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RESEARCH ARTICLE

Inter-annual Variability in Growth and Maturation of the Swordtip Squid *Uroteuthis edulis* in Yilan Bay off Northeastern Taiwan

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Abstract

The swordtip squid *Uroteuthis edulis*, distributed in the temperate and tropical neritic waters in the Indo-Pacific region, is a crucial component of marine ecosystems and is a target species of fisheries in the Northwest Pacific. Although studies have elucidated the growth and maturation of the squid in the southern East China Sea (ECS) shelf, few have assessed the population biology of the squid in waters in the vicinity of the southern ECS. We collected samples of swordtip squid from a trawler in Yilan Bay (YLB) between January 2011 and December 2012 to examine the growth and maturation of the squid based on statolith microstructures and the inter-annual variability in certain parameters as well as the potential underlying mechanisms. The average dorsal mantle length (ML) of the squid was significantly higher in 2011 than in 2012 in both sexes. The ML-body weight relationship differed significantly between 2011 and 2012 in both sexes. Squid hatching peaked in summer (June and August)in 2011 and spring (March and April) in 2012. The average ML-at-age data were described using the exponential function and power function for female and male squid, respectively. Female squid matured to 139 mm at 133 days in 2011 and to 133 mm at 137 days in 2012. Male squid matured to 160 mm at 151 days in 2011 and to 148 mm at 133 days in 2012. However, the ML- and age-at-maturity of the squid in YLB were lower than those of the squid in the southern ECS shelf. These results indicate that YLB is one of the feeding grounds for squid that have hatched in the southern ECS shelf and have been transported southward intermittently to YLB. Further study of the population structure and potential population connectivity of the squid in the entire ECS shelf is warranted to obtain data for the development of effective conservation and management measures for the squid and its fisheries in the Northwest Pacific.

Keywords: Neritic squid, *Uroteuthis edulis*, Statolith, Yilan Bay, Northwest Pacific

1. Introduction

Identification of population (or stock) structures of marine fishery resources is a key component of fisheries ecology and is essential for fisheries management [1]. An insufficient understanding of the population structure may lead to overexploitation of fisheries, adversely affecting the sustainability of the marine fishery population [2]. The relevant population structure parameters reflect the resilience of populations that face increasing pressure from fisheries and climate changes, and the parameters provide substantial information for developing conservation and management measures [3,4].

Marine fishery resources contribute substantially to human food security [5]. Cephalopods play a critical role in sustaining trophic webs in pelagic ecosystems. They typically prey on small fishes, crustaceans, and other cephalopods (i.e.,

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cannibalism). Cephalopods are preyed on by pelagic fishes (e.g., sharks, tunas and billfishes), marine mammals (e.g., whales, dolphins and seals), and seabirds [6,7]. Although cephalopods are a target of commercial fisheries worldwide, global cephalopod landings disproportionately rely on a limited number of oceanic squid species [8]. The development of commercial fisheries, however, may directly influence the biomass and structure of squid populations and indirectly influence the species that interact with squids in the trophic web [9]. Therefore, obtaining an understanding of the population structure and population connectivity of these commercially exploited squid species will provide essential information that can be used as a reference for developing conservation and management measures relevant to these species and their ecosystems [10–12].

The swordtip squid *Uroteuthis* (*Photololigo*) *edulis* is a neritic squid distributed in the temperate and tropical coastal waters of the Indo-Western Pacific, from the coastal waters of Japan in the north to the surrounding waters of Australia in the south [13]. The swordtip squid is a critical component of marine ecosystems in Northwest Pacific regions and is a target species for many commercial fisheries, especially those in the East China Sea (ECS) and Tsushima Strait [8,14]. Studies on swordtip squid populations in the ECS have mainly examined the growth and maturation of seasonal spawning groups and seasonal cohorts. Based on the distribution and occurrence time of mature females, the species spawning grounds are suggested to be located between 25.5°N and 26.5°N and between 121.5°E–122.5°E. Wang et al. (2008) revealed that the peak spawning seasons of the squid are spring and autumn, with the spring spawning squid exhibiting smaller size than the autumn spawning ones [15]. According to statolith microstructure analysis in 2002–2004, the lifespan of the swordtip squid is approximately 9 months. The swordtip squid hatches throughout the year, with the peak hatching periods occurring from March to April and from October to November [16]. Growth rates differ among the seasonal cohorts of the swordtip squid; the winter cohort generally grows more rapidly and attains a larger size than the summer cohort [17]. Comparisons of the life-history traits of female squid between the waters off southern Japan and northern Taiwan revealed potential population connectivity of the swordtip squid in the two regions [18]. Recent studies have provided novel scenarios for possible spawning grounds and migration routes of the swordtip squid in the waters off southern Japan. Squid may hatch in the southern ECS shelf and be then transported by currents to the northern region (off southern Japan) [19–21]. The distinct sizes of the squid occurring in different seasons may be related to the differing spawning ground locations and migration routes [22–24]. Data on the population structure and potential population connectivity of the squid in waters in the vicinity of southern ECS can provide substantial information for developing conservation and management measures for the squid and relevant fisheries in the Northwest Pacific region. However, such data are limited.

Squid have a short life span, and their annual abundance and distribution typically exhibit wide fluctuations in rapid response to varying environmental conditions [25–27]. Variation in the life-history traits of micro-cohorts (seasonal cohorts) of several loliginid squid species has been studied [17,28–30]. However, although inter-annual variability may explain the inconsistency in the results of growth studies on squid, few studies have assessed the inter-annual variability in the growth and maturation of squid [31–33].

Yilan Bay (YLB) is located off northeastern Taiwan, where oceanographic conditions are strongly affected by seasonal intrusions of the Kuroshio Current (KC) [34]. YLB has been suggested to be suitable spawning and feeding grounds for several marine fishes [35] and is a major fishing ground in Taiwan [36,37]. The potential movement of the Japanese anchovy *Engraulis japonicus* between the southern ECS shelf and YLB has been studied [38]. Inter-annual fluctuations in the oceanographic conditions of YLB may substantially influence the abundance and life-history traits of the swordtip squid populations inhabiting YLB. Therefore, this study examined the inter-annual variability in the growth and maturation of the swordtip squid in YLB to provide essential information on the population structure of the swordtip squid in the Northwest Pacific.

2. Materials and methods

2.1. Squid samples

Squid samples were collected monthly from January 2011 to December 2012 from a sampling vessel in the Dasi Fishing Port of Yilan County. The sampling vessel was a daily trip trawl vessel operated in YLB, with fishing grounds in the waters surrounding Gueishan Island (24.80°N–24.88°N and 121.88°E–121.97°E; Fig. 1). A minimum of 30 individuals were collected each month, with the actual sample size depending on the harvest of the fishermen. The squid samples were transported to the

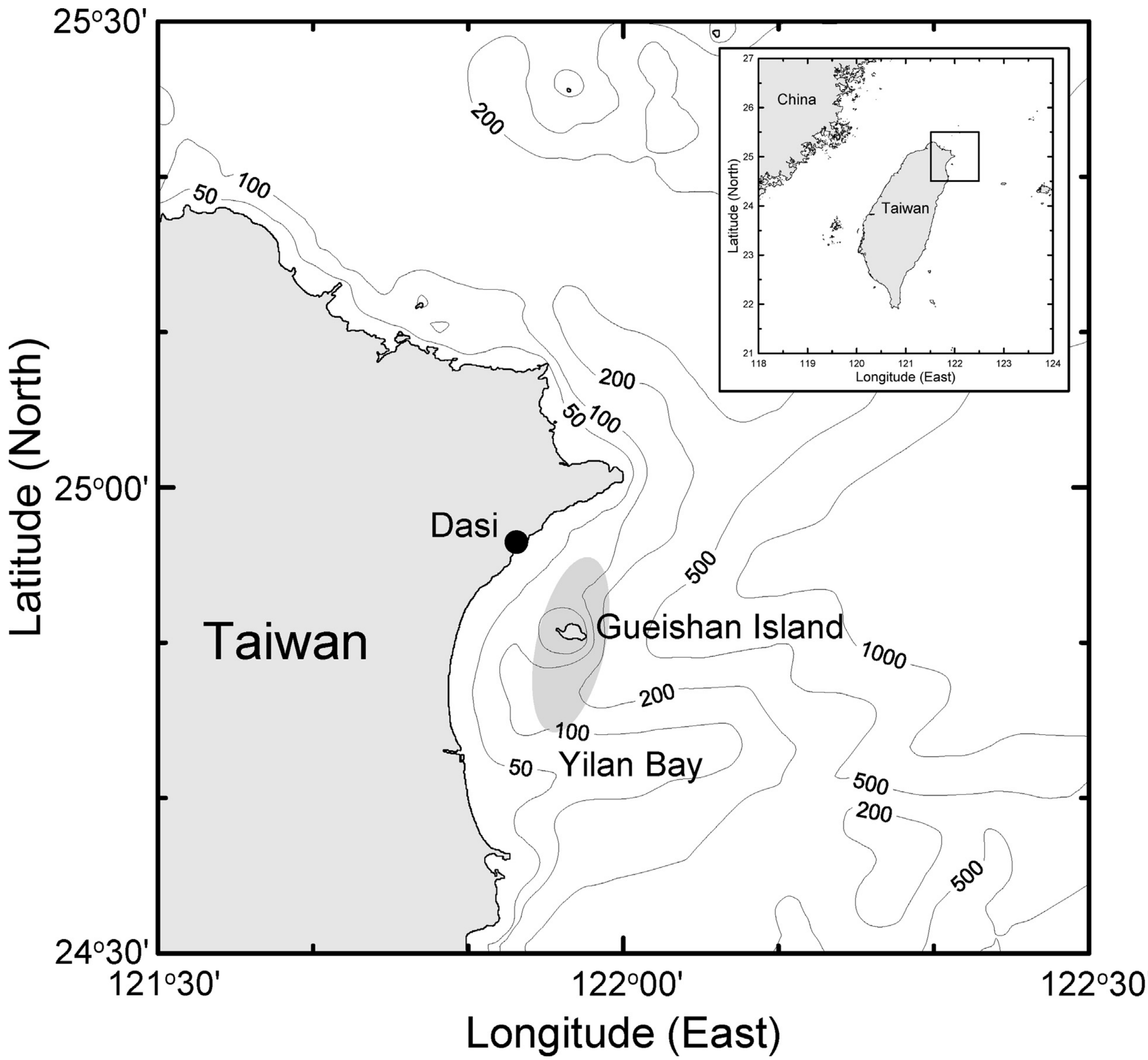

Fig. 1. Map showing potential fishing grounds (grey shaded areas) for the sampling vessel in Yilan Bay off northeastern Taiwan. (The sampling location Dasi Fishing Port is shown).

laboratory at National Taiwan Ocean University (Keelung) and were immediately preserved in a freezer (−20 °C).

The squid samples were thawed before examination in the laboratory. The swordtip squid *U. edulis* were identified on the basis of a pair of photophores on the ink sac and morphological features [13]. The squids were then sexed, and the following parameters were measured: dorsal mantle length (ML), body weight (BW), and gonad weight (GW; comprising the sums of the weight of ovaries, oviducts and oviducal glands, and the nidamental gland in the female squid and the testes and Needham complex in the male squid). The length and weight measurements were taken to the nearest 1 mm and 1 g, respectively. For each squid, the sexual maturity stage was assigned according to the maturity scale [39]: stage I (juvenile); stage II (immature); stage III (maturing); stage IV (mature); and stage V (spent). The statoliths of each squid were extracted, washed with water, and stored in 96-well plates with liquid paraffin.

2.2. Age determination

The statolith (left) was cleaned with xylene (~1 min) and ethanol (~1 min), dried and embedded in a mold with resin. After hardening, the resin block was cut to an appropriate size and mounted on a glass slide. A transverse plane of the statolith was obtained by grinding it from the anterior side. The prepared statoliths were examined under a compound microscope (Olympus BX-50) equipped with a CCD camera. Frames of statolith images were captured from the nucleus to the margin of the rostrum and saved as digital files. Multiple frames of each statolith image were merged to form an entire statolith image through Photoshop software. The growth increments of the statolith were determined and marked along the longest axis from the nucleus to the edge of the rostrum using PowerPoint.

The growth increment period of the statoliths of the swordtip squid has not been experimentally validated; however, indirect evidence (growth rate compared with that obtained from tag and recovery experiments) regarding the daily growth increments of the swordtip squid was reported [40]. Thus, in the present study, the number of increments (NI) was considered equivalent to the age of the squid in days, and hatching dates were determined by subtracting the estimated daily age from the capture date.

2.3. Growth model

The relationship between ML and BW of *U. edulis* was fitted using the following power function:

$$BW = aML^b,$$

where BW is the body weight (g), ML is the mantle length (mm), and a and b are coefficients to be estimated.

Average ML-at-age data were calculated for the squid (by sex and by year) and fitted to six growth functions, as follows:

Linear function: $Y = a + bX$

Exponential function: $Y = a \times e^{(bX)}$

Power function: $Y = aX^b$

Logistic function: $Y = \frac{a}{1+e^{-b(X-c)}}$

von Bertalanffy growth function (VBGF): $Y = a(1 - e^{-b(X-c)})$

Gompertz growth function: $Y = ae^{b(1-e^{-cX})}$,where Y is ML, X is the age in days.

Additionally, the Schnute function was also tested.

Schnute function:

$$Y = \left[L_1^{g_2} + \left(L_2^{g_2} - L_1^{g_2}\right) \times \left(\frac{1 - Exp\left(-g_1 \times (t - t_1)\right)}{1 - Exp\left(-g_1 \times (t_2 - t_1)\right)}\right)\right]^{\left(1/g_2\right)}$$

where t_1 and t_2 are the minimum and maximum ages of the squid samples, respectively. L_1 and L_2 denote the estimated size at the minimum and maximum ages, respectively. The growth function parameters (a, b, c, g_1 and g_2) were estimated using the least squares method (for linear models) and a non-linear estimation method (for non-linear models).

The best-fit growth function was determined using the Akaike information criterion (AIC) [41] as follows:

$$\text{AIC} = -2LL + 2k,$$

where LL is the expected logarithm of the maximum likelihood, and k is the number of estimated parameters in each function.

2.4. Maturation parameters

The gonadosomatic index (GSI) for the squid was calculated as follows:

$$GSI = \frac{GW}{(BW - GW)} \times 100\%$$

where GW is the gonad weight of the squid, and BW is the body weight of the squid.

Maturity ogives, which represent the proportion of mature individuals at a given age or length, for the squid were estimated through the logistic function,

$$Y = \frac{1}{1 + e^{-a(X-b)}}$$

where Y is the proportion of mature individuals within a particular age (10-day intervals) or ML (20 mm intervals) class, X is the age or ML class, a is the slope of the function, and b is the age or ML at which 50% of individuals matured [42]. Parameters a and b were estimated through non-linear estimation using the simplex method.

Differences in the ML-BW relationship of the squid between sexes were examined through analysis of covariance (ANCOVA). Parameter calculations and statistical analyses were performed using R version 3.1.1 [43]. Statistical significance was set at the 5% level for the tests.

3. Results

3.1. ML composition

A total of 1112 specimens (614 females and 498 males) and 2785 specimens (1661 females and 1124 males) of the swordtip squid were collected in 2011 and 2012, respectively (Table 1). For the squid collected in 2011, the ML ranged between 39 and 254

Table 1. Summary information for Uroteuthis edulis samples in Yilan Bay off northeastern Taiwan between January 2011 and December 2012. (F: females, M: males).

Year month	Collected (N)		Aged (N)		ML range (mm)		BW range (g)	
	F	M	F	M	F	M	F	M
2011								
Jan.	13	9	11	7	104–238	89–233	55–482	39–366
Feb.	9	2	7	1	75–160	46–68	25–158	8–21
Mar.	37	40	29	33	44–137	42–172	6–101	6–184
Apr.	66	45	58	37	44–153	39–126	8–132	8–87
May	69	26	55	19	73–220	72–168	22–311	20–140
Jun.	49	85	44	73	53–194	43–143	14–244	8–143
Jul.	33	33	28	25	60–184	58–175	25–205	13–157
Aug.	46	76	44	66	84–208	66–189	34–278	20–198
Sep.	27	12	24	10	62–254	54–171	16–457	13–270
Oct.	91	66	88	61	39–212	46–189	7–301	7–202
Nov.	119	54	113	53	59–216	58–183	12–280	13–172
Dec.	58	47	56	46	51–247	50–161	9–513	8–161
2012								
Jan.	83	54	81	54	46–276	39–199	7–577	5–258
Feb.	70	64	59	56	42–178	35–131	7–214	4–84
Mar.	254	135	85	52	37–210	39–169	5–337	6–193
Apr.	103	40	82	35	46–185	49–143	8–242	10–110
May	62	20	61	19	60–172	66–133	12–188	15–88
Jun.	310	182	79	54	24–230	24–184	3–336	2–193
Jul.	141	141	102	62	55–228	57–202	12–427	12–235
Aug.	154	126	83	40	38–207	52–194	4–245	8–214
Sep.	258	158	107	37	46–210	49–139	7–288	7–102
Oct.	59	35	51	35	42–138	45–114	5–107	6–52
Nov.	107	121	62	60	45–207	49–169	6–373	7–165
Dec.	60	48	60	48	38–246	45–151	4–546	8–130

mm and the BW ranged between 6 and 513 g, whereas for the squid collected in 2012, the ML ranged between 24 and 278 mm and the BW ranged between 2 and 577 g. In 2011, the smallest individual was collected in October (a female with a length of 39 mm and a weight of 7 g), and the largest individual was collected in September (a female with a length of 254 mm and a weight 457 g). In 2012, the smallest individual was collected in June (a female with a length of 24 mm and a weight of 3 g), and the largest individual was collected in January (a female with a length of 276 mm and a weight of 577 g).

The monthly ML composition of the squid had similar seasonal variation in both sexes (Fig. 2). The squid with a greater ML were collected in January, May, July, and August in both sexes. The average ML of the squid in 2011 was significantly greater than that of the squid in 2012 in both sexes (females [average ± standard deviation]: 103.5 ± 38 mm and 88.6 ± 36 mm in 2011 and 2012, respectively; $t = 8.619$, $p < 0.001$; males: 93.6 ± 32 mm and 86.1 ± 30 mm in 2011 and 2012, respectively; $t = 4.458$, $p < 0.001$).

The ML-BW relationship of the squid was described using a power function (Fig. 3). The ML-BW relationship significantly differed between 2011 and 2012 in females (ANCOVA, $F_{1,\ 2271} = 10.387$, $p = 0.0013$) and males (ANCOVA, $F_{1,\ 1618} = 9.166$, $p = 0.0025$).

Females:

2011 $BW = 0.0010ML^{2.3599}$ ($n = 614$, $R^2 = 0.9638$)

2012 $BW = 0.0006ML^{2.4362}$ ($n = 1{,}661$, $R^2 = 0.9617$)

Males:

2011 $BW = 0.0013ML^{2.2826}$ ($n = 498$, $R^2 = 0.9412$)

2012 $BW = 0.0008ML^{2.3787}$ ($n = 1{,}124$, $R^2 = 0.9470$)

3.2. Hatching date distribution

The growth increments of 988 swordtip squids (557 females and 431 males) in 2011 and 1464 swordtip squids (912 females and 552 males) in 2012 were successfully determined based on the statolith microstructure (Table 1). The age ranges of the squid collected in 2012 (53–189 days in females and 53–177 days in males) were wider than those of the squid collected in 2011 (72–167 days in females and 80–171 days in males).

The squid collected in 2011 hatched between July 2010 and September 2011 (Fig. 4), with the main hatching months being December 2010, March 2011, May–June 2011, and August 2011. The squid collected in 2012 hatched between July 2011 and

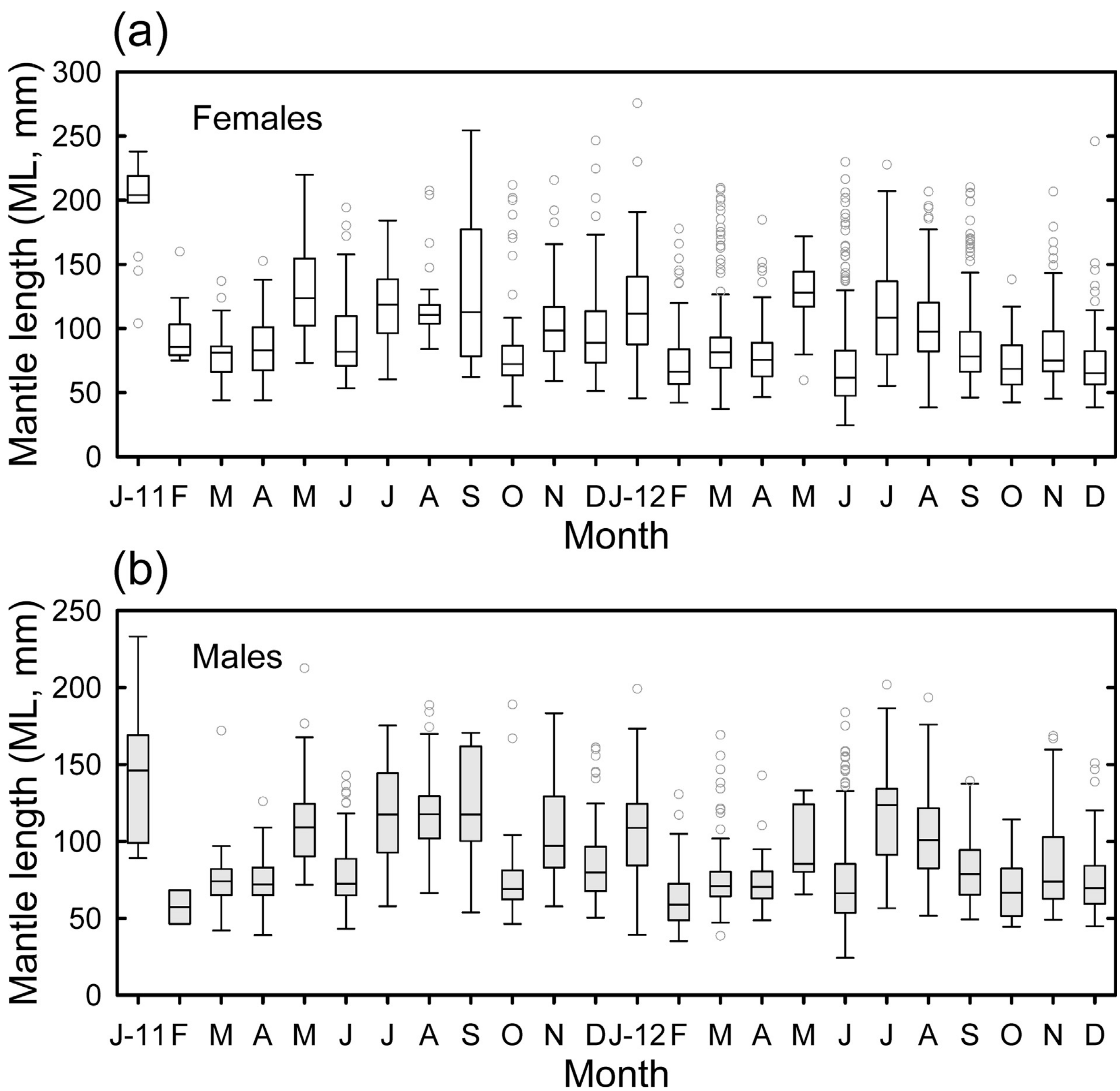

Fig. 2. Monthly mantle length composition of the swordtip squid in Yilan Bay off northeastern Taiwan from January 2011 to December 2012. (box range, first and third quartiles; band, median; whiskers, 1.5 interquartile; circle, outliers. a, females; b, males).

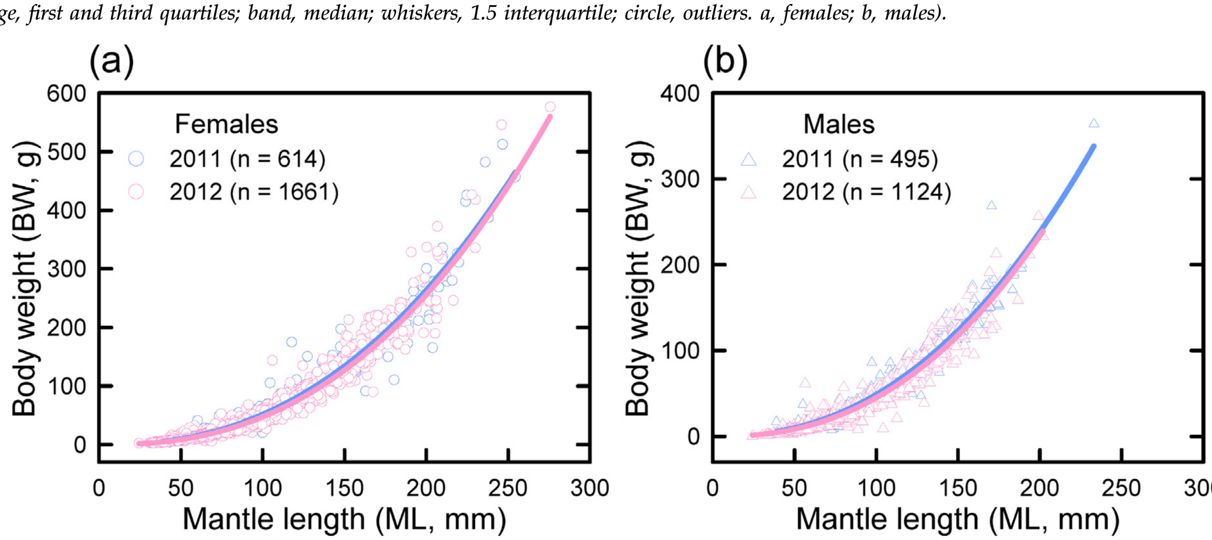

Fig. 3. Relationship between mantle length and body weight for the swordtip squid in Yilan Bay off northeastern Taiwan in 2011 and 2012. (a, females; b, males).

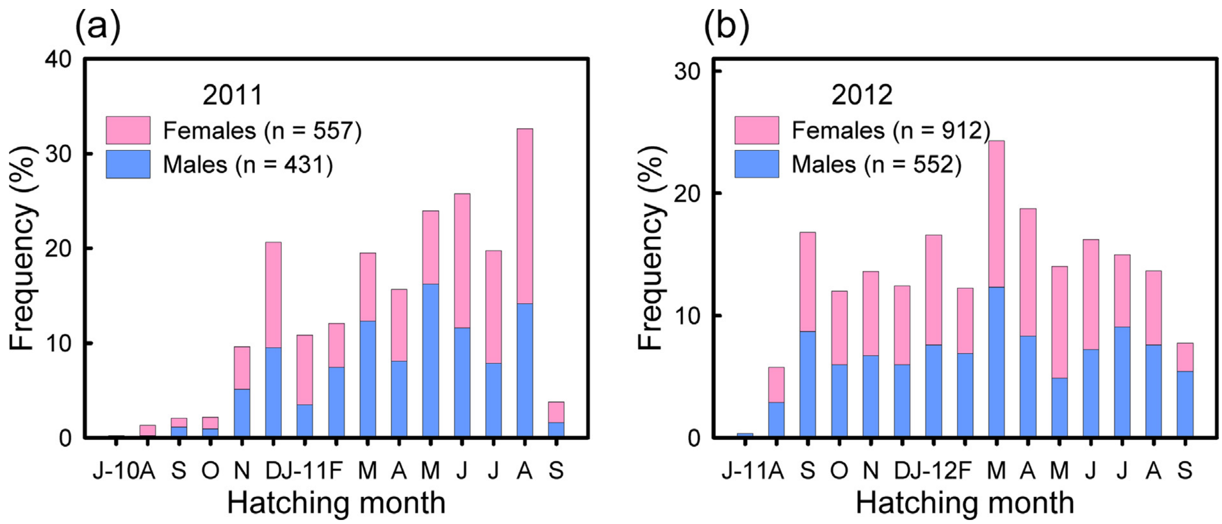

Fig. 4. Frequency distribution of back-calculated hatching months of the swordtip squid in Yilan Bay off northeastern Taiwan in (a) 2011 and (b) 2012.

September 2012 (Fig. 4), with the main hatching months being September 2011, January 2012, March 2012, and June−July 2012.

3.3. Growth pattern

The ML-at-age was calculated for the squid (by sex and by year) and fitted to the growth function (Fig. 5). The parameters of asymptotic growth functions (the logistic, von Bertanlanffy, Gompertz and Schnute functions) failed to converge for the average ML-at-age data in females. In both 2011 and 2012, according to the AIC values, the average ML-at-age data were optimally described using the exponential function and power function for females and males, respectively (Table 2). The ML-at-age data in males revealed a higher variation than those in females (Fig. 5). For females, a high variation in the ML-at-age data was observed after 130 days for individuals in 2011, whereas a high variation in the ML-at-age data was noted after 140 days for individuals in 2012.

3.4. Maturation

Mature female individuals were found nearly year-round, with peaks in May and November in 2011 and in March and May in 2012 (Fig. 6). Mature male individuals were also found nearly year-round, with peaks in November to December, May,

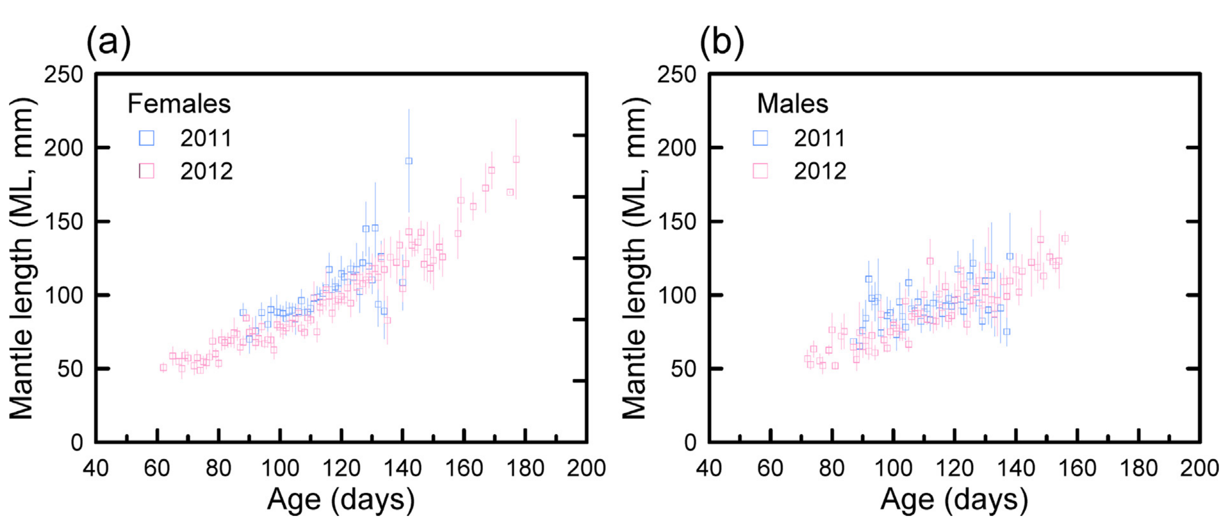

Fig. 5. Mantle length-at-age data (average and standard error) for the swordtip squid in Yilan Bay off northeastern Taiwan in 2011 and 2012. (a, females; b, males).

Table 2. Parameters and Akaike's information criterion (AIC) of fitted growth functions of the mantle length-at-age data for Uroteuthis edulis in Yilan Bay off northeastern Taiwan.

Sex/Fit	2011						2012					
	n	Parameters				AIC	n	Parameters				AIC
		a/L_1	b/L_2	c/g_1	g_2			a/L_1	b/L_2	c/g_1	g_2	
Female												
Linear (2)	44	−28.598	1.149			362.3	93	−24.467	1.088			696.4
Exponential (2)	44	30.091	0.011			360.9	93	25.330	0.011			662.5
Power (2)	44	0.364	1.189			361.9	93	0.293	1.221			683.7
Logistic (3)	44	–	–	–			93	–	–	–		
VBGF (3)	44	–	–	–			93	–	–	–		
Gompertz (3)	44	–	–	–			93	–	–	–		
Schnute (4)	44	–	–	–			93	–	–	–		
Male												
Linear (2)	48	47.033	0.405			378.1	72	−7.712	0.859			535.5
Exponential (2)	48	55.801	0.004			378.2	72	28.367	0.010			537.3
Power (2)	48	8.751	0.498			378.0	72	0.515	1.089			533.4
Logistic (3)	48	105.5	0.037	56.8		379.7	72	215.0	0.002	134.0		537.5
VBGF (3)	48	106.2	0.031	42.2		379.7	72	–	–	–		
Gompertz (3)	48	0.456	5.448	0.034		379.7	72	16.073	3.054	0.007		537.4
Schnute (4)	48	63.306	101.448	−0.078	25.841	380.2	72	55.019	127.912	−0.013	2.061	539.3

and August in 2011 and in January, March, and November in 2012.

The average GSI with age (in months) exhibited a similar pattern in the female squid in both 2011 and 2012, with maturation beginning at 4 months and maturation being attained (maturity stage IV) at 6 months (Fig. 7). In male squid, maturation began at 3 months, and maturation was attained (maturity stage IV) at 5 and 6 months for 2011 and 2012, respectively.

Age and ML at maturity of the squid were estimated using a logistic function for each sex by age group and size class. The functions by age group explained 97.1% and 97.6% of the variance in the maturity of females in 2011 and 2012, respectively (Fig. 8a) and explained 80.3% and 98.8% of the variance in the maturity of males in 2011 and 2012, respectively (Fig. 8b). Females matured at 133 days in 2011 and at 137 days in 2012 (4 days longer). By contrast, the males matured at 151 days in 2011 and at 146 days in 2012 (5 days shorter).

The functions by size class explained 99.1% and 99.7% of the variance in the maturity of females in 2011 and 2012, respectively (Fig. 9a) and explained 95.0% and 80.9% of the variance in the maturity of males in 2011 and 2012, respectively (Fig. 9b). ML-at-maturity for females in 2011 was 139 mm, which was more than that for individuals in 2012 (133 mm).

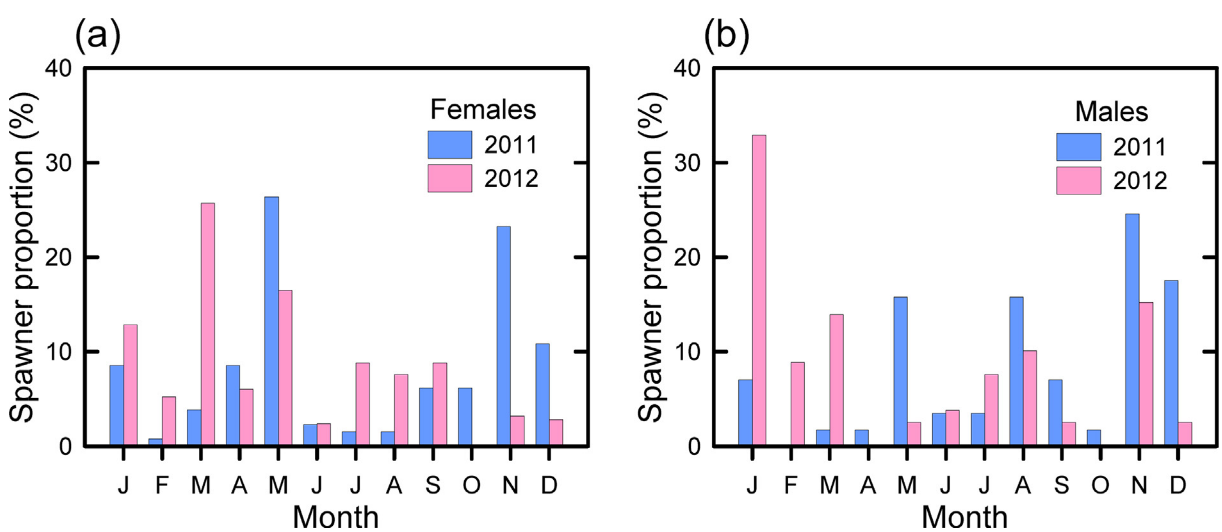

Fig. 6. Percentage of squid spawners (mature individuals) by month of the total spawners in 2011 and 2012. (a, females; b, males).

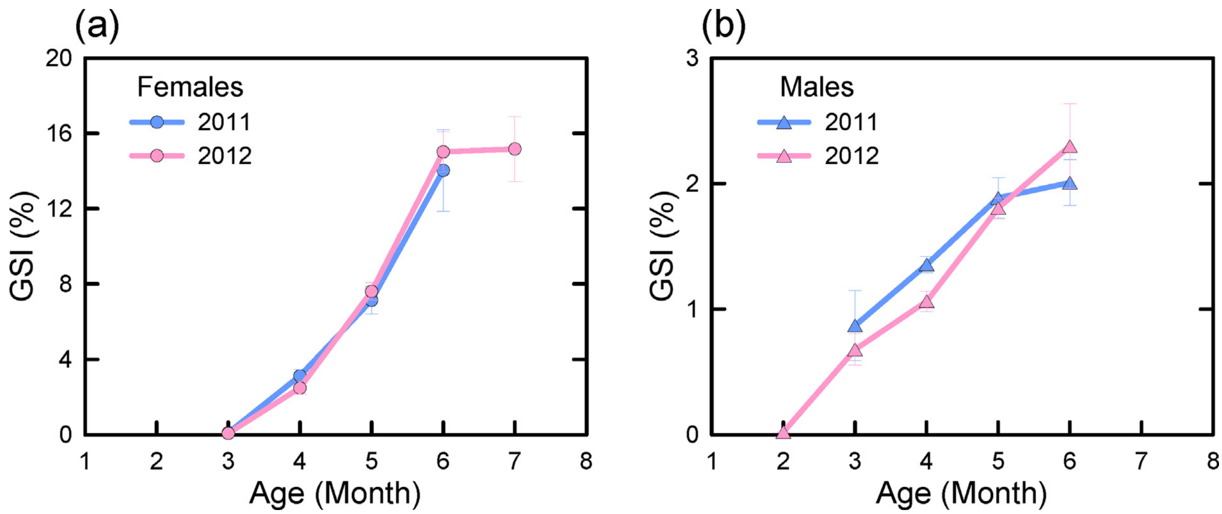

Fig. 7. Gonadosomatic index (GSI) by age group (in month, average and standard deviation) of the swordtip squid in Yilan Bay off northeastern Taiwan in 2011 and 2012. (a, females; b, males).

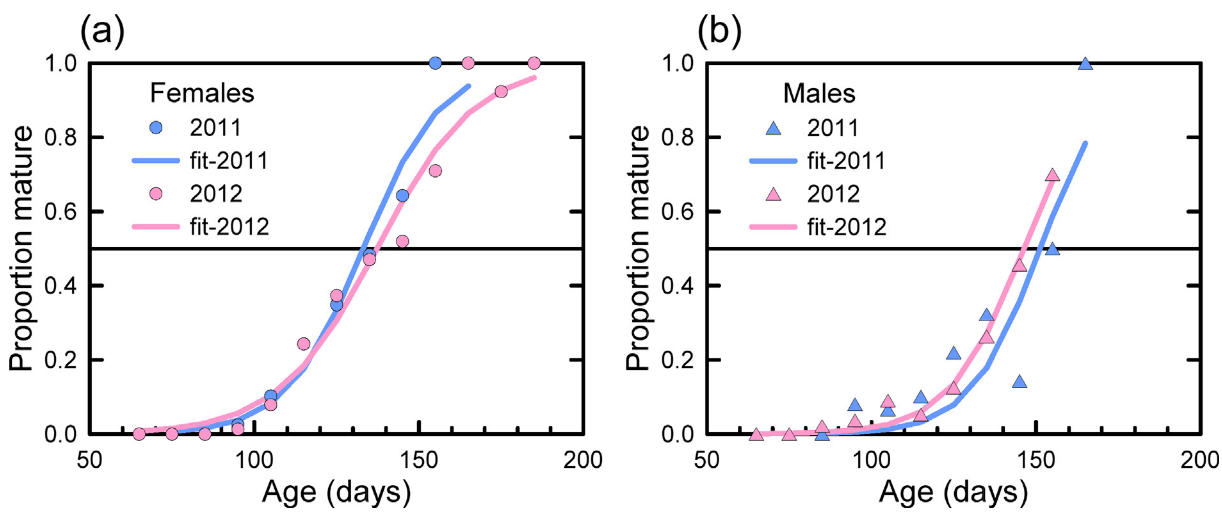

Fig. 8. Percentage of mature individuals by age group and estimated maturity ogives of the swordtip squid in Yilan Bay off northeastern Taiwan in 2011 and 2012. (a, females; b, males).

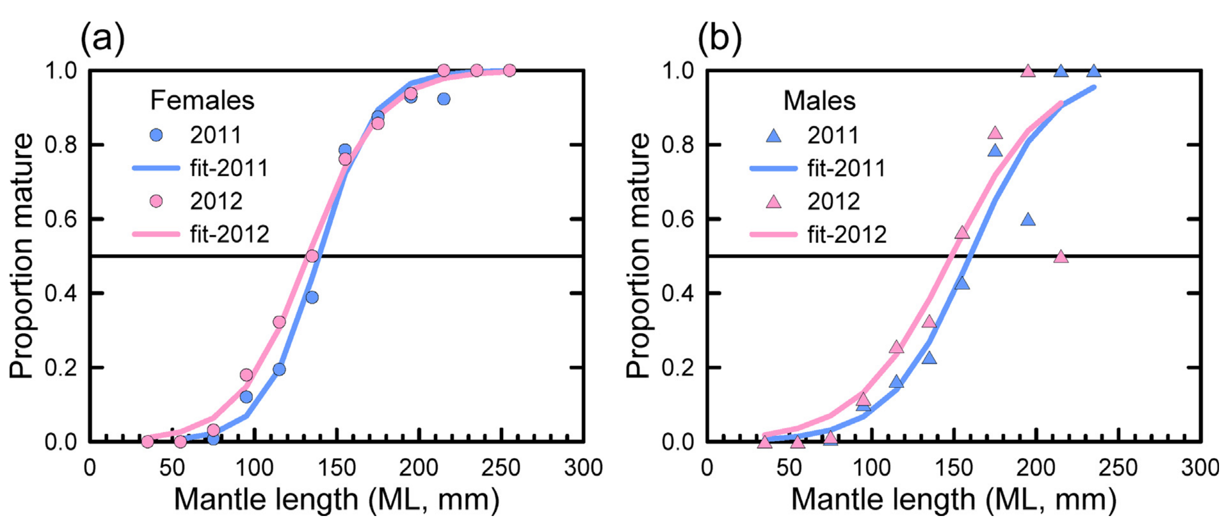

Fig. 9. Percentage of mature individuals by size group and estimated maturity ogives of the swordtip squid in Yilan Bay off northeastern Taiwan in 2011 and 2012. (a, females; b, males).

ML-at-maturity for males in 2011 was 160 mm, which was more than that for individuals in 2012 (148 mm).

4. Discussion

The swordtip squid is the target species of torchlight net fishing vessels in the ECS shelf [15,16] and is one of the main targets of trawl vessel fishing in the ECS shelf and YLB. This study examined the growth and maturation of the swordtip squid in YLB, and the results revealed significant interannual variability in the parameters examined. These results provide essential information on the swordtip squid population in YLB and extend our understanding of the swordtip squid population in the ECS shelf.

4.1. Age and growth of swordtip squid in YLB

The age and growth of the swordtip squid populations have previously been studied in the western North Pacific region. The squid population in the waters off southern Japan is typically larger in size (maximum ML: ~300 mm in females and ~400 mm in males) and has a lifespan of approximately 1 year based on the results of statolith microstructure analysis [40]. The squid population in the southern ECS shelf has a size structure (maximum ML: 316 mm in females and 433 mm in males) similar to that of the population in southern Japan and a lifespan of approximately 9 months [16]. In the present study, the squid population in YLB exhibited a smaller size structure (maximum ML: 278 mm in females and 233 mm in males) and a younger age structure (maximum age: 189 days in females and 177 days in males) than the squid populations in the southern ECS shelf and southern Japan.

Squid is a short-lived species that exhibits considerable plasticity in life-history traits between geographical stocks, with individuals inhabiting temperate or subtropical waters being larger, older and matured later than those inhabiting tropical waters [44,45]. The variabilities in life-history traits between geographical stocks (or seasonal cohorts) of squid are typically attributed to the varying environmental conditions of their habitats [28,29,46,47]. The latitudinal differences in oceanographic conditions between southern Japan and the southern ECS shelf, such as differences in currents, topography, and wind, may partly explain the disparities in the age structure and growth patterns of the swordtip squid [18,48]. However, further research on the influence of the environment, at annual and seasonal scales, on the life-history traits of squid is warranted.

In addition to a short lifespan, squid generally possesses a semelparous life cycle; that is, adults die after spawning [49]. Squid typically has a rapid growth rate until they reach full maturity, after which their growth rate decreases and they exhibit an asymptotic growth trajectory [50]. Therefore, the growth patterns of squid are most effectively described using non-asymptotic functions [51,52]. In the present study, the ML-at-age data of all squid samples (which may comprise numerous micro-cohorts) were optimally described using the exponential and power functions for females and males, respectively, in 2011 and 2012. By contrast, in a previous study, the growth pattern was described using logistic functions for both sexes of the warm- and cold-season brood of the squid in the waters off southern Japan [40]. However, the ML-at-age data for the squid in Japan were calculated using a five-class moving average of ML for each 10-increment class, which might considerably reduce the temporal and individual variations in squid ML data. The growth patterns were optimally described using exponential functions for both sexes of the squid in the southern ECS shelf [16]. Furthermore, a study reported that the winter cohort grew faster and reach a larger size than the summer cohort [17]. Studies have proposed that squid growth is influenced by sea water temperature [53,54] and food availability [44]. Moreover, distinct seasonal cohorts (micro-cohorts) of squid have been reported to exhibit different growth patterns, in which individuals hatched in cold- or warm-water conditions (cohort) display distinct life history strategies that can partly be explained by the environmental conditions [17,28,29,45]. Further research on variation in the growth patterns between micro-cohorts of the swordtip squid in YLB and the possible influence of environmental conditions is warranted.

4.2. Inter-annual variability in growth and maturation

The squid in YLB exhibited a smaller size structure and younger age structure than those in the southern ECS shelf. Furthermore, this study revealed considerable inter-annual fluctuations in the size structure and hatching seasons of the squid in YLB. Regarding the monthly ML composition of the squid in YLB, a similar pattern was found for large-sized individuals collected in winter (December to January) and in early summer (May and July−August) in 2011 and 2012. However, the

ML of the squid collected in 2011 was greater than that of the squid collected in 2012 in both sexes.

Additionally, the spawning seasons for the squid in YLB in spring (April to May) and autumn (October to November) were similar to those for the squid in the southern ECS shelf [15]. However, the main spawning season for the squid in YLB was inconsistent between 2011 and 2012; it occurred in spring (May) and autumn (November) in 2011 and in spring (March and May) in 2012. The hatching season for the squid in YLB differed from that for the squid in the southern ECS shelf, which peaked in spring (March to April) and autumn (October to November) [16]. The hatching season for the squid in YLB varied considerably between 2011 and 2012; it peaked in summer (June and August) in 2011 and in spring (March and April) in 2012.

Furthermore, ML-at-maturity was smaller (~136 and 154 mm in females and males, respectively) and age-at-maturity was younger (~135 and 148 days in females and males, respectively) for the squid in YLB than for the squid in the southern ECS shelf (164−186 mm and 121−169 mm in females and males, respectively, and ~210 and ~190 days in females and males, respectively) [15,16]. Additionally, slight inter-annual fluctuations in size- and age-at-maturity were noted in the squid in YLB (Figs. 8 and 9).

These results indicate potential population connectivity between the squid populations in the two areas (namely, the southern ECS shelf and YLB; Fig. 10). YLB may be one of the feeding grounds for the squids hatched in the southern ECS shelf that have been transported southward intermittently to YLB. Nevertheless, ambient oceanographic conditions, such as ocean currents and associated hydrographic processes, fluctuate seasonally and inter-annually and may greatly influence

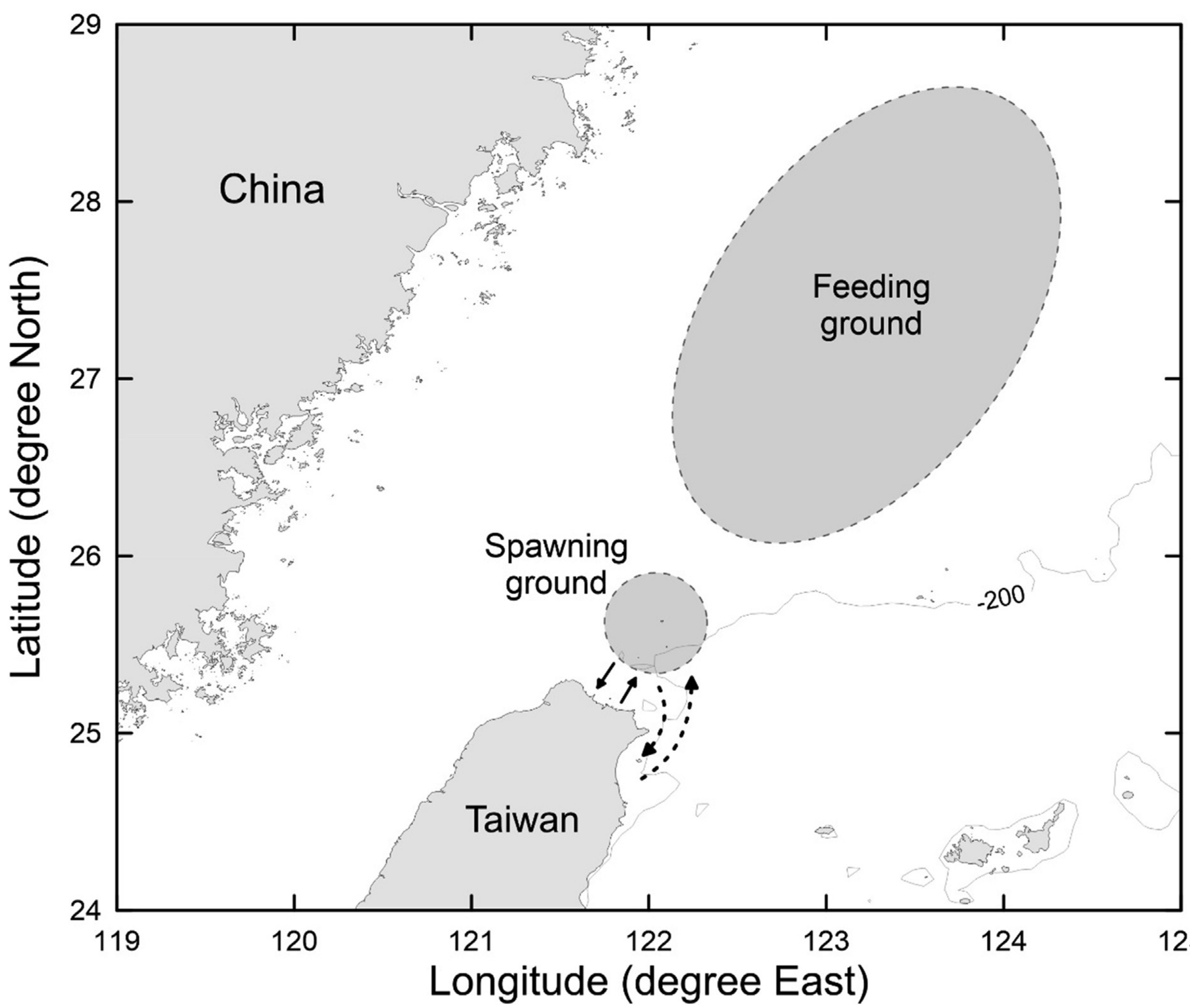

Fig. 10. Schematic of the potential movement of the swordtip squid in southern East China Sea and Yilan Bay. (The spawning and feeding grounds for the squid in the East China Sea is shown).

connectivity as well as the growth and maturation of the squid in YLB.

Temporal and spatial variations in the growth and maturation characteristics have been studied in several squid species [17,28,29,31,44–46]. Most previous studies have focused on variability in the growth and maturation parameters of squid at an intra-annual scale (monthly or seasonally) and have proposed influencing factors related to environmental conditions [17,28,29,45]. By contrast, studies on inter-annual variability in the growth and maturation parameters of squid are limited [31–33,44], although studies have provided substantial information on the population dynamics of squid and the possible influence of long-term changes in environmental conditions on the squid populations [27,55]. In addition, intra-annual and inter-annual variability in the life-history traits of squid have been attributed to the characteristics of its short lifespan, which typically exhibits high plasticity and susceptibility to variation in ambient environmental conditions [27,55].

In this study, both the age and ML group of the females highly explained the proportion of maturity in the 2 years under study (2011 and 2012; >97.1%). By contrast, the ML group of the males explained the proportion of maturity more favorably in 2011 (age, 80.3%; ML, 95.0%), whereas the age group explained the proportion of maturity more favorably in 2012 (age, 98.8%; ML, 80.9%). In addition to potential environmental influence, the possibility of male dimorphism in loliginid squid should be considered [56]. Male loliginid squid exhibit body size-related alternative reproductive tactics (ARTs), which may facilitate reproductive success during sexual selection [57–60]. The inter-annual difference in ML at maturity for the male squid in YLB (160 mm in 2011 and 148 mm in 2012) might be a consequence of the variation in the composition of the distinct ART male squid (consort and sneaker) [61,62].

YLB is located off the northeastern coast of Taiwan and is one of the crucial fishing and nursery grounds for marine fishes in Taiwan [34–36]. The waters of YLB are mainly affected by the ECS shelf waters (coastal countercurrent) along the coast of Taiwan and mix with the KC, which flows northward off YLB [63,64]. The seasonal movement of the KC modifies the flow pattern and related hydrographic process in this region. In summer, the KC flows northeastward along the continental shelf break off northeastern Taiwan. In winter, a portion of the KC flows onto the continental shelf and leads to significant hydrographic processes off northern Taiwan [65]. Therefore, the oceanographic conditions of the waters of YLB show intra-annual and inter-annual variations (Fig. S1) and are partly affected by the seasonal movements of the KC [66]. However, further research is warranted to examine the dynamics of these flow patterns and hydrographic processes in YLB and their potential influences on the life-history traits of squid.

4.3. Conclusions

This study examined the growth and maturation of the swordtip squid in YLB and inter-annual variability in the related parameters. The results revealed that potential connectivity between the squid populations in YLB and the southern ECS shelf. However, the population connectivity and the growth and maturation parameters of the squid in YLB may be influenced by seasonal and inter-annual fluctuations in oceanographic conditions. The results of this study provide substantial information on the population structure and connectivity of the squid in YLB and the southern ECS shelf, which may support the planning of effective conservation and management measures for the squid and relevant fisheries in the Northwest Pacific.

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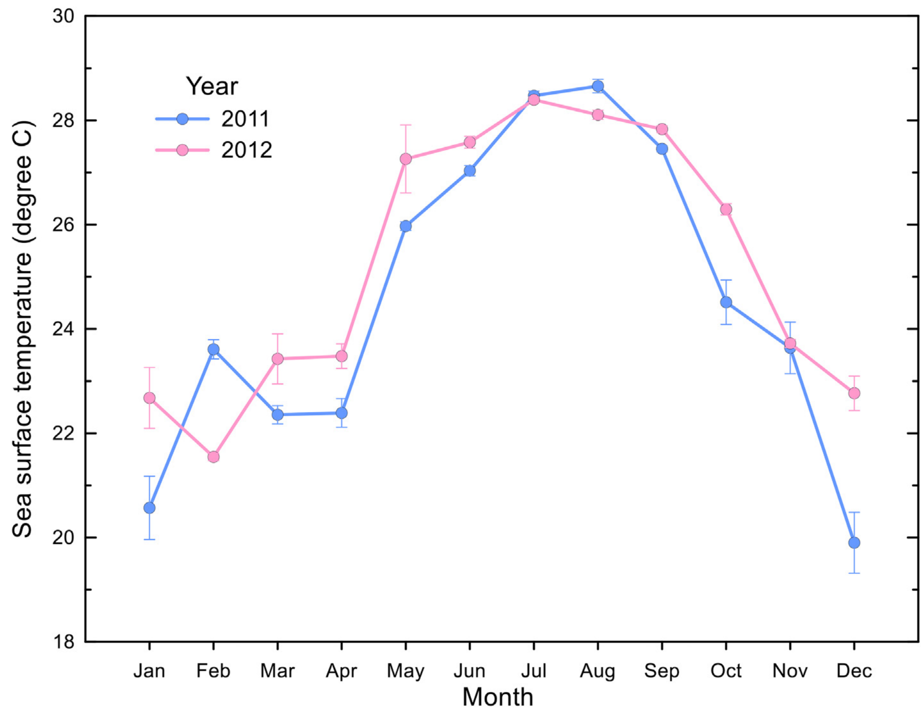
Appendix A. Figure S1. Monthly sea surface temperature (average and standard error) in Yilan Bay in 2011 and 2012.



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