

Age, growth, reproductive biology, color pattern, and ontogenetic divergence of two closely related rockfishes (*Sebastes koreanus* and *S. nudus*) off the coasts of the Shandong Peninsula, China*

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Abstract The live-bearing genus *Sebastes* is renowned for its outstanding species richness and color diversity, and its speciation has been a point of interest. This study investigated the age, growth, reproductive biology, color pattern and ontogenetic divergence of a pair of closely related rockfishes from the coasts of the Shandong Peninsula, namely, *Sebastes koreanus* ($n=879$) and *S. nudus* ($n=257$). Marginal increment analysis of sectioned otoliths showed that annulus formation occurred once a year between June and July in both species. The sex-pooled growth curves of *S. nudus* and 3 populations of *S. koreanus* differed significantly from each other. No apparent latitudinal cline in growth parameters was found in *S. koreanus*. For both species, the peak parturition periods were from April to May, and the peak copulation periods were from November to December. *S. nudus* has a highly variable and conspicuous color pattern while *S. koreanus* has a stable and dull color pattern. This difference, together with the overlapping distribution and the close relationship, make *S. koreanus* and *S. nudus* an ideal model to investigate the color-driven speciation of the *Sebastes*. We confirmed that *S. nudus* changes its body color with age and season and fully expresses the carotenoid-based nuptial coloration when the fish reaches first maturity. Moreover, our comparisons of morphological traits that are likely related to survival and quality of these fishes suggested that *S. nudus* may suffer higher predation risk and foraging difficulty beginning at age 3. In light of the ontogenetic development of the color pattern in *S. nudus*, we suggested that the full expression of nuptial coloration most likely triggers the strong selective pressure to enhance swimming performance, anti-predator defense and foraging capacity of *S. nudus* through predator-prey interactions. By understanding all these details, we further inferred a hypothesis that both color pattern and bathymetric segregation play key roles in facilitating the speciation of demersal rockfishes.

Keyword: *Sebastes*; growth; color pattern; speciation

1 INTRODUCTION

The live-bearing genus *Sebastes* (rockfish) is one of the most speciose genera of marine fishes with approximately 110 species known worldwide, the majority of which are distributed in temperate to Arctic waters throughout the North Pacific (Hyde and Vetter, 2007; Nelson et al., 2016). Most of the rockfishes are important components of both commercial and recreational fisheries within their range (Love et al., 2002). Although the large assemblage of *Sebastes* has been proposed to be the

modern result of an ancient explosive speciation event (Johns and Avise, 1998), speciation mechanisms may still be active in *Sebastes* (Alesandrini and Bernardi, 1999). Many closely related species within the genus show only low levels of genetic divergence, and several examples of natural hybridization among them have been reported, suggestive of incipient

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speciation or recent speciation events (Roques et al., 2001; Narum et al., 2004; Hyde and Vetter, 2007; Kai and Nakabo, 2008; Artamonova et al., 2013).

The scarcity of geographical barriers to gene flow in marine ecosystems poses a challenge to the traditional view of speciation, with its emphasis on geographical isolation (Palumbi, 1994). Fully allopatric speciation can occur across barriers such as the Isthmus of Panama (Lessios and Cunningham, 1990), but these features are not common enough to explain all marine speciation events (Puebla, 2009; Ingram, 2010). Despite the recent examples of self-recruitment (e.g., Johansson et al., 2008), the prevalence of pelagic larval phases in marine taxa provides ample potential for gene flow covering long oceanic distances on a time scale of a few thousands of years (Lessios et al., 1998; Bowen et al., 2001; Mora and Sale, 2002; Craig et al., 2006; Lessios and Robertson, 2006; Shanks, 2009). Ecological speciation (reproductive isolation resulting from divergent natural selection) seems to be widespread in marine taxa (Rocha et al., 2005; Puebla, 2009; Ingram, 2010) due to its potential to operate within any taxonomic group, under any geographic mode and involve diverse types of interactions between organisms and their environment (Orr and Smith, 1998; Doebeli and Dieckmann, 2000; Schluter, 2001; Rundle and Nosil, 2005). Many closely related *Sebastes* occur in broad sympatry (Orr et al., 2000; Love et al., 2002; Jin, 2006). Therefore, the considerable diversity in the absence of geographical barriers has sparked interest in the factors promoting speciation in *Sebastes* (Alesandrini and Bernardi, 1999; Hyde and Vetter, 2007; Hyde et al., 2008; Ingram, 2010; Tuset et al., 2016).

As speciation in marine taxa remains poorly understood (Palumbi, 1994), it is difficult to pinpoint the mechanisms of speciation in *Sebastes*. However, the extensive literature on ecological speciation in the lake-dwelling cichlid fishes (e.g., Endler, 1983; Allender et al., 2003; Seehausen and Schluter, 2004) provide valuable insights for investigating the speciation mechanisms of *Sebastes*, as both *Sebastes* and cichlids are renowned for their outstanding species richness and color diversity, as well as numerous co-occurring species (Alesandrini and Bernardi, 1999; Maan and Sefc, 2013). As in several cichlid assemblages, depth segregation and coloration differences suggested that ecological and sexual selection may play important roles in this system (Endler, 1983; Alesandrini and Bernardi, 1999;

Allender et al., 2003; Kocher, 2004; Seehausen and Schluter, 2004). Several studies have suggested that closely related species and color morphotypes of rockfishes undergoing speciation differ primarily in color pattern, which is in turn usually associated with depth distribution (e.g., Hyde et al., 2008; Artamonova et al., 2013). Previous evolutionary studies have paid considerable attention to the role of bathymetric segregation in the speciation of rockfishes (Hyde et al., 2008; Ingram, 2010; Artamonova et al., 2013). Unexpectedly, despite the increasing reports of clear coloration differences between closely related *Sebastes* (e.g., Hyde et al., 2008; Artamonova et al., 2013), there is hardly any empirical research that has investigated how coloration acts on the speciation and adaptive evolution of *Sebastes* or how coloration and other potential speciation factors, e.g., bathymetric segregation, can interact.

Numerous studies in some speciose families of teleosts, e.g., *Cichlidae* and *Poeciliidae*, have suggested that body color can play important roles in social communication, competition, mate choice, predation and foraging and are therefore subject to potentially strong selective pressures (Endler, 1983; Godin and Dugatkin, 1996; Coullidge and Alexander, 2002; Godin and McDonough, 2003; Maan and Sefc, 2013). Moreover, there is growing evidence that strongly divergent selections generated through predator-prey interactions (predation and foraging) could lead to rapid adaptive divergence in body shape, especially the fitness traits closely related to survival and body condition such as foraging morphology, predator defense morphology, etc. (Langerhans et al., 2004; Andersson et al., 2006; Eklöv and Svanbäck, 2006; Domenici et al., 2007; Langerhans, 2009). Therefore, though many closely related species and color morphotypes within *Sebastes* show only low levels of genetic divergence (Roques et al., 2001; Narum et al., 2004; Hyde and Vetter, 2007; Hyde et al., 2008; Kai and Nakabo, 2008; Artamonova et al., 2013), the color-driven divergent selection generated through predator-prey interactions (Langerhans et al., 2004; Andersson et al., 2006; Eklöv and Svanbäck, 2006; Domenici et al., 2007; Langerhans, 2009) may also lead to rapid adaptive divergence in body shape of rockfishes and, consequently, accelerate their speciation and adaptive radiation. However, the strength of the color-driven divergent selection may vary, because in many teleosts, color patterns vary not only between species but also within a species (e.g., sexual dichromatism and polychromatism), as well as

within individuals (e.g., nuptial coloration), depending on their age and sexual maturity (Macedonia et al., 2002; Leclercq et al., 2010; Maan and Sefc, 2013). Thus, in terms of understanding the potential mechanism of color-driven speciation in *Sebastes*, it is important to ascertain and analyze some aspects of the biology of closely related species or color morphotypes of *Sebastes* such as age, growth, maturity, coloration and its variation, as well as some morphological traits likely related to survival and body condition.

In this study, we selected a pair of very closely related rockfishes, *Sebastes koreanus* and *S. nudus*. Though not perfectly sympatric, the distributions of *Sebastes koreanus* and *S. nudus* are overlapping in the coastal areas of Shandong Peninsula and the southern part of the Korean Peninsula, according to previous records (Kai and Nakabo, 2013; Yu and Kim, 2014; Fang et al., 2015; Yu et al., 2015). After the pelagic larval and early juvenile stages, they dwell on demersal rocky reefs and display a migratory movement towards deeper waters during ontogeny, known as the “bigger-deeper” distribution pattern (e.g., Polloni et al., 1979), which is a common theme among rockfishes (Love et al., 1991; Jin, 2006). *Sebastes koreanus* and *S. nudus* are morphologically and meristically similar (Kai and Nakabo, 2013; Fang et al., 2015). Their color patterns, however, are distinct (Kai and Nakabo, 2013; Yu and Kim, 2014; Fang et al., 2015). *Sebastes nudus* appears to show a bolder color pattern (dark base color vs. conspicuous yellow markings) than *Sebastes koreanus* (light brown base color vs. dark brown bands or dots). *Sebastes nudus* shows much variation in its coloration among individuals (even within a population), mainly included in the size, number, and distribution of the conspicuous yellow markings (carotenoid pigments) on the body, head, and fins (Kai and Nakabo, 2013; Yu and Kim, 2014; present study). However, *Sebastes koreanus* shows little to no color variation among populations (Fang et al., 2015; Yu et al., 2015; present study) and even from juvenile to mature stages (Yu et al., 2015). The body color characteristics of *Sebastes koreanus* and *S. nudus* make them an ideal model to study the action of color-driven divergent selection on morphological traits in the rockfishes living in same environment and sharing a similar gene pool. Moreover, few other studies have attempted to analyze and compare the growth of these two *Sebastes* species, in part because of their problematic species identification. Recently, researchers have reviewed

and re-described the two species and clarified their species identification (Kai and Nakabo, 2013; Fang et al., 2015). These efforts have provided an important basis for the reliable studies on the age and growth of these species.

Using specimens of *S. koreanus* and *S. nudus* collected off the coasts of Shandong Peninsula, China, the objectives of the present study were to: (i) ascertain their age and growth from otoliths; (ii) investigate their reproductive seasonality; (iii) investigate the ontogenetic, seasonal and sexual variations in the body color pattern of *S. nudus*; and (iv) determine when divergence in some phenotypic traits occurs between the two closely related species. By understanding these details, we further hoped to infer a possible mechanism of speciation by natural selection in rockfishes.

2 MATERIAL AND METHOD

2.1 Collection and preparation

A total of 879 *Sebastes koreanus* and 257 *S. nudus* specimens were purchased live or, occasionally, freshly dead directly from local fishers from 2013 to 2016 (Table 1). The purchased fishes were fished by fish traps or occasionally, angling off the coasts of Shandong Peninsula, China (Fig.1). Specimens for validating otolith annuli and reproductive seasonality analysis were sampled monthly from 2013 November to 2014 November in Qingdao, southern coast of Shandong Peninsula. To generally reflect the annual migration trends of the two species, we purchased the 24-hour catches in fish traps in the very nearshore of sample locations-1 and -2 in Qingdao (Fig.1) (the water depth at the sites varies between 4 and 7 m, which is close to the shallower limit of distribution of the two species) for ≤ 3 times per month (Table 2). Specimens were also sampled seasonally off the coast of Rongcheng (eastern Shandong Peninsula) and Penglai (northern Shandong Peninsula) from 2015 to 2016 (Table 1). Species identification was carried out by morphological features as described by Kim et al. (2005) and Fang et al. (2015) for *S. koreanus* and Kai and Nakabo (2013) for *S. nudus*.

For fish color analysis, to reduce, or possibly, avoid the possible body color variations caused by changes in feeding and illumination conditions (e.g., Oshima and Yokozeki, 1999; Kasai and Oshima, 2006; Alishahi et al., 2015) after the wild fish have been landed, we photographed the just caught *S. nudus* individuals as soon as possible outdoors in a shaded

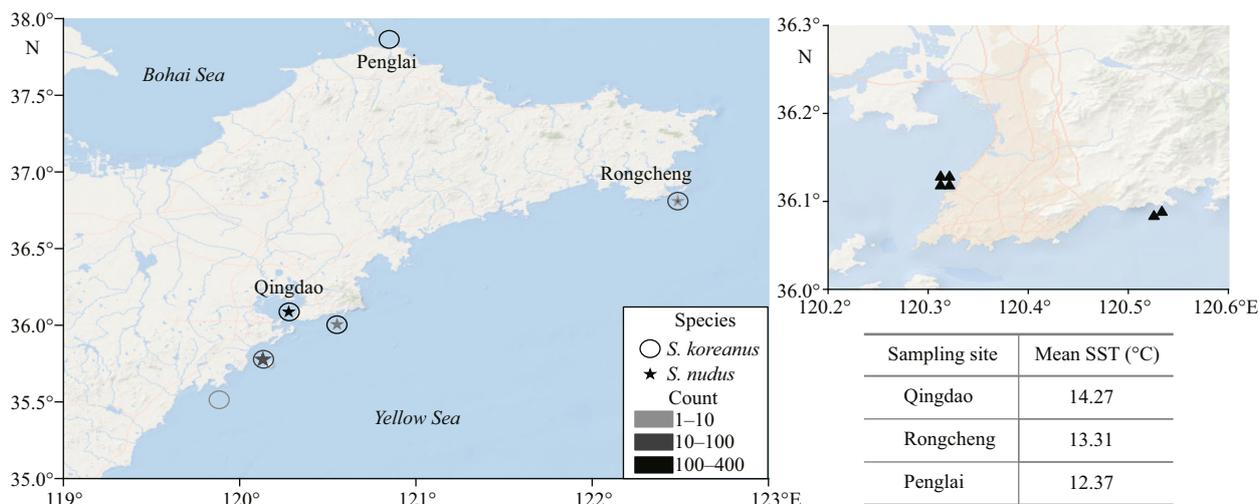


Fig.1 The sampling sites for *S. koreanus* (enclosed star) and *S. nudus* (open circle) off the coasts of Shandong Peninsula, China. Close triangles indicate the fixed fish traps in the very nearshore of sampling sites-1 and -2 in Qingdao. The mean sea surface temperatures (SSTs) from Jan 2013 to Dec 2016 off the coast of Qingdao, Rongcheng and Penglai (daily SST data were available at ftp://data.remss.com/SST/daily_v04.0/mw_ir/ and read by Python version 3.4) are given.

Table 1 The number of individuals and range of standard length of *S. koreanus* and *S. nudus* by sampling month

Month	Sampling location	Sex	<i>S. koreanus</i>		<i>S. nudus</i>	
			<i>n</i>	Standard length (mm)	<i>n</i>	Standard length (mm)
2013 Nov.	Qingdao	Male	8	67–88	1	82
		Female	31	68–114	5	145–179
		Unidentified	3	42–86	0	
Dec.	Qingdao	Male	17	65–101	8	133–156
		Female	16	65–122	10	102–188
		Unidentified	17	80–105	0	
2014 Jan.	Qingdao	Male	6	66–84	10	95–120
		Female	15	62–85	8	92–158
		Unidentified	0		0	
Feb.	Qingdao	Male	1	88	20	98–164
		Female	2	77–115	27	98–175
		Unidentified	0		0	
Mar.	Qingdao	Male	12	75–116	1	116
		Female	19	67–122	1	144
		Unidentified	0		0	
Apr.	Qingdao	Male	32	71–112	10	103–165
		Female	35	79–137	1	99
		Unidentified	0		0	
May	Qingdao	Male	6	68–107	11	104–155
		Female	5	95–122	15	102–183
		Unidentified	12	48–73	0	
Jun.	Qingdao	Male	50	74–111	20	97–146
		Female	69	64–126	10	93–154
		Unidentified	0		0	

To be continued

Table 1 Continued

Month	Sampling location	Sex	<i>S. koreanus</i>		<i>S. nudus</i>	
			<i>n</i>	Standard length (mm)	<i>n</i>	Standard length (mm)
Jul.	Qingdao	Male	20	66–109	13	90–136
		Female	31	75–116	15	95–157
		Unidentified	0		0	
Aug.	Qingdao	Male	7	81–101	6	173–210
		Female	7	83–109	5	123–202
		Unidentified	2	92–112	0	
Sep.	Qingdao	Male	27	68–121	4	110–142
		Female	45	76–140	5	97–161
		Unidentified	4	72–88	0	
Oct.	Qingdao	Male	80	74–124	14	76–159
		Female	100	80–144	16	91–158
		Unidentified	0		0	
Nov.	Qingdao	Male	0		10	132–169
		Female	0		9	127–161
		Unidentified	0		0	
2015 Jul.	Rongcheng	Male	2	111–140	0	
		Female	1	111	0	
		Unidentified	0		0	
	Penglai	Male	2	109–110	0	
		Female	0		0	
		Unidentified	0		0	
Sep.	Rongcheng	Male	25	79–143	2	101–180
		Female	17	95–144	0	
		Unidentified	0		0	
	Penglai	Male	52	71–129	0	
		Female	43	76–137	0	
		Unidentified	3	71–106	0	
Dec.	Rongcheng	Male	0		0	
		Female	1	145	0	
		Unidentified	0		0	
2016 May	Rongcheng	Male	23	80–111	0	
		Female	15	78–115	0	
		Unidentified	1	63	0	
	Penglai	Male	8	85–125	0	
		Female	7	76–137	0	
		Unidentified	0	0	0	
Total			879	42–144	257	76–210
Mean±SD		Male	378	93±12	130	129±23
		Female	459	97±14	127	132±24
		Unidentified	42	78±19	0	
		Combined	879	95±14	257	130±23

Table 2 Age-groups of the monthly samples of *S. koreanus* and *S. nudus* collected by the fixed fish traps in the very nearshore of sampling sites-1 and -2 in Qingdao

Sample site	Month	Age-groups (year)		Purchase frequency (time/month)
		<i>S. koreanus</i>	<i>S. nudus</i>	
1	2014 Jan.	1-3	-	2
	Feb.	2	2	2
	Mar.	2-7	3, 4	2
	Apr.	2-4, 7, 8	2	2
	May	3-7	3-5	3
	Jun.	1-11	2-4, 6, 7	3
	Jul.	1-10	2-6	3
	Aug.	2-8	2, 3	3
	Sep.	2-4	2	2
	Oct.	1, 2, 4	-	2
	Nov.	1	-	1
2	2013 Nov.	1-3	-	1
	2014 Apr.	3-5, 8	2-4, 6	1
	May	2-6, 8-10	3, 6, 8, 9	1
	Aug.	2-7	5, 6,	1
	Sep.	1-6	3, 4, 5	1
Oct.	1, 2, 4	2	1	

- means no sample taken from the fixed fish traps during that month.

area. In view of the possible fading of body color following death, only live individuals ($n=188$ or 73.2% of *S. nudus* sample size) were selected to be photographed. Digital photographs were taken following methods suggested by Stevens et al. (2007), namely, the use of a high-resolution camera, the inclusion of a color standard in each image, the avoidance of file types that compress images, and manual control of exposure times and white balancing. We photographed the right and the left-side views of each individual alongside an X-Rite mini color checker card (X-Rite Inc.) in RAW format using a Nikon D90 digital camera (Nikon Inc.). The digital camera was fitted with a Nikon 24–85 mm zoom lens (Nikon Inc.) and attached to a tripod (Manfrotto Co.). Thin pins and bamboo skewers were used for fin spreading following the method suggested by Motomura and Ishikawa (2013). To reduce the reflected light spots from the body surface, we placed a semi-translucent white cloth around the specimen to soften the sunlight and wiped the body surface lightly while photographing (Motomura and Ishikawa, 2013).

All specimens of *S. koreanus* and *S. nudus* were measured, weighed, and sexed in the laboratory immediately upon collection. For each individual collected, total length (TL) and standard fish length (SL) were measured to the nearest mm, while total body weight (TW), eviscerated weight (EW), gonadal weight (GW) and gastrointestinal weight (GAW) were measured to the nearest 0.01 g. Here, the GAW included the weight of the gut itself as well as the weight of the gut contents. Caudal fin length (CFL) was taken as the TL minus the SL. Pectoral fin length (PFL), longest dorsal spine length (DSL) and mouth breadth (MB) were measured to the nearest mm in 111 *S. koreanus* and 156 *S. nudus*. Traits were selected based on their likely relationship to foraging and/or swimming ability (CFL, PFL, MB), as well as predator defense (DSL) (e.g., Malmquist, 1992; Ruzzante et al., 2003, 2011). The sex of each individual was determined by visual observation of the gonads. In small specimens, gonads were observed by a light microscope to aid sex determination. Only adults were selected to determine reproductive and feeding seasonality. Reproductive seasonality was indicated by the gonadosomatic index (GSI) calculated as: $GSI = GW \times 100 / EW$. Timing of reproduction is often related to feeding seasonality of adults, allowing needed energy reserves (Guillemot et al., 1985). Hence, monthly variation in feeding condition was indicated by the digestosomatic index (DSI) calculated as: $DSI = GAW \times 100 / EW$. The eviscerated weight was used because it is a more adequate body mass indicator than total weight, as it is not affected by individual variation in the mass of the digestive tract, liver and reproductive organs (Peres and Vooren, 1991).

All sagittae were dissected, cleaned, air-dried at room temperature and stored in plastic tubes for subsequent examination. We used the right otolith for age determination when it was available and the left when the right was not utilizable.

2.2 Age determination and growth analysis

Sagittae were embedded in epoxy resin and cross-sectioned transversely to a thickness of approximately 800 μm with an Isomet low-speed diamond bladed saw, before mounting on glass slides. These sections were polished with a fine grit polishing pad and velvet polishing pad (Buehler) until the core was distinctly visible. Then, the otolith sections were viewed and imaged with a digital camera fitted to a Nikon SMZ1000 dissecting microscope under transmitted

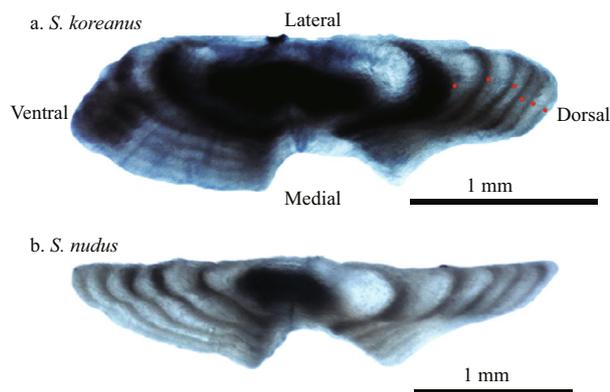


Fig.2 Photographs of cross-section otolith of *S. koreanus* (a) (6-year-old female, 96 mm SL) and *S. nudus* (b) (5-year-old male, 134 mm SL)

Red dots denote annulus.

light at 40× magnification (Fig.2). The images were then enhanced in Adobe Photoshop CS5 Extended as described by Campana et al. (2015) to maximize annuli visibility prior to age determination.

Annuli (outer margins of the opaque zone) were read twice (one month apart) in a random order without prior knowledge of the size or species. Deviations were counted a third time. Only counts with at least two agreements were used in subsequent analyses.

Annulus formation was verified by marginal-increment analysis technique (e.g., Kadison et al., 2010). For all age-2 and older fish, the marginal increment ratio (MIR) was calculated as:

$$\text{MIR} = (R - R_n) / (R_n - R_{n-1}),$$

where R is the radius (the distance between the focus and the otolith edge), R_n is the distance between the focus and the last annual band and R_{n-1} is the distance between the focus and the penultimate annual band. Once MIRs were obtained for all of the otoliths, the monthly mean values were plotted separately for *S. koreanus* and *S. nudus* to determine the annual patterns of band formation. For age-1 fish, which had no second annulus, the expected distance between the first and second annuli was calculated as described by Kadison et al. (2010). The marginal increment ratios for all fish age-1 and older were pooled and plotted as monthly means to verify and determine the timing of annulus formation.

Relative ages derived from otolith ageing were converted to absolute ages according to the reproductive seasonality, the date of capture, and the period of annulus formation (see Results). The von Bertalanffy growth function was fitted to the length-at-age data by species, population and sex:

$$\text{SL}_t = \text{SL}_\infty \times F07B1 - e^{(-k(t-t_0))} F07D,$$

where SL_∞ is the asymptotic length, k is the growth coefficient, and t_0 is the hypothetical age at zero length. The analysis of the residual sum of squares (ARSS) (Chen et al., 1992) was employed to compare growth curves between populations, species and sexes. In addition, the ratio of male to female SL (SL ratio) was used as an index of sexual size dimorphism (Lenarz and Echeverria, 1991). Here, we used the average SL of mature fish measured in this study to calculate the SL ratio.

2.3 Bodycoloration analysis

The side-view images of *S. nudus* specimens were calibrated with the X-rite ColorChecker Passport software (V.1.0.2). For better measurement, we further enhanced the contrast between conspicuous yellow markings and their surroundings by converting the fish coloration to black-and-white mode within Adobe Photoshop CS5 Extended. Here, we selected Adobe Photoshop CS5 Extended software due to its flexible and strong performance in selection techniques (see Adobe Photoshop CS5 Help at <https://helpx.adobe.com/photoshop/archive.html>). The main steps in processing the image within the software are shown in Fig.3.

For each processed image, the total area of the markings (white area) and the total area of fish surface outside the markings (black area) were measured using Image-Pro Plus (V.6.0). The yellow marking ratio (YMR, the ratio between the total area of yellow markings and the total body surface area) was calculated as:

$$\text{YMR} = A_{\text{white}} / (A_{\text{white}} + A_{\text{black}}),$$

where A_{white} is the white area value, and A_{black} is the black area value in the processed image.

A paired-samples t -test of YMR derived from left side-view images and right side-view images indicated no significant difference ($t = -0.617$, $P > 0.05$). Then, the left side-view images were processed once again in a random order one month later. A paired-samples t -test of YMR derived from the two separate handlings revealed no significant difference ($t = 0.224$, $P > 0.05$). Hence, the YMR value derived from the first handling of the left side-view image of each individual was used in subsequent analyses.

Two-way analyses of variance (ANOVA) were performed to examine the age-group × month, sex × age-group and sex × month interactions on the YMR, separately. When no significant interaction term was detected by the two-way ANOVA ($P > 0.05$), the simple main effect of each factor (age-group, month and sex)

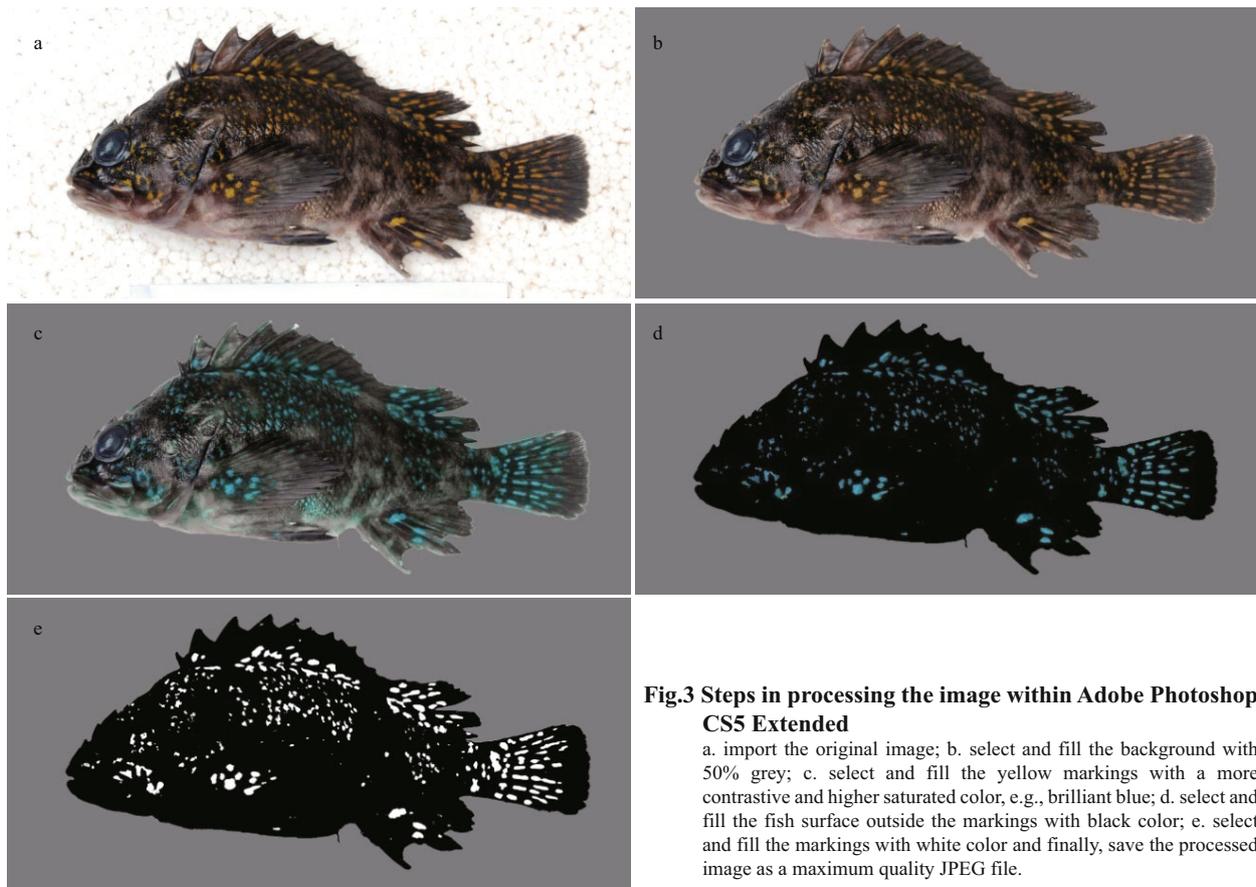


Fig.3 Steps in processing the image within Adobe Photoshop CS5 Extended

a. import the original image; b. select and fill the background with 50% grey; c. select and fill the yellow markings with a more contrastive and higher saturated color, e.g., brilliant blue; d. select and fill the fish surface outside the markings with black color; e. select and fill the markings with white color and finally, save the processed image as a maximum quality JPEG file.

was analyzed separately by one-way ANOVA. Significant one-way ANOVA was followed by a Duncan's test for multiple comparisons. To investigate the possible seasonal sexual dimorphism in coloration, the sexual difference in the mean YMR value within each month was assessed, respectively, using independent-samples Student's *t*-test. The mean YMR values were plotted by age to display the variation trend. Then, the monthly mean YMR values for male, female and sex-pooled *S. nudus* were plotted separately.

2.4 Morphological trait analysis

To evaluate the scaling relationship for each morphological variable with body size, we calculated separate reduced major axis (RMA) regressions for CFL, PFL, DSL and MB on SL for each of the species examined. Reduced major axis regression is the most appropriate method for the evaluation of structural relationships between variables when both are subject to measurement error (Rayner, 1985; LaBarbera, 1989). All data were \log_{10} transformed prior to analysis, allowing the exponent of each scaling relationship to be determined as the slope of its RMA regression. The RMA regression was applied using the RMA Software for Reduced Major Axis

Regression (V. 1.17) by Bohonak (2004). Deviations from isometry and homogeneity of slopes between the species were examined by inspection of the 95% confidence intervals of the slope estimates.

The morphological variables measured above were used to obtain 4 morphometric ratios (CFL/SL, PFL/SL, DSL/SL and MB/SL) that are considered potentially important for describing the swimming performance, predator avoidance or hunting capacity of fish (Wańkowski, 1979; Ringler, 1983; Blouw and Hagen, 1984; Fisher and Hogan, 2007; Nanami, 2007; Leavy and Bonner, 2009). As there were no significant sex \times age-group interactions on the 4 morphological ratios within each species (two-way ANOVA, in all cases, *S. koreanus* $P > 0.05$ and *S. nudus* $P > 0.05$), the sex-pooled data were used in subsequent analyses. To examine the ontogenetic trajectories of the 4 morphometric ratios, we plotted the mean ratios by age within each species. To determine the age at which interspecific divergence in these ratios begins to appear, Student's *t*-tests were used to assess the interspecific differences of each ratio by age.

All statistical analyses were performed with a significance level of 0.05 using SPSS (V.19.0). Prior to each ANOVA and *t*-test, the variables were tested

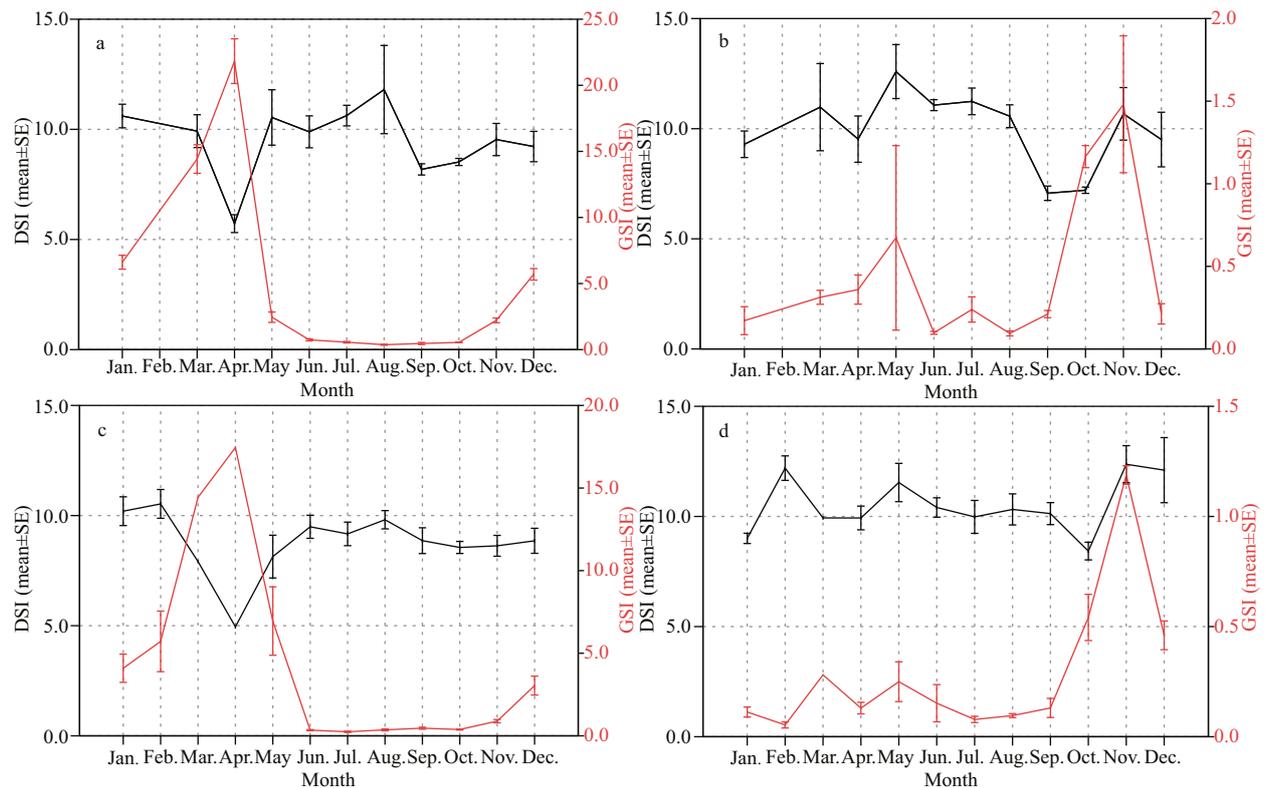


Fig.4 Monthly variations in gonosomatic index (GSI) and digestosomatic index (DSI) of *S. koreanus* females (a), males (b), and *S. nudus* females (c), males (d)

for normality (Kolmogorov-Smirnov test) and homogeneity of variance (Levene's test) and data were log-transformed if necessary.

3 RESULT

3.1 Reproductive and feeding seasonality

Only adults sampled from Qingdao were used to determinate reproductive and feeding seasonality. In the 641 sexed *S. koreanus*, the youngest mature male was age-1 (67 mm SL), and the youngest mature female was age-2 (71 mm SL). In the 255 sexed *S. nudus*, the youngest mature male was age-2 (100 mm SL), and the youngest mature female was age-2 (99 mm SL). For both species, all age-3 and older individuals were classified as mature.

Monthly changes of GSI and DSI are plotted in Fig.4. The monthly variations in the GSI for both species indicated that the peak parturition periods of both species were from April to May (Fig.4a, c), and the peak copulation periods of both species were from November to December (Fig.4b, d).

The mean DSI values of *S. koreanus* females (Fig.4a) and *S. nudus* females (Fig.4c) showed the minimum levels at the peak parturition periods and experienced different degrees of decline (very rapid

for the former, moderate for the latter) just before their peak copulation periods. Moreover, the low-level period (just before the peak copulation period) of the mean DSI of *S. koreanus* males lasted approximately 2 months (September–October) (Fig.4b) while the low-level period of *S. nudus* males lasted only approximately 1 month (October) (Fig.4d).

3.2 Age and growth

1 133 otoliths (99.8%) were used in the age and growth analyses because they were not only readable but also provided at least two agreements among separate readings. The dorsal face of the sectioned otoliths (Fig.2) seemed to provide a better individualization of the growth increments owing to their greater sharpness, higher contrast between fast and slow growth bands and larger distance between them.

The plot of monthly mean MIR across all age-groups showed that the highest mean MIR occurred in May and lowest in July for both *S. koreanus* and *S. nudus*, suggesting that one growth ring formed on an annual basis for the two species (Fig.5).

Having considered the peak parturition periods, 1st May was assigned as the birth date for both species in this study. Relative ages derived from ageing were then converted to absolute ages. Ages of *S. koreanus*

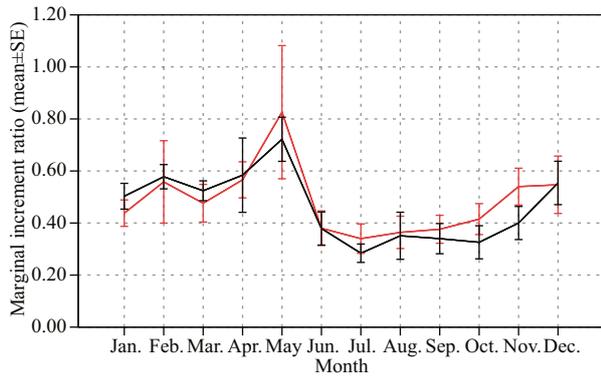


Fig.5 Monthly mean marginal increment ratio (\pm SE) of otoliths for *S. koreanus* and *S. nudus*

ranged from 0.52 to 15.35 years, and ages of *S. nudus* ranged from 0.56 to 11.03 years.

No significant differences in growth curves were found between the sexes for *S. nudus* (ARSS, $P > 0.05$) and each population of *S. koreanus* (ARSS, in all cases, $P > 0.05$). However, the ARSS indicated that the sex-pooled growth curves of *S. nudus* and 3 populations of *S. koreanus* differed significantly from each other (in all cases, $P < 0.05$). Therefore, sexes-combined von Bertalanffy growth curves are depicted in Fig.6, and the growth parameters are shown in Table 3. The average ratio of male to female SL is 0.96 for *S. koreanus* and 0.98 for *S. nudus*.

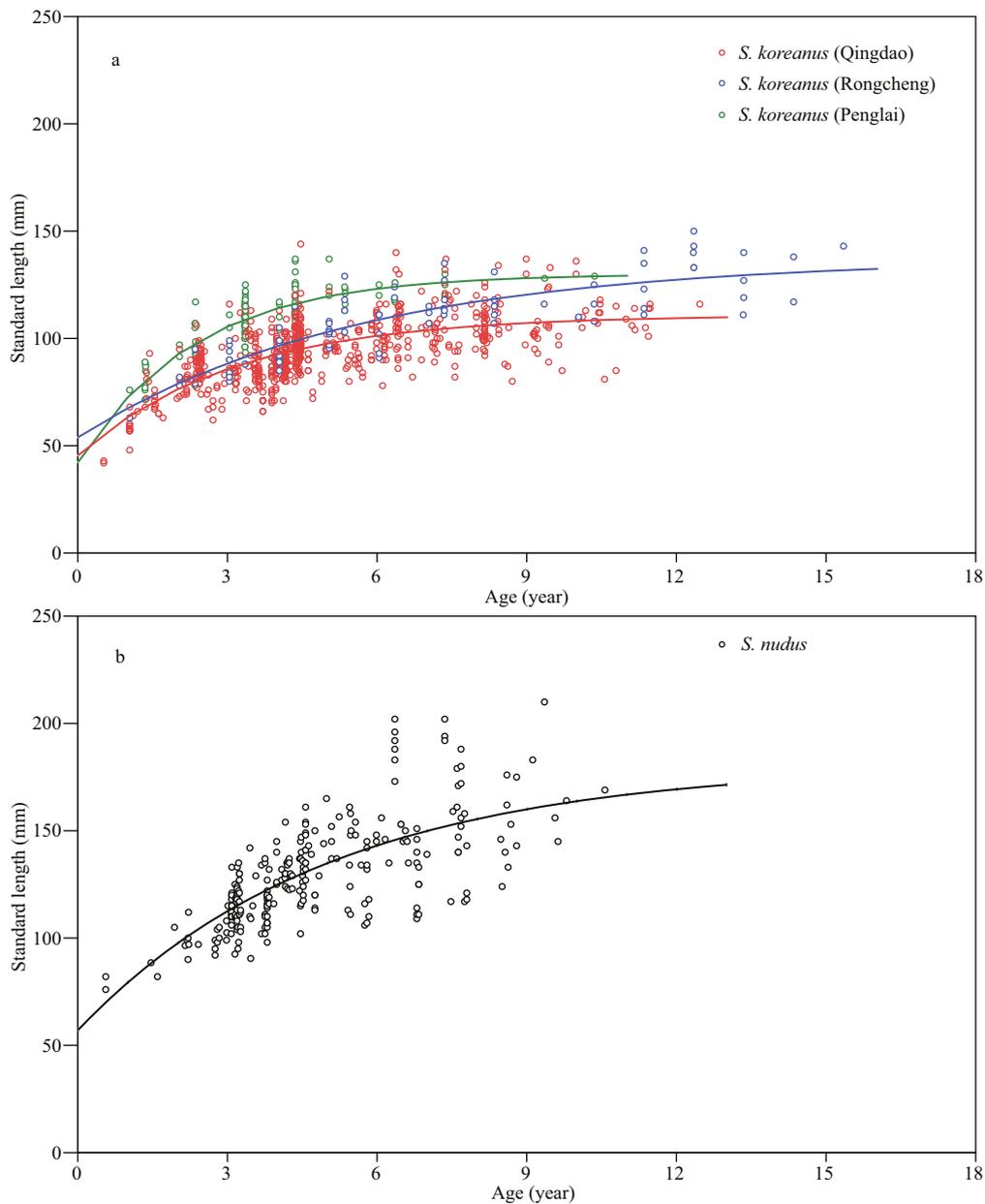


Fig.6 Von Bertalanffy growth curves in standard length of *S. koreanus* and *S. nudus*

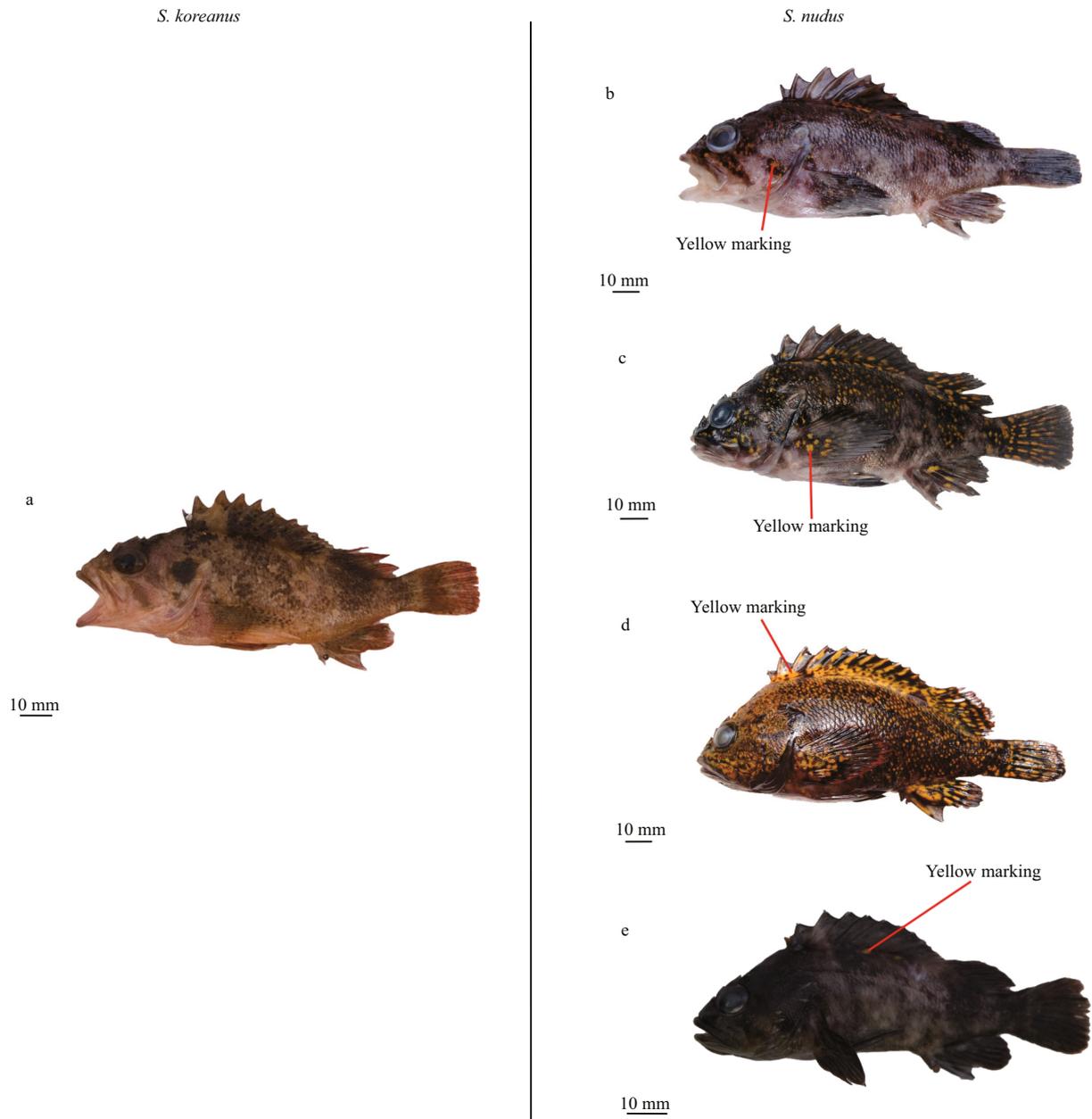


Fig.7 Live body color morphotypes of *S. koreanus* and *S. nudus*

a. *S. koreanus*, adult fish, 105 mm SL; b. *S. nudus*, adult fish, 122 mm SL, YMR=0.049; c. *S. nudus*, adult fish, 120 mm SL, YMR=0.097; d. *S. nudus*, adult fish, 117 mm SL, YMR=0.343; e. *S. nudus*, age-1 juvenile fish, 82 mm SL, YMR=0.001.

Table 3 Von Bertalanffy growth parameters of *S. koreanus* and *S. nudus*

Species	SL _∞	k	t ₀	R ²	n
<i>S. koreanus</i> (Qingdao)	110.882	0.321	-1.644	0.484	680
<i>S. koreanus</i> (Rongcheng)	137.181	0.179	-2.791	0.716	84
<i>S. koreanus</i> (Penglai)	130.044	0.427	-0.922	0.676	115
<i>S. nudus</i>	180.849	0.198	-1.921	0.489	257

3.3 Body coloration analysis

Sebastes nudus has a highly variable and conspicuous (dark base color vs. conspicuous yellow markings) color pattern (Kai and Nakabo, 2013; present study), differing from the stable and dull (light brown base color vs. dark brown bands or dots) color pattern of *S. koreanus* (Jin, 2006; Yu et al., 2015; present study) (Fig.7). Interestingly, for *S. nudus*,

Table 4 Intercepts, slopes and their 95% confidence intervals of RMA-regression of morphological variables regressed on SL of *S. koreanus* and *S. nudus*

Regression abscissa	Regression ordinate	Species	Intercept	Intercept 95% confidence intervals	Slope	Slope 95% confidence intervals	R ²	Allometry
SL	CFL	<i>S. koreanus</i>	-0.693	-0.763, -0.623	0.985	0.950, 1.020	0.731	0
SL	CFL	<i>S. nudus</i>	-0.798	-0.919, -0.677	1.047	0.990, 1.104	0.876	0
SL	PFL	<i>S. koreanus</i>	-0.401	-0.515, -0.288	0.939	0.884, 0.995	0.905	-
SL	PFL	<i>S. nudus</i>	-0.680	-0.781, -0.577	1.071	1.022, 1.119	0.921	+
SL	DSL	<i>S. koreanus</i>	-0.652	-0.780, -0.525	0.890	0.828, 0.953	0.799	-
SL	DSL	<i>S. nudus</i>	-1.284	-1.436, -1.132	1.223	1.151, 1.295	0.846	+
SL	MB	<i>S. koreanus</i>	-1.305	-1.451, -1.158	1.298	1.226, 1.370	0.851	+
SL	MB	<i>S. nudus</i>	-1.306	-1.417, -1.195	1.305	1.254, 1.359	0.927	+

Allometry is indicated as isometric (0), negatively (-) or positively (+) allometric.

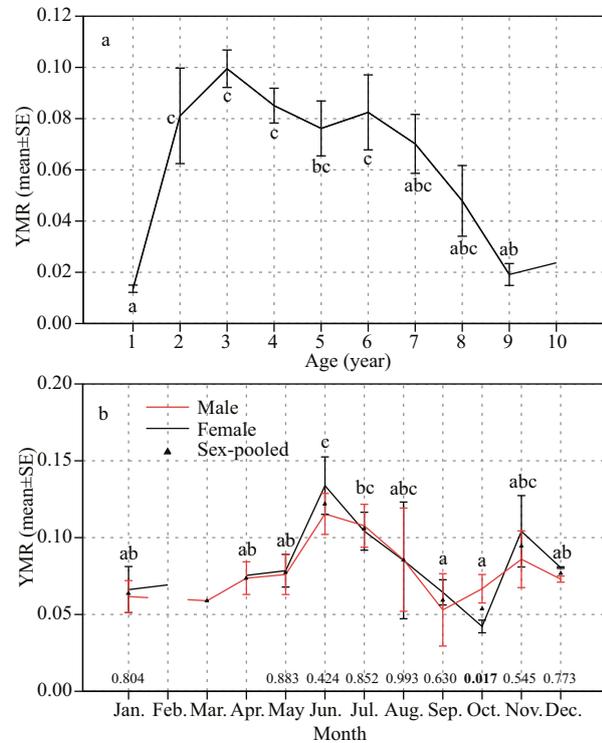


Fig.8 Mean yellow marking ratio (±SE) by age-group of *S. nudus* (a); monthly mean yellow marking ratio (±SE) of male and female *S. nudus* and monthly mean yellow marking ratio of sex-pooled *S. nudus* (b)

In (a), letters near the bars indicate significant differences between age-groups; those not sharing a common letter were significantly different (Duncan's test, $P < 0.05$); in (b), P -values based on a two-tailed Student's t -test using the log-transformed data between sexes within each age-group are given on the top of the x -axis. Only significant values ($P < 0.05$) are in bold. P -values were not present in the February–April groups due to insufficient sample sizes for the K-S normality test. Letters near the bars indicate significant differences between monthly mean yellow marking ratio of sex-pooled *S. nudus*; those not sharing a common letter were significantly different (Duncan's test, $P < 0.05$).

irregular distinct yellow markings often extend onto head and pectoral, anal, caudal, and dorsal fins (Fig.7c) but sometimes are indistinct (Fig.7b & e), or

oppositely, very conspicuous on almost the whole body except the ventral surface (Fig.7d).

Two-way ANOVAs indicated no significant age-group×month ($P > 0.05$), sex×age-group ($P > 0.05$) and sex×month ($P > 0.05$) interaction effects on the YMR. Then, the one-way ANOVAs showed significant differences in YMR among the various age-groups ($P < 0.05$) and months ($P < 0.05$) and no significant differences between the sexes ($P > 0.05$). The mean YMR values of *S. nudus* were plotted by age in Fig.8a. The age-1 group showed the smallest value while the age-3 showed the largest value. The mean YMR value rose rapidly from age-1 to age-2 and then declined gradually from age-3 to age-9. Multiple comparisons showed significant differences (Duncan's test, $P < 0.05$, respectively) between the age-1 group and the age-2~6 groups (Fig.8a).

The monthly mean YMR values were plotted separately by sex in Fig.8b. For both sexes, the monthly variations in the YMR data exhibited similar bimodal patterns with a major peak in June and a minor peak in November. The mean YMR values for both sexes increased gradually from January to May, rose rapidly from May to the major peak in June, and declined dramatically until September for males and October for females. Then, the mean YMR values for both sexes rose again to the minor peak in November and decreased in December. The Student's t -test indicated that significant difference ($P < 0.05$) between the sexes occurred only in October throughout the year (Fig.8b).

3.4 Morphological trait analysis

Regression analyses for both *S. koreanus* and *S. nudus* showed strong correlations between each of the 4 variables examined (CFL, PFL, DSL and MB) and SL (mean $R^2 = 0.857$, Table 4, Fig.9a, b, c, d). The

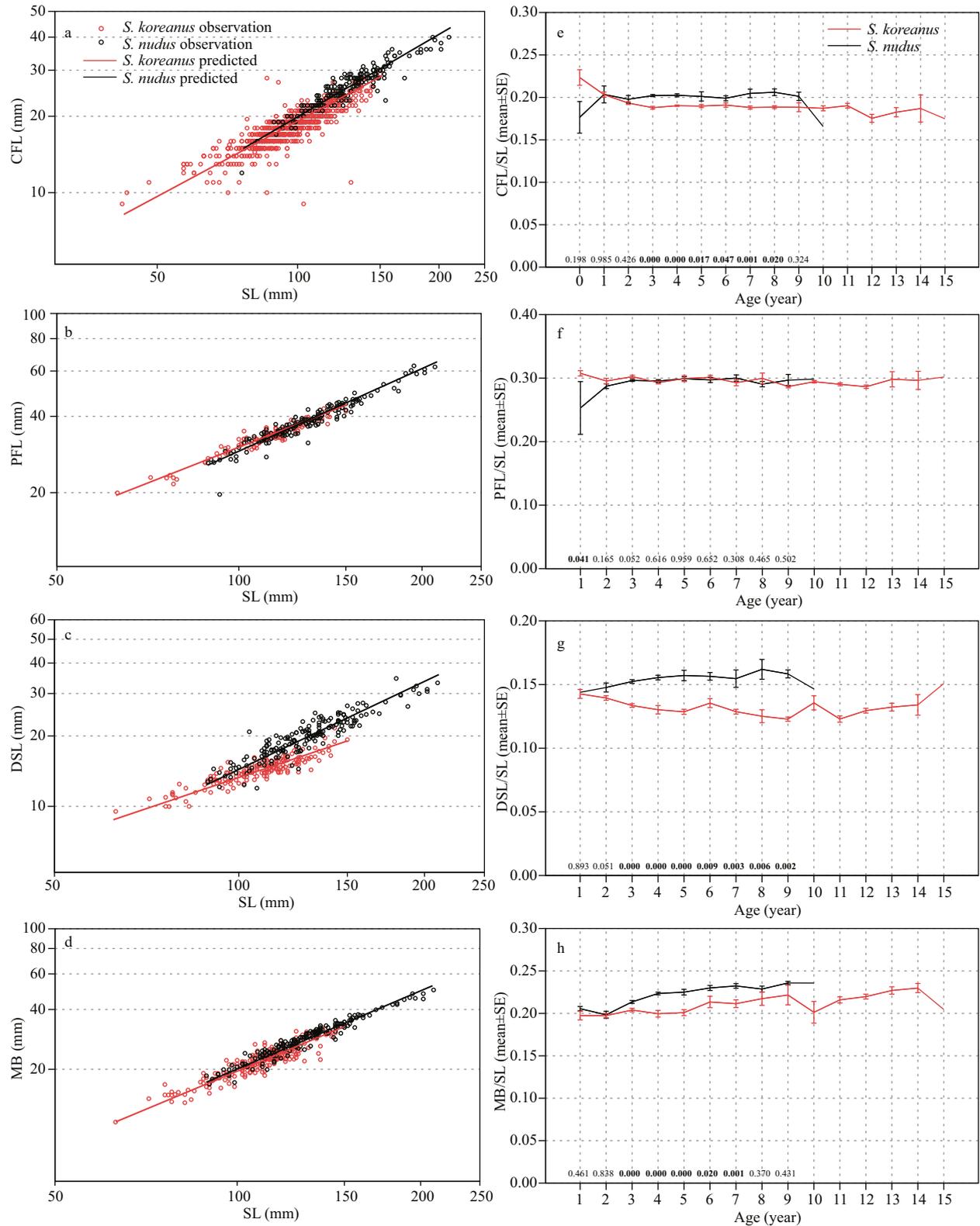


Fig.9 Plots of log-log RMA regressions based on original body measurements, comparing scaling of CFL, PFL, DSL and MB on SL in *S. koreanus* and *S. nudus* (a–d) (see Table 2 for parameters of scaling equations); error bar plots of CFL/SL, PFL/SL, DSL/SL and MB/SL by age-group for *S. koreanus* and *S. nudus* (e–h)

P-values based on a two-tailed Student’s *t*-test between species within each age-group are given on the top of *x*-axis. Only significant values (*P*<0.05) are in bold. *P*-values were not present in the 10–11 age-groups due to insufficient sample sizes for the K-S normality test.

intercept, slope and confidence intervals for each of the species are given in Table 4. The slope value of the CFL regression for *S. nudus* (1.047) is somewhat higher than the slope value of the CFL regression for *S. koreanus* (0.985), with both exhibiting isometry of CFL with respect to SL (95% CI of regression slope for each species overlaps predicted slope of 1 for isometry, Table 4). *S. nudus* exhibited positive allometry of PFL on SL (95% CI>1, Table 4), whereas *S. koreanus* showed negative allometry of PFL on SL (95% CI<1, Table 4). Similarly, *S. nudus* exhibited positive allometry of DSL on SL (95% CI>1, Table 4), whereas *S. koreanus* showed negative allometry of DSL on SL (95% CI<1, Table 4). Both species showed positive allometry of MB with respect to SL (95% CI>1, Table 4). Interestingly, in all variables, *S. nudus* had higher slope values (Table 4).

The age-related trends in morphometric ratios (CFL/SL, PFL/SL, DSL/SL and MB/SL) of *S. koreanus* and *S. nudus* were displayed in Fig.9. For CFL/SL, *S. koreanus* and *S. nudus* showed two opposite trends during the early phases of growth (<age-3): a general decrease in *S. koreanus* and a general increase in *S. nudus*. However, no interspecific significant difference was detected in CFL/SL from age-0 to age-2 (Student's *t*-test, $P>0.05$, Fig.9e). *S. nudus* was characterized by significantly higher CFL/SL mean values beginning at age-3 and continuing through age-8 (Student's *t*-test, $P<0.05$, Fig.9e).

Relative to PFL/SL, *S. koreanus* had a significant higher mean value than *S. nudus* at age-1 (Student's *t*-test, $P<0.05$, Fig.9f) while no significant interspecific difference was detected from age-2 to age-9 (Student's *t*-test, $P>0.05$, Fig.9f).

No significant interspecific difference was detected in DSL/SL at age-1 and age-2 (Student's *t*-test, $P>0.05$, Fig.9g). However, *S. nudus* was characterized by significantly higher DSL/SL mean values beginning at age-3 and continuing through age-9 (Student's *t*-test, $P<0.05$, Fig.9g).

Relative to MB/SL, both species showed a general increase with age (Fig.9h). No significant interspecific difference was detected at age-1 and age-2 (Student's *t*-test, $P>0.05$, Fig.9h). *S. nudus* was characterized by significantly higher MB/SL mean values beginning at age-3 and continuing through age-7 (Student's *t*-test, $P<0.05$, Fig.9h). No statistically significant interspecific difference was found at age-8 and age-9 (Student's *t*-test, $P>0.05$, Fig.9h), but *S. nudus* still had higher mean values than *S. koreanus*.

4 DISCUSSION

In the present study, *S. koreanus* specimens were collected easily and steadily by local fisheries off the south, east and north coasts of Shandong Peninsula. Similarly, *S. nudus* specimens were collected easily and steadily by local fisheries off the south coast of Shandong Peninsula. However, *S. nudus* were collected very rarely off the east coast of Shandong Peninsula and never off the north coast of Shandong Peninsula during the sample period. These findings are consistent with previous reports on the distributions of the two *Sebastes* (Kai and Nakabo, 2013; Fang et al., 2015; Yu et al., 2015).

To our knowledge, this study is the first validation of age determination from otoliths of *S. koreanus* and *S. nudus* and adds important biological knowledge to age, growth, reproductive biology and color pattern of these species. Excellent precision in independent ring counts on sectioned otoliths in our study provides accurate age estimates. The annual periodicity of formation of growth ring on otoliths was confirmed in the two species, which enabled analysis of their age and growth. In general, marginal increment analysis showed that annulus formation occurred once a year between June and July (early summer) in both species, suggesting that water temperatures likely correlate with the pattern of marginal increment growth.

Our results indicate that *S. nudus* grows to a larger size than *S. koreanus*, but that the longevities of the two species can be similar. Significant differences in growth curves were observed among the 3 populations of *S. koreanus*. *S. koreanus* exhibits a relatively shallow depth distribution (2–30 m) and a narrow latitudinal distribution (Fang et al., 2015; Yu et al., 2015) where environmental and biological factors may have a greater influence on its populations. Several studies on *Sebastes* explored the relationships between growth parameters (k and SL_{∞}) and latitude or water temperature. Boehlert and Kappenman (1980) and Love and Westphal (1981) noted that the growth coefficient increased with latitude in *S. serranooides* and *S. diploproa*. Pearson and Hightower (1990) reported increase in asymptotic length and decrease in growth coefficient of *S. entomelas* with increasing latitude. In the present study, given the latitudes and mean ambient water temperatures of the 3 populations of *S. koreanus* (Fig.1), we found there was no apparent latitudinal cline in growth parameters. However, the most southern (Qingdao) *S. koreanus* population showed the smallest SL_{∞} value of

110.882 cm and a high k value of 0.321/a (although this k value is somewhat lower than the Penglai k value of 0.427/a). According to previous studies, the southern coastal waters of Shandong Peninsula seems to be the southern border of the distributions of both *S. koreanus* and *S. nudus* (Kai and Nakabo, 2013; Fang et al., 2015; Yu et al., 2015). Therefore, the potential high temperature stress may impact the growth performance of the most southern (Qingdao) *S. koreanus* population, including increasing the growth rate of young fish, inducing earlier sexual maturity (see result, the youngest mature *S. koreanus* male caught in Qingdao was only age-1), as well as decreasing the asymptotic length. Moreover, since the Rongcheng population showed the highest SL_{∞} value and longevity (Fig.6) among the 3 populations of *S. koreanus*, we speculated that this population may be under the lowest fishing pressure.

The adult size of female rockfish is often larger than males (Six and Horton, 1977; Love and Westphal, 1981; Love et al., 1990; Laidig et al., 2003). Although females may have a slightly greater growth parameter SL_{∞} than males, both species in the present study did not show clear sexual difference in growth curves based on the ARSS results. Territorial behaviour has now been observed for several demersal rockfishes (Larson, 1980; Hallacher and Roberts, 1985; Markevich, 1988; Shinomiya and Ezaki, 1991), and larger males tend to hold larger territories (Shinomiya and Ezaki, 1991). Lenarz and Echeverria (1991) suggested that the tendency for the ratio of male to female SL to be high for demersal species of *Sebastes* may be related to an increased tendency for territorial behaviour by demersal males. Hence, the demersal lifestyle of both *S. koreanus* and *S. nudus* may partly explain why their SL ratios were relatively high, like the average SL ratio of the demersal rockfishes (0.97) calculated by Lenarz and Echeverria (1991).

Both *S. koreanus* and *S. nudus* are cool-temperate fishes adopting the semi-settled lifestyle (Jin, 2006; Kai and Nakabo, 2013; Yu et al., 2015). Although no long-range movements or migratory patterns have been noted for the two rockfishes, they both tend to exhibit short-range, seasonal vertical migrations (Tang and Ye, 1990; Han and Lu, 2003; Ma and Hou, 2013) that may be interpreted as adaptations to the well-defined seasonal temperature fluctuations in temperate coastal waters. The large deep dwellers (i.e., the older fish) of the *S. koreanus* and *S. nudus* gradually migrated into the shallow areas with rising nearshore water temperature in spring and

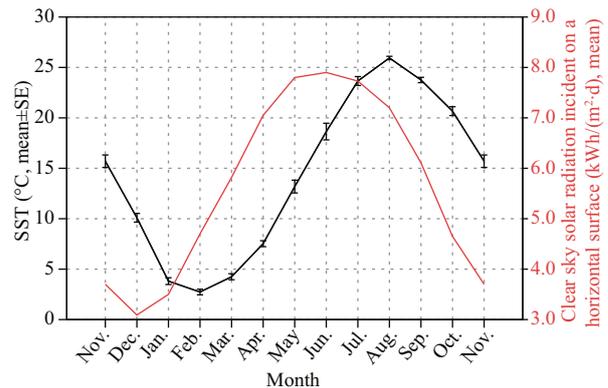


Fig.10 Monthly mean sea surface temperatures (SST) from Nov. 2013 to Nov. 2014 off the coast of Qingdao

Daily SST data were available at ftp://data.remss.com/SST/daily_v04.0/mw_ir/ and read by Python version 3.4) and monthly mean clear sky solar radiation incident on a horizontal surface at the coast of Qingdao in the 22-year period (Jul. 1983–Jun. 2005) (data were available at NASA Surface meteorology and Solar Energy: <https://eosweb.larc.nasa.gov/>).

earlysummer (approximately March–June) (Table 2, Fig.10). They gradually migrated back into their warmer, deeper habitats with declining nearshore water temperature in late autumn and winter (approximately October–next February) (Table 2, Fig.10). Other than temperature, food availability is a possible cue for their seasonal vertical migrations because their main prey items, small-sized demersal fishes (e.g., gobies) and crustaceans, exhibit the similar seasonal migration pattern (Tang and Ye, 1990; Jin, 2006; Ma and Hou, 2013). It is highly plausible that their overwintering migrations also represent mating migrations, with peak periods of copulation of both species occurring in winter (November–December). In view of the bigger-deeper distribution patterns and seasonal shallow-deep migrations of both *S. koreanus* and *S. nudus*, we suggest that individuals tend to mate with fish of a similar size. In other words, the small-sized shallow dwellers may rarely encounter the large deep dwellers except during the nearshore aggregations in summer (May–July) (Table 2).

Based on analyses of YMR, we confirmed that *S. nudus* changes its body color with age and season. The age-1 juvenile fish showed a clearly lower YMR than the older fish, while the age-3 fish showed the highest YMR (Fig.8a). Interestingly, the youngest mature fish were age-2, and all fish were mature by age-3 for *S. nudus*. These facts suggested that the bold color pattern may begin to fully express when the young fish reach first maturity.

For both sexes of *S. nudus*, the monthly variations

in the YMR data exhibited similar bimodal patterns (Fig.8b). Color changes in fish are often related to environmental stress, and light intensity is one of the most important factors regulating pigment distribution through hormone regulation (Fujii, 2000; Yasir and Qin, 2009). Additionally, the light intensity decreases along the depth gradient. In this study, the sunlight intensity in Qingdao reached its peak in June (Fig.10) when the *S. nudus* migrated into the very nearshore from their relatively deep habitats (Table 2). Consequently, although the ambient light intensity of the *S. nudus* cannot be measured precisely, the ambient light intensity may reach the peak in June. Moreover, the major peak of monthly mean YMR also appeared in June (Fig.8b). Taken together, these results support a general positive correlation between the ambient light intensity and the YMR. In view of the bigger-deeper distribution pattern of *S. nudus*, this positive correlation accounts well for the gradual decreases of the mean YMR by age-group after the first maturity (Fig.8a).

Nuptial coloration is widespread among fishes and is generally more pronounced in the males (Andersson, 1994; Sköld et al., 2008). In *Sebastes*, sexual visual communication (via color patterns, visual sensitivity, etc.) may play a more important role in mating, as relatively elaborate courtship displays reflecting males' body condition were usually observed as an initial and essential stage of mate selection in rockfishes (Helvey, 1982; Shinomiya and Ezaki, 1991; Karageorge and Wilson, 2017). In this study, the monthly mean YMR of both sexes of *S. nudus* displayed a minor peak (Fig.8b) during the peak copulation period in November (Fig.4). Throughout the year, the monthly mean YMR of males was significantly higher than the monthly mean YMR of females only in October, which was just before the peak copulation period (Fig.8b). Having considered this evidence, we speculated that *S. nudus* may show a typical carotenoid-based nuptial coloration. During the copulation season, the nuptial coloration may make the *S. nudus* more visually conspicuous and thus reduce the mate searching costs and maximize the efficiency of courtship displays in the relatively deep and murky environments. Previous observations confirmed that in *Sebastes*, males are relatively more active than females during the mating season (Helvey, 1982; Shinomiya and Ezaki, 1991; Eschmeyer et al., 2010). In view of the lowest-level period of DSI just before the peak copulation period (Fig.4), we speculated that both *S. koreanus* and *S. nudus* males

may stop feeding during the mating season. The males may spend more time and energy on mate searching and courtship activities rather than on food searching during this period. Within each sex, *S. nudus* showed a shorter low-level duration and smaller decrease in DSI than did *S. koreanus* during the copulation period (Fig.4). Moreover, Li et al. (2014) recently studied the visual sense of 4 reef fishes and indicated that *S. nudus* may have better visual acuity and scotopic vision than *S. koreanus*. All these facts imply that the bolder nuptial coloration and better visual sense of *S. nudus* may together enhance the efficiency of mate searching and sexual selection and thus reduce the energy and time costs.

Although conspicuous coloration may confer mating advantages, it is also hypothesized to impose one or more fitness costs. In fact, several empirical studies involving sexual dichromatism, color morphotypes, or closely related species suggested that conspicuous coloration may inadvertently attract the attention of potential predators and thus may be costly in terms of increasing individual predation risk (e.g., Endler, 1983, 1992; Grafen, 1990; Johnstone, 1995; Godin and Dugatkin, 1996; Godin and McDonough, 2003). On the other end of predator-prey interactions, conspicuously colored individuals may also be visually conspicuous to their prey and thus suffer greater foraging difficulty (Grether and Grey, 1996; Macedonia et al., 2002; Baird, 2008). Hence, the conspicuously colored individuals of *S. nudus* may suffer more fitness costs such as higher predation risk and greater foraging difficulty than their closely related sympatric congener, *S. koreanus*.

Predator-prey interactions can generate divergent selection in several different ways and are presumed to represent a major source of evolutionary diversification (Kerfoot and Sih, 1987; Langerhans et al., 2004; Langerhans, 2007). Strong divergent selection generated through predator-prey interactions may contribute to rapid phenotypic plasticity and evolution of morphological traits that facilitate survival (Langerhans et al., 2004; Andersson et al., 2006; Eklöv and Svanbäck, 2006; Domenici et al., 2007; Langerhans, 2009). Predators often generate phenotypic selection favouring enhanced survival abilities of prey, such as better swimming performance (e.g., Langerhans et al., 2004), stronger anti-predator defense (e.g., Ruzzante et al., 2011), etc. Moreover, divergent selection imposed by differences in foraging difficulty may also cause adaptive divergence in foraging morphology such as feeding organs (e.g.,

Malmquist, 1992; Berner et al., 2008) and swimming organs (e.g., Berner et al., 2008; Sharpe et al., 2008), etc. The morphological traits that we have identified in comparisons of *S. koreanus* and *S. nudus* have several potential implications for locomotion, foraging and anti-predator defense. *Sebastes* are relatively active swimmers in scorpaenid fishes and primarily use their caudal structures and pectoral fins for propulsion and maneuvering (Chen, 1986; Jin, 2006). Like many other ambush predators of rockfish, both *S. koreanus* and *S. nudus* have rounded caudal fins. The expanded caudal area may increase the drag but increase the thrust-production for rapid acceleration in ambush predation and escape from potential predators (Massare, 1994). Therefore, both CFL/SL and PFL/SL are probably positively associated with swimming performance (Berbel-Filho et al., 2016). Based on these assumptions, the results of Student's *t*-tests in CFL/SL and PFL/SL suggested that relative to same-aged *S. koreanus*, *S. nudus* did not show a better swimming performance than *S. koreanus* during their juvenile stage (Fig.9e & f). However, *S. nudus* tended to be a stronger swimmer than same-aged *S. koreanus* as they became mature adults (Fig.9e & f). Both *S. koreanus* and *S. nudus* are equipped with sharp, hollow spines connected to venom glands. These species typically erect their dorsal spine in response to piscivorous predators (Jin, 2006). Hence, in the case of predation avoidance related to predator gape limitation, longer dorsal spines are the important adaptation to increase chances of survival (Abrahams, 2005; Ruzzante et al., 2011). Based on this assumption, the results of Student's *t*-tests in DSL/SL suggested that, relative to same-aged *S. koreanus*, *S. nudus* may suffer a higher predation risk beginning at age-3 (Fig.9g). Both *S. koreanus* and *S. nudus* tend to swallow their prey whole (verified by visual observation) and thus are gape-limited predators (Jin, 2006). Generally, maximum prey size and foraging success are positively correlated with mouth size (especially, mouth breadth) in *Sebastes* (Roberts, 1979; Hallacher and Roberts, 1985; Anderson, 1994). Relative to same-aged *S. koreanus*, *S. nudus* was characterized by significantly greater mouth breadth beginning at age-3 (Fig.9h). These results, together with the results of CFL/SL, imply that clear differences in foraging may occur beginning at age-3.

However, our comparisons of scaling patterns between *S. koreanus* and *S. nudus* identified significant differences with respect to the scaling of PFL and

DSL relative to SL (Table 4). Moreover, despite the similar scaling patterns of CFL and MB for the two species, *S. nudus* always have higher slope values (Table 4). These data suggested a strong selective pressure to enhance swimming performance, anti-predator defense and foraging capacity in *S. nudus*. In view of the ontogenetic development of color pattern in *S. nudus* (Fig.8), we suggest that the full expression of the bold color pattern, which begins at the age of first maturity, most likely triggers the strong selective pressure on *S. nudus* through predator-prey interactions. The divergences in swimming performance, anti-predator defense and foraging capacity, together with the differences in feeding intensity during copulation season, may account well for the divergence in the growth trajectories between *S. koreanus* and *S. nudus*.

Although a recent taxonomic review has suggested that *S. nudus* and *S. pachycephalus* are sister species, their reproductive barrier is not yet completely effective, and their body color patterns are somewhat indistinguishable (Kai and Nakabo, 2013). No specimen of *S. pachycephalus* was encountered during our study. Moreover, there is no report of this species from the coasts of the Shandong Peninsula after its recent taxonomic review (Kai and Nakabo, 2013). Therefore, *S. nudus* may be the unique member from the *Sebastes pachycephalus* complex (Kai and Nakabo, 2013) inhabiting the coastal areas of Shandong Peninsula. However, the mitochondrial COI gene sequence analysis indicated that *S. nudus* maybe the species most closely related to *S. koreanus* among other closely related *Sebastes* species (Table 5, Fig.11). In all, the dramatic difference in color pattern polymorphisms, the broadly overlapping distribution and the very close phylogenetic relationship together make *S. koreanus* and *S. nudus* an ideal model to investigate the role of color-driven divergent selection and ecological adaptation in the speciation of the *Sebastes*.

It is becoming increasingly clear that, in conjunction with a solid understanding of their phylogenetic relationships, *Sebastes* spp. offers a unique opportunity to study speciation patterns in the marine realm, both modern and historic (Hyde and Vetter, 2007; Hyde et al., 2008; Ingram, 2010). In the present study, all the evidence strongly supports the hypothesis that both color pattern and bathymetric segregation play key roles in facilitating the speciation of demersal rockfishes. Color pattern polymorphisms are relatively common in *Sebastes* (e.g., Kai and Nakabo, 2013;

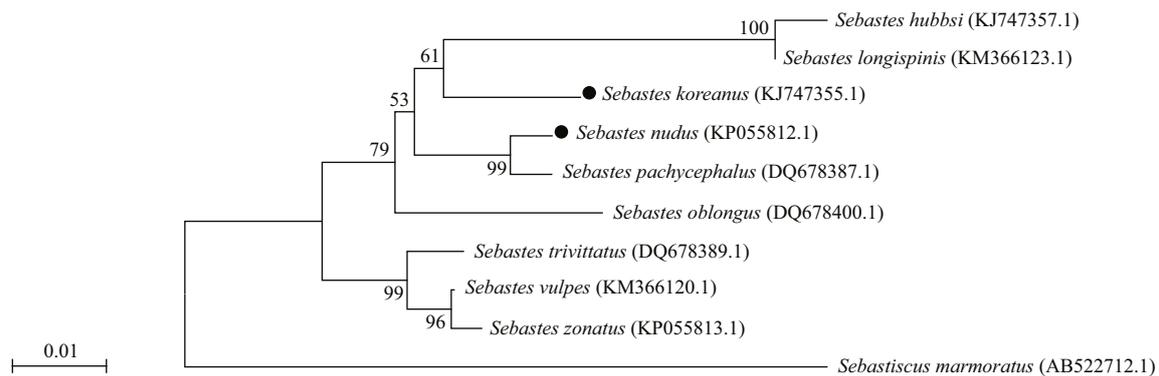


Fig.11 Neighbor-joining tree based on mitochondrial COI gene sequences available in GenBank, showing the relationships among 9 closely related *Sebastes* species in clade NWPs (*Sebastiscus marmoratus* as an out group)

The sequences were aligned using Clustal W, and the tree was constructed using the Kimura 2-parameter model and 1 000 bootstrap replications in the software MEGA 6.06. Parentheses indicate the NCBI registration number.

Table 5 Genetic distance based on the mitochondrial COI gene sequences among 9 closely related *Sebastes* species in clade NWPs

	<i>Lon</i> *	<i>Hub</i>	<i>Kor</i>	<i>Nud</i>	<i>Pac</i>	<i>Obl</i>	<i>Tri</i>	<i>Zon</i>
<i>S. longispinis</i>								
<i>S. hubbsi</i>	0.005 3							
<i>S. koreanus</i>	0.049 7	0.055 5						
<i>S. nudus</i>	0.051 6	0.057 5	0.032 6					
<i>S. pachycephalus</i>	0.051 6	0.057 5	0.034 5	0.008 9				
<i>S. oblongus</i>	0.061 4	0.067 4	0.042 1	0.038 3	0.040 2			
<i>S. trivittatus</i>	0.067 3	0.073 3	0.042 0	0.038 2	0.036 3	0.046 0		
<i>S. zonatus</i>	0.065 2	0.071 2	0.042 0	0.042 0	0.040 1	0.047 8	0.014 3	
<i>S. vulpes</i>	0.063 3	0.069 3	0.038 2	0.038 2	0.036 3	0.046 0	0.010 7	0.003 5

* *Lon*: *S. longispinis*; *Hub*: *S. hubbsi*; *Kor*: *S. koreanus*; *Nud*: *S. nudus*; *Pac*: *S. pachycephalus*; *Obl*: *S. oblongus*; *Tri*: *S. trivittatus*; *Zon*: *S. zonatus*. Bold number highlight the genetic distance between *S. koreanus* and *S. nudus*.

Frale et al., 2015). The vast majority of this genus inhabit coastal or littoral zones (Nelson et al., 2016) that are well characterized by broad-spectrum sunlight and high luminous intensity. *Sebastes* have many visual predators (Mills et al., 2007), and themselves prey upon visually well-equipped organisms such as crustaceans and other fish (Guthrie, 1986). Hence, visual factor tends to play a more important role than any other sensory factors in inter- and intraspecific communication as well as predator-prey interactions and be an alternative force driving evolutionary process in *Sebastes*. A fish's boldness in coloration could reliably indicate its overall quality, as relatively conspicuous-colored fish tend to be better informed about potential predators, more likely to survive encounters with them, and feed at higher rates or more persistently than dull-colored fish. Bold coloration in rockfish thus appears to be an honest signal of high quality (Johnstone, 1995) such as high efficiency in mate searching, good swimming

performance, good anti-predator defense and good foraging capacity. All these advantages may together make conspicuous-colored fish grow faster and attain a bigger size than dull-colored fish. Moreover, in view of the prevalence of the bigger-deeper phenomenon (Love et al., 1991), demersal lifestyle (Hyde and Vetter, 2007) and seasonal shallow-deep migration pattern (Tang and Ye, 1990) in *Sebastes*, we suggest that the conspicuous-colored adults are likely to migrate into deeper areas than dull-colored adults during mating period. The spatial separation (bathymetric segregation) of mating ground between color phenotypes may gradually develop through the strong divergent color-driven ecological and sexual selection and result in individuals reproducing and populations establishing in separate habitats. Migration of suboptimal phenotypes or competition between phenotypes may favour assortative mating, reducing gene flow and ultimately allowing speciation along the depth gradient (Doebeli and Dieckmann, 2003).

5 CONCLUSION

In summary, this study first ascertained the age, growth, reproductive and feeding seasonality and color pattern of two very closely related rockfishes, *S. koreanus* and *S. nudus*. Based on the body color analyses, we confirmed that *S. nudus* changes its body color with age and season and fully expresses the carotenoid-based nuptial coloration when reaching first maturity. Moreover, our comparisons of morphological traits that are likely related to survival and quality of these fishes suggested that *S. nudus* might suffer higher predation risk and foraging difficulty beginning at age 3. In view of the ontogenetic development of the color pattern in *S. nudus*, we suggested that the full expression of nuptial coloration most likely triggers the strong selective pressure to enhance swimming performance, anti-predator defense and foraging capacity of *S. nudus* through predator-prey interactions. By understanding all these details, we further inferred a hypothesis that both color pattern and bathymetric segregation play key roles in facilitating the speciation of demersal rockfishes. We expect that in future, empirical research on color-driven speciation in *Sebastes* will become more integrative, and aspects of biology such as age, growth and reproductive biology should doubtlessly be integrated into this research. In this way, we can take full advantage of the *Sebastes* species flock as a tool for understanding the evolution of biological diversity.

6 DATA AVAILABILITY STATEMENT

The digital photographs of fish and otoliths are only available upon request to the corresponding author, Dr. YE Zhenjiang (yechen@ouc.edu.cn). All other data are available within the paper.

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