung, unpublished results). Our findings suggest that the seasonal canopy-forming *Sargassum* habitat in Hong Kong could play a potential nursery role as a transient juvenile habitat of *S. boops*.

Low genetic differentiation between populations from Hong Kong and Japan

There was no clear genetic structure between Hong Kong and Japan populations in *Cytb* haplotype network (Fig. 4). Both Hong Kong and Japan populations were rich in haplotype *Cytb*2. All pairwise F_{ST} values were low (-0.02413–0.04120) and similar to the F_{ST} values (-0.0411–0.0615) in Noguchi et al. (2012) and can be classified as “little genetic differentiation (F_{ST})” following Hartl and Clark (1997). Low but significant F_{ST} value was obtained between Kochi and Hong Kong, suggesting that the Kochi population might be significantly differentiated from that of Hong Kong. But such results might also be due to excessive singleton haplotypes in geographic populations affecting the results of the permutation test. Indeed, *Cytb* is relatively conservative compared to the control region of the mitochondrial genome, RFLP, and microsatellites (genetic markers commonly used for population genetics), which might result in the observed low and insignificant pairwise F_{ST} values. Genetic structure of the *S. boops* populations need to be further studied with hypervariable gene markers.

The low differentiation among all localities suggests that juveniles of *S. boops* in Hong Kong might be either the offspring of the Japanese population or derived from a single genetic population around the NW Pacific. Based on records of immediate post-birth larvae, *S. boops* is assumed to utilize the Okinawa Trough as its spawning ground (Uchida et al. 1958; Mochizuki 1977; Noguchi et al. 2012; Takai et al. 2014; Sassa and Konishi 2015). During the spawning season

(October to March), the warm Kuroshio Current and the Tsushima Current might contribute to the transport of *S. boops* offspring from the Okinawa Trough to both sides of the Japanese Archipelago, which in turn may facilitate genetic homogeneity among the geographic populations (Noguchi et al. 2012; Takai et al. 2014). During the spawning season of *S. boops*, the typical East Asian monsoon (northeasterly monsoon) in winter usually drives the colder and fresher flows southward along the coast of China, *i.e.*, the southward China Coastal Current (Fig. 1a), and consequently this current holds back the northward intrusion of the Kuroshio Branch Current (Jan et al. 2010). *Scombrops boops* larvae were reported in the southern East China Sea (Sassa and Konishi 2015). Therefore, it is plausible to assume that larvae of *S. boops* might drift along the China Coastal Current, disperse through the Taiwan Strait and arrive in the coastal waters of Hong Kong. After the disappearance of the seasonal *Sargassum* habitat since the arrival of the wet season, these juveniles may move to their next transient habitats or migrate back to the deeper water habitat as adults, *i.e.*, the mesopelagic zone in temperate or subtropical areas, *e.g.*, Japan and Taiwan. Likewise, a similar migration pattern was also suggested for *S. gilberti*, which is a closely related species of *S. boops*. The juveniles of *S. gilberti* undertake a long-distance migration from northern Japan, where they use high productive waters during their early life stage, to southern Japanese waters, where they complete their development into adulthood (Itoi et al. 2011). Our findings on *S. boops* have provided additional evidence on the life history characteristics of this genus.

The South China Sea has a known maximum depth of 5,559 m. The continental shelf of the South China Sea might provide suitable habitats for the mesopelagic adults of *S. boops*. Our finding of its small juveniles in Hong Kong suggests that there could be an unreported population of *S. boops* in the mesopelagic area of the South China Sea. If so, then the low genetic differentiation between Hong Kong's juvenile samples and Japanese populations might due to the high migratory rate between the populations that overcome the effect of genetic drift; or insufficient time for subpopulations to reach genetic equilibrium after a recent range expansion event (Slatkin 1993). However, no adult specimen of *S. boops* has been reported in the mesopelagic zone of the South China Sea. To bridge this knowledge gap, further research on the diversity and ecology of deepwater fishes in the South China Sea region is needed.

CONCLUSIONS

This study represents the first report of a deepwater temperate fish, *S. boops*, in littoral waters of Hong Kong, making it the southern-most record of *Scombroproboops boops*. Our findings showed that the occurrences of these juveniles were limited to the dry-wet transitional season (March to May), which is also the peak season for the canopied-forming *Sargassum* beds along the coastal water of Hong Kong. The high genetic relatedness between Hong Kong specimens and Japan populations, suggesting that these juveniles *S. boops* found in Hong Kong might be either the offspring of the Japanese population or derived from a single genetic population around the North West Pacific. This paper highlighted that subtropical littoral habitats, in particular the seasonal *Sargassum* habitat, could be one of the important transient juvenile habitats for this temperate deepwater species.

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Authors' contributions: Jiehong Wei: Data curation, Formal analysis, Investigation, Visualization, Writing-Original draft. Jiarui Gu: Writing- Original draft. Min Liu: Conceptualization, Data curation, Writing- Review & Editing. Bai-an Lin: Investigation. Gabriel Y. Lee: Investigation. Tak-Cheung Wai: Writing- Review & Editing. Paul K.S. Lam: Supervision, Writing- Review & Editing. Meng Yan: Investigation, Writing- Original draft. Priscilla T.Y. Leung: Conceptualization, Data curation, Investigation Writing- Review & Editing, Project administration, Supervision, Writing- Review & Editing.

Competing interests: The authors declare that they have no conflict of interests.

Availability of data and materials: The collected specimens were deposited in the State Key Laboratory of Marine Pollution, City University of Hong Kong, Hong Kong, China. *COI* sequences and *Cytb* haplotypes of the Hong Kong specimens could be found in the NCBI Genbank. Accession number of *COI* sequences: MK987135–MK987174; Accession number of *Cytb* haplotypes: MK987120–MK987134. Fasta files of *COI* sequences and *Cytb* haplotypes used in this study could be found in DataSet S1. *Cytb* haplotype information could be found in DataSet S2.

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Ethics approval consent to participate: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors. All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgments.

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Supplementary materials

DataSet S1. Sequences of *COI* and *cytb*. (download)

DataSet S2. *Cytb* haplotypes from each sampling site.
(download)