



# Environmental influence on life-history traits in male squid *Uroteuthis edulis* with alternative reproductive tactics

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## Abstract

Squid are characterized by flexible life-history traits (LHTs) that change in response to changing oceanic parameters. Male alternative reproductive tactics (ARTs), characterized by large-sized ‘consorts’ versus small-sized ‘sneakers’, are commonly observed in loliginid species. This study reports on LHTs flexibility in male squids displaying ARTs. LHTs of consorts and sneakers in *Uroteuthis edulis*, including body size, age, growth rate and gonado-somatic energy allocation, were compared among seasonal and geographical groups from Japan and Taiwan. The ratio of consorts to sneakers was highest in the group spawning in the ‘Japan-warm’ season (June–November), followed by that of the ‘Japan-cold’ season (December–May), and lowest in Taiwan (spring and autumn). LHTs were compared among cohorts separated by hatching season and catch location (Jwarm, Jcold and Taiwan cohorts). Mean body size of consorts showed no difference among cohorts, although Taiwan consorts were relatively younger than Japan consorts. Mean size and age of sneakers decreased with increased water temperature at hatching. Growth rates of consorts and sneakers were slightly different among cohorts, in accordance with differences of statolith increment widths during their early life stage (50–150 days). Growth rates of both consorts and sneakers were highest in the Taiwan cohort, followed by the Jwarm cohort, with the Jcold cohort lowest. Sneakers invested more both in mantle and gonadal weights than consorts in all cohorts. Gonado-somatic energy allocation patterns of consorts and sneakers were consistent at different temperatures. LHTs of *U. edulis* consorts and sneakers were strongly influenced by temperature, with higher flexibility in sneakers than consorts.

**Keywords** Squid biology · Alternative reproductive tactics · Environmental influence · Life-history traits · Male dimorphism

## Introduction

Considerable flexibility in squid life-history traits (LHTs) has been assumed to be one of the pivotal factors contributing to the increase of squid stocks worldwide, which appears

to be a result of the ability of squids to adapt successfully to environmental changes (Pecl et al. 2004; Pecl and Jackson 2005; Hoving et al. 2013; Doubleday et al. 2016). There is great variability in LHTs in a wide range of squid species (Pierce et al. 2005; Ichii et al. 2009; Ching et al. 2019), which is considered to be a mixture of intrinsic variability and the influence of environmental factors, especially water temperature and food availability (Vidal et al. 2002; Pecl and Jackson 2005; Pierce et al. 2008; Yu et al. 2015). Significant differences in growth and size-at-maturity have been observed in different geographical and seasonal cohorts for various squid species (Arkhipkin et al. 2000; Jackson and Moltschanivskyj 2002; Jackson et al. 2003; Ceriola and Jackson 2010). For example, squid that hatch in warmer temperatures grow faster and mature earlier than those in colder waters (Jackson and Moltschanivskyj 2002; Moreno et al. 2007; Ibáñez et al. 2015; Chemshirova et al. 2021), indicating the strong influence of environmental conditions

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on squid growth and maturation, particularly during the early life stages (Vidal et al. 2002; Chen and Chiu 2003; Forsythe 2004). In addition, energy allocation between somatic growth and reproduction also exhibits great variation (McGrath Steer and Jackson 2004; Pecl et al. 2004). Many squid species continue to grow after reproductive maturation (Arkhipkin et al. 1999; Wang et al. 2010), but energy allocation to somatic growth decreases progressively (Forsythe 2004). Reproductive investment varies and could be a function of the environmental conditions experienced, especially during the hatching period (Pecl and Moltshanskiy 2006).

Large sex-specific differences in LHTs are common in many squid species (Arkhipkin 1996; Jackson et al. 2005). Male squids vary more in somatic growth, while females vary more in reproductive investment, since males tend to invest more energy in somatic growth to fight for mating opportunities, while females invest more in egg production (McGrath Steer and Jackson 2004; Pecl et al. 2004; Lin et al. 2015). These differences are more complex in coastal loliginid squid species, which typically display male dimorphism associated with two alternative reproductive tactics (ARTs) (Iwata and Sakurai 2007; Iwata et al. 2018; Apostólico and Marian 2018; Marian et al. 2019). One type of male ART is the ‘consort’, where the male is generally larger than mature females and, therefore, has an advantage when competing for females with larger body size. Consorts conduct ‘male-parallel’ copulations with high fertilization success (Hanlon et al. 1997; Iwata et al. 2005; Naud et al. 2016; Shashar and Hanlon 2013). The other male ART is the ‘sneaker’, where the male is generally smaller than mature females and avoids male–male competition and courtship behaviors. Sneakers conduct ‘head-to-head’ copulations which result in a lower number of egg fertilizations per female than that of consorts (Hanlon et al. 1997; Iwata et al. 2005; Naud et al. 2016; Shashar and Hanlon 2013).

In *Loligo vulgaris* and *L. forbesi*, smaller and younger mature males have a high gonado-somatic index (GSI), with relatively large gonads but small spermatophores; while larger and older males have a low GSI, with a small gonad but large spermatophores (Rocha and Guerra 1996). Gonadal investment is also higher in sneaker males than in consort males in *Doryteuthis plei* (Apostólico and Marian, 2019), but the opposite is true in *Heterololigo bleekeri*, and there are no differences in GSI between consorts and sneakers in *L. reynaudii* (Iwata et al. 2021). Although a proximate mechanism of squid male dimorphism associated with ARTs remains elusive, it is crucial to distinguish male squids by ARTs when it comes to understanding correctly about the response of male squid LHTs to different environmental conditions, due to the intrinsic differences in body size and reproductive characters between males using one or other of the two different ARTs.

The swordtip squid *Uroteuthis edulis* is an ideal model species to study the effects of environmental conditions on the LHTs of males with ARTs. First, *U. edulis* is distributed widely, from southern Japan, across the South China Sea to the Philippine Islands and perhaps even the continental shelf of northern Australia (Jereb and Roper 2010). This wide distribution from a temperate area with strong seasonality of water temperature to a stable warm subtropical area provides contexts to study environmental impacts on the LHTs in natural populations. Second, *U. edulis* is a commercially important fishery species based in the northwestern Pacific area (FAO 2016), which allows easy access to abundant samples with a wide size range throughout the year. Third, the previous studies have shown great variability in *U. edulis* LHTs in different environments. Female squids in Japanese populations have a higher growth rate when they hatch in a warm season than they do if they hatch in a cold season, and they mature at a younger age and smaller size in Taiwan than in Japan (Pang et al. 2020). Also, in Japanese waters, male squids that hatch in a warm season display a higher growth rate than those hatching in a cold season (Natsukari et al. 1988); and male squids in northern Taiwan caught in spring mature at a smaller size than those caught in autumn (Wang et al. 2008). However, these previous studies considered all mature male squids as one group. To investigate male *U. edulis* LHTs in a holistic way, the ART adopted by each male should be taken into consideration. In addition, by also comparing the LHTs of male *U. edulis* off Japan and Taiwan simultaneously, this would contribute to a better understanding of the environmental influences on this species.

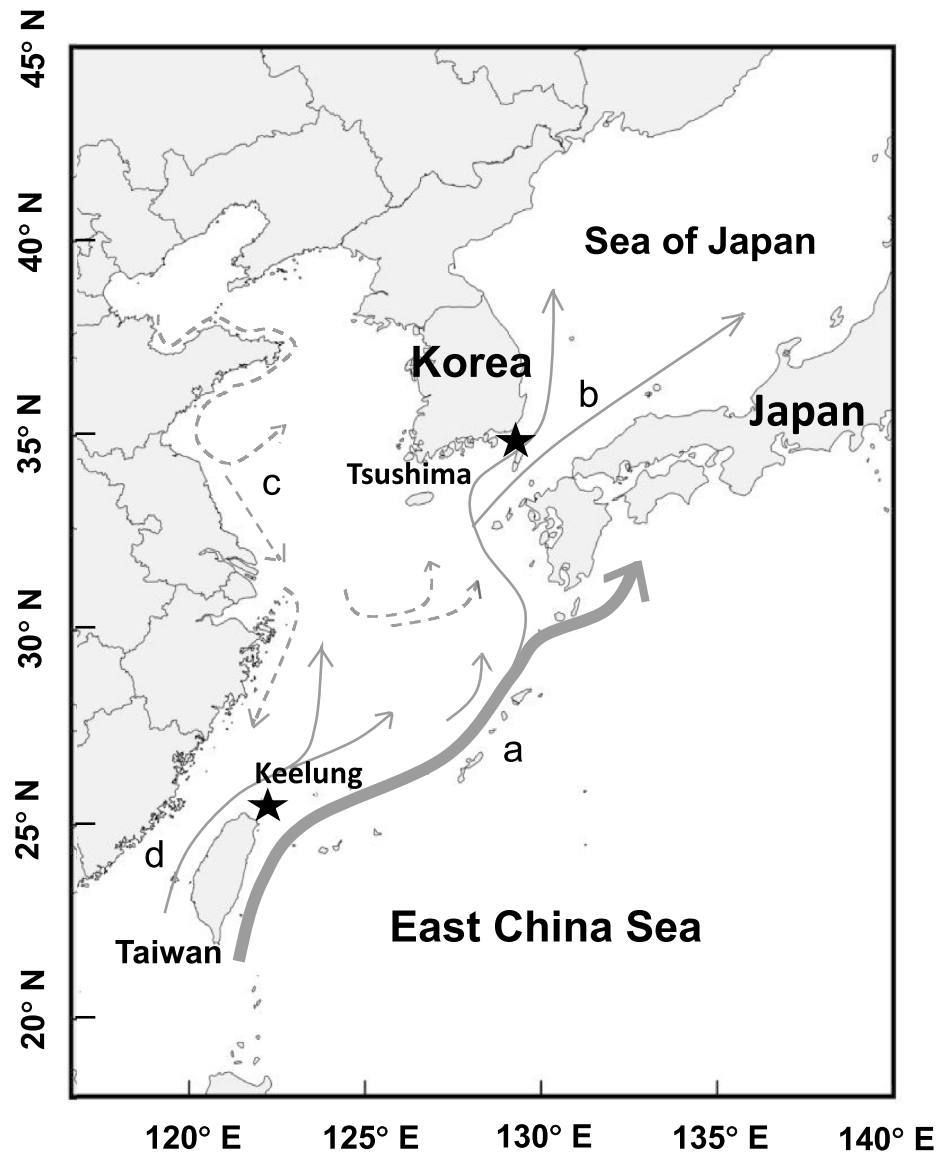
Therefore, this study focuses on variations in LHTs of male *U. edulis* squids with two ARTs (consort and sneaker) in terms of growth, maturation and gonado-somatic energy allocation. To identify the impacts of different environments on the variability of male LHTs, individuals collected in the temperate waters of southern Japan and the subtropical waters of northern Taiwan were compared within each year group.

## Materials and methods

### Sampling

Samples of *Uroteuthis edulis* Hoyle, 1885, from Japanese waters were collected each month from May 2017 to August 2020, using inshore set-nets located off northern Tsushima Island (depth 30–36 m, 34.33–34.39° N, 129.17–129.30° E, Fig. 1). Fishermen separated the squid into six size classes, with about 4 kg of squid sampled from each size class (about 15 individuals for the largest class and 120 for the smallest). Measurement data were scaled by the total catch weight of each size class on any given sampling date

**Fig. 1** Sampling localities (stars) off the Tsushima Islands (Japan) and off Keelung (Taiwan). **a** Kuroshio current; **b** Tsushima warm current; **c** East China Sea mainland coastal current; **d** Taiwan Strait warm current



to avoid size selection biases. Squid from Taiwanese waters were obtained by bottom-trawl during two main spawning seasons in May–July and September–November from 2017 to 2019, at 110 m depth in the southern East China Sea (25.50–26.00° N, 121.50–122.50° E, Fig. 1). As the catches in Taiwan were small and unsorted, all collected squid were taken to the lab as samples for further analysis.

Sea surface temperature (SST) in the waters off northern Taiwan is warmer and less variable throughout the year (19.7–29.7 °C, mean 25.2 °C) compared to that in the waters off southern Japan, which is cooler and more variable between months (14.4–29.2 °C, mean 20.7 °C; Japan Meteorological Agency, Fukuoka Regional Headquarters (2021)). Monthly catch data of Japanese squid were divided into two spawning groups on the basis of annual mean SST:

a Japan-cold-spawning group (JCSG, December–May) and a Japan-warm-spawning group (JWSG, June–November). All squid collected from Taiwan were considered as a single spawning group (TSG): the SST in this area had a similar range to that of the JWSG.

### Biological data and age determination

For each *U. edulis* male squid, measurements were taken of mantle length (ML, to the nearest 1 mm), body weight (BW, wet-weight to the nearest g), mantle weight (MW, wet-weight of the muscular mantle and fins, stripped of the head, arms, internal organs and gladius, to the nearest g), and total gonad weight (GW, sum of testis weight and accessory gland weight, to the nearest 0.1 g). Statoliths were

removed from each individual, cleaned with distilled water, air dried, and stored in microtubes until processing. Sexual maturity stages were categorized based on the three stages reported for *Loligo plei* (Perez et al. 2002). Mature males of *U. edulis* were classified as either consort or sneaker, according to the shape of their spermatangia, which were obtained by inducing the spermatophoric reaction in spermatophores collected from the spermatophore sac (Iwata and Sakurai 2007; Apostólico and Marian 2018; Iwata et al. 2018). For each spawning group, the proportion of mature individuals was determined, along with the ratio of consorts to sneakers among them (Table 1).

Growth increments on the statoliths of *U. edulis* are assumed to be deposited daily (Natsukari et al. 1988), as in other loliginid squids (Patterson 1988; Villanueva 2000; Jackson and Forsythe 2002; Jackson 2004; Arkhipkin 2005). Representative sub-samples were selected from across the size distribution of male squids for statolith microstructure analysis and age determination. Statoliths were attached to a microscope slide using Crystalbond 509, ground on both sides along a transverse plane using fine waterproof sandpapers (#1000–4000), and polished with cloth before observation. Statolith microstructure was examined by light microscope under transmitted light at  $\times 400$  magnification. The hatching ring was defined as the first thick black ring around the nucleus (Arkhipkin 2005). Growth increments of each statolith were manually read from the hatching ring to the edge of the rostrum using a light microscope connected to a video monitor and an otolith reading system. The number of statolith increments and increment width were recorded simultaneously (Otolith 8 software, Ratoc System Engineering Co., Ltd.). The number of statolith growth increments was counted twice, with an interval of at least 3 months between readings. Only when the counts differed by less than 10%, the mean of the two counts was used as the estimated squid age in days. When increment definition was poor, or the statolith was over-ground, the sample was discarded.

Individual hatching dates were back-calculated from the date of capture, using estimated age at capture as determined by statolith growth increments. According to the hatching dates, males from Japanese waters were grouped into a Japan-cold cohort (Jcold, hatching between December and May) and a Japan-warm cohort (Jwarm, hatching between

June and November). As statolith increment width reflects the growth rate of the individual on each day (Arkhipkin 2005), a statolith 10-day mean increment width and standard deviation were calculated for consorts and sneakers from all cohorts to observe changes of growth rate throughout the life of the cohort.

## Data analysis

Instantaneous growth rate in ML ( $G_L$ ) and BW ( $G_W$ ) was calculated for each male using the following formulae:-

$$G_L = (\ln L - \ln L_0) / (T - T_0) \times 100$$

$$G_W = (\ln W - \ln W_0) / (T - T_0) \times 100,$$

where  $L$  is ML (mm),  $W$  is BW (g) and  $T$  is time (day) at capture. The ML at hatching ( $L_0$ ) of *U. edulis* is 2.2 mm (Toyofuku and Wada 2018). There are no reports of BW at hatching ( $W_0$ ) in this species, so it was assumed to be 1.7 mg based on the mean wet-weight of ripe eggs in *U. edulis* (Pang et al. 2020). The growth rates for each maturity status among the different cohorts, and for each cohort among different maturity statuses, were compared using one-way ANOVA and Tukey's pairwise post hoc test.

A geometric regression model was used to analyze gonado-somatic energy allocation. To represent somatic and gonadal growth of each individual, MW and GW were selected, respectively. MW was used to represent somatic growth instead of BW, because GW is included in BW. Two sets of data were applied to the geometric regression model: log-transformed ML was used as the independent variable, and either log-transformed MW or GW was the dependent variable. The standardized residual of MW or GW was calculated for each individual by subtracting the predicted value of the geometric model from the actual log-transformed MW or GW at the same value of log-transformed ML. These provide size-independent estimates of the relative condition of somatic or gonadal tissues. Thus, individuals with a higher MW or GW for their length, and accordingly higher residuals, were considered to show better body condition (BC) or reproductive condition (RC), respectively, in terms of somatic or gonadal growth. Two scenarios were analyzed: (1) to compare

**Table 1** Male *U. edulis* composition of the three sampled spawning groups

Spawning group	Number of sampled individuals				C:S ratio	Mature: total
	Total	Immature	Consorts	Sneakers		
JWSG	6184	3025	2245	914	2.456	0.511
JCSG	4944	2767	672	1505	0.447	0.440
TSG	709	210	49	450	0.109	0.697

JWSG Japan-warm-spawning group, JCSG Japan-cold-spawning group, TSG Taiwan spawning group

energy allocation patterns among ARTs in the same environmental context, gonado-somatic energy allocation was compared among immature males, consorts, and sneakers within each cohort, and one-way ANOVA and pairwise post hoc test (Tukey method) were used to observe the difference in energy allocation; (2) to compare energy allocation patterns among environmental contexts within each ART, data of the same ART from different cohorts were applied to understand the influence of temperature on gonado-somatic allocation by one-way ANOVA and Tukey's pairwise post hoc test. To determine if energy allocation to somatic and gonadal tissues was a function of an energetic trade-off in different environments, the standardized residuals derived from the ML versus MW (abbreviated below as 'ML-MW') and ML versus GW ('ML-GW') relationships of each cohort were compared for consorts and sneakers using Pearson correlation analysis.

## Results

### Catch information and hatching period

A higher proportion of mature individuals was found in the warmer environments: the TSG had the highest proportion of mature individuals, followed by JWSG, with JCSG the lowest. The ratio of consorts to sneakers in each cohort differed greatly, with relatively more consorts in the Jwarm cohort, followed by the Jcold cohort, and relatively few in the Taiwan cohort (Table 1).

In the Japanese cohorts, the majority of consorts hatched during the warm period and matured mostly in the next warm period. Sneakers hatched throughout the warm and cold periods, but more sneakers were always caught in the cold period than the warm (Table 2). In the

Taiwanese population, the hatching months of consorts and sneakers largely overlapped.

### Age, size and growth rate

The mean ML of consorts showed no significant difference among cohorts ( $F=2.608$ ,  $P=0.076$ ), but the mean age of consorts in the Taiwan cohort was significantly younger than that of consorts in the Japanese cohorts ( $F=50.841$ ,  $P<0.0001$ ). The mean ML of sneakers was largest in the Jcold cohort, followed by Jwarm, with the Taiwan cohort the smallest ( $F=23.623$ ,  $P<0.0001$ ); while the mean age of sneakers was youngest in the Jwarm cohort and oldest in the Taiwan cohort ( $F=60.455$ ,  $P<0.0001$ ). Sneakers matured at a smaller size and a younger age than consorts in all cohorts. The size range of sneakers clearly overlapped with that of immature males and partly with consorts for all cohorts (Fig. 2). The age range of sneakers completely overlapped with that of both immature males and consorts.

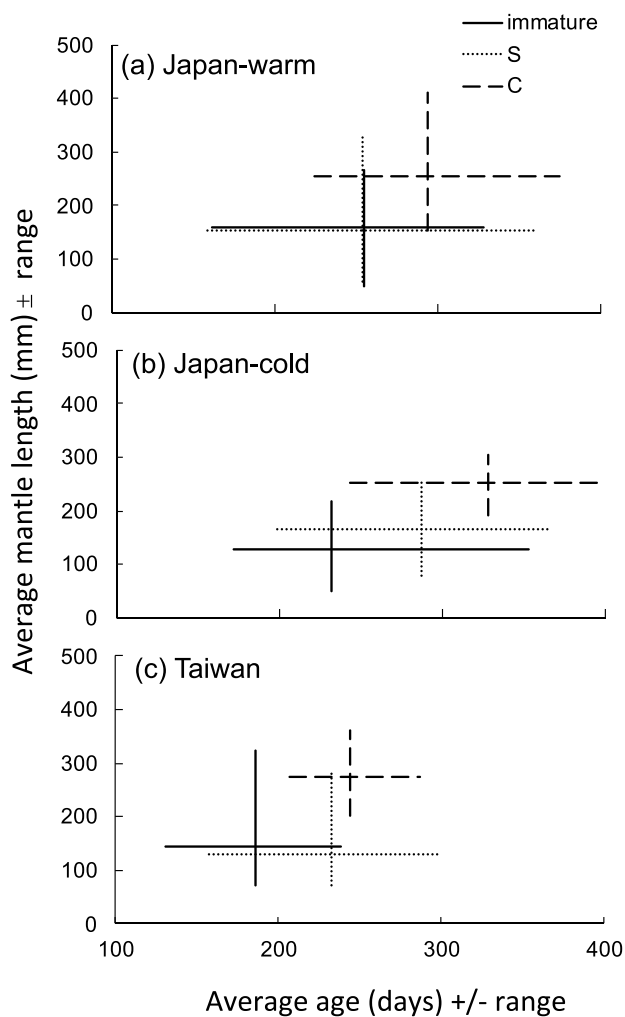
Growth rates in ML ( $G_L$ ) and BW ( $G_W$ ) differed among cohorts (Fig. 3). For consorts and sneakers, the Taiwan cohort showed the highest growth rates (both  $G_L$  and  $G_W$ ), followed by the Jwarm and Jcold cohorts (consorts:  $G_L$   $F=72.58$ ,  $P<0.0001$ ;  $G_W$   $F=73.12$ ,  $P<0.0001$ ; sneakers:  $G_L$   $F=42.29$ ,  $P<0.0001$ ;  $G_W$   $F=46.20$ ,  $P<0.0001$ ). The Taiwanese immature males, too, had the highest growth rate, followed by the Jcold and then Jwarm cohorts ( $G_L$ :  $F=226.67$ ,  $P<0.0001$ ,  $G_W$ :  $F=205.34$ ,  $P<0.0001$ ). This is consistent with the result that the statolith increment widths of the Taiwanese cohort were wider than those of the Japanese cohorts, especially during the early stage of life (50–150 days) (Fig. 4).

Growth rates also varied for different maturity statuses within each cohort. In the Jwarm cohort, the growth rate of consorts was slightly lower than that of immature males and sneakers ( $G_L$ :  $F=4.42$ ,  $P=0.013$ ;  $G_W$ :  $F=26.49$ ,

**Table 2** Size and age characteristics of sampled individuals of different hatching cohorts in each spawning group

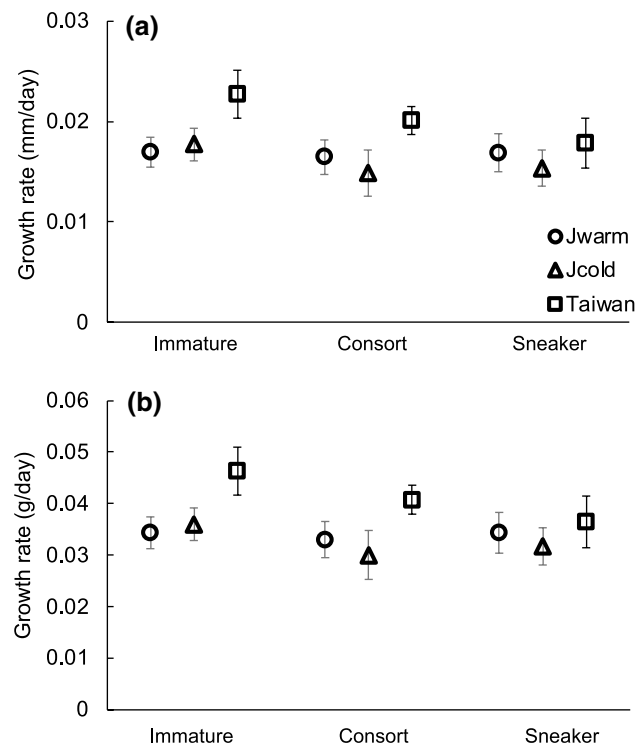
Cohort	Number of sampled individuals	Hatching period	Mean ML (mm) $\pm$ SD	Mean age (days) $\pm$ SD
(a) Consorts				
Jwarm	113 (JWSG)	Jun–Nov	254.4 $\pm$ 45.5	294.4 $\pm$ 30.5
	47 (JCSG)	Jun–Oct		
Jcold	4 (JWSG)	Dec	251.1 $\pm$ 31.0	328.7 $\pm$ 46.0
	15 (JCSG)	Dec–May		
Taiwan	32 (TSG)	Aug–Mar	273.3 $\pm$ 39.1	243.9 $\pm$ 20.0
(b) Sneakers				
Jwarm	52 (JWSG)	Jul–Nov (JWSG)	152.8 $\pm$ 47.1	254.4 $\pm$ 37.3
	101 (JCSG)	Jun–Oct (JCSG)		
Jcold	24 (JWSG)	Dec–Apr (JWSG)	166.3 $\pm$ 37.6	287.2 $\pm$ 39.5
	101 (JCSG)	Dec–May (JCSG)		
Taiwan	102	Aug–Mar	128.5 $\pm$ 37.0	233.0 $\pm$ 35.8





**Fig. 2** Relationship between age and length of immature males, consorts (C), and sneakers (S) in different cohorts. Horizontal lines show age range; vertical lines show mantle length range

$P < 0.0001$ ). In the Jcold cohort, immature males had the highest growth rate ( $G_L$ :  $F = 33.16$ ,  $P < 0.0001$ ;  $G_W$ :  $F = 42.00$ ,  $P < 0.0001$ ), and sneakers had the same  $G_L$  as consorts but a slightly higher  $G_W$ . Accordingly, sneakers had slightly wider statolith increment widths in the early life stage (~200 days) than those of consorts in the Jwarm and Jcold cohorts (Fig. 4a, b). In the Taiwanese cohort, immature males had the highest  $G_L$  (followed by consorts, with sneakers the lowest;  $F = 77.09$ ,  $P < 0.0001$ ); and also the highest  $G_W$ , but consort and sneaker males showed no difference in  $G_W$  ( $F = 69.08$ ,  $P < 0.0001$ ). Similarly, Taiwanese consorts had much wider statolith increment widths around 50–150 days than those of sneakers during the same period (Fig. 4c).

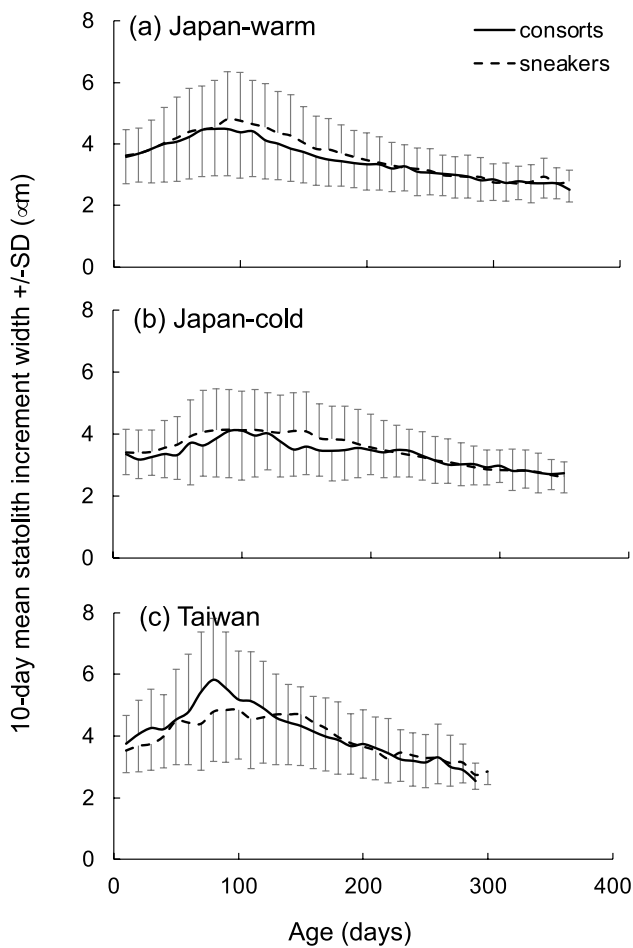


**Fig. 3** Growth rate of males of different maturity status in different cohorts: **a** growth rate in mantle length ( $G_L$ , mm/day); **b** growth rate in wet-weight ( $G_W$ , g/day)

### Energy allocation

Body condition and reproductive condition were compared among different maturity statuses in three cohorts (Fig. 5). In the Jwarm cohort, sneakers had the best body condition, followed by immature males, with consorts the poorest ( $F = 16.123$ ,  $P < 0.0001$ ); and sneakers had the best reproductive condition, followed by consorts, and immature males the poorest ( $F = 132.084$ ,  $P < 0.0001$ ). In the Jcold cohort, sneakers had the best body condition, followed by immature males, with consorts the poorest ( $F = 30.038$ ,  $P < 0.0001$ ). There was no difference in reproductive condition between consorts and immature males, while sneakers had the highest reproductive condition ( $F = 30.406$ ,  $P < 0.0001$ ). In the Taiwan cohort, consorts showed the poorest body condition ( $F = 13.15$ ,  $P < 0.0001$ ), while sneakers and immature males had the same level of body condition. Similarly, sneakers showed the greatest reproductive condition, followed by consorts, and immature males the poorest ( $F = 73.97$ ,  $P < 0.0001$ ). In general, sneakers had better body and reproductive condition than consorts in all cohorts.

Gonado-somatic energy allocation of consorts and sneakers in different cohorts are shown in Fig. 6. For both consorts and sneakers, the poorest body condition was observed in the Jwarm cohort (consorts:  $F = 10.34$ ,  $P < 0.0001$ ; sneakers:



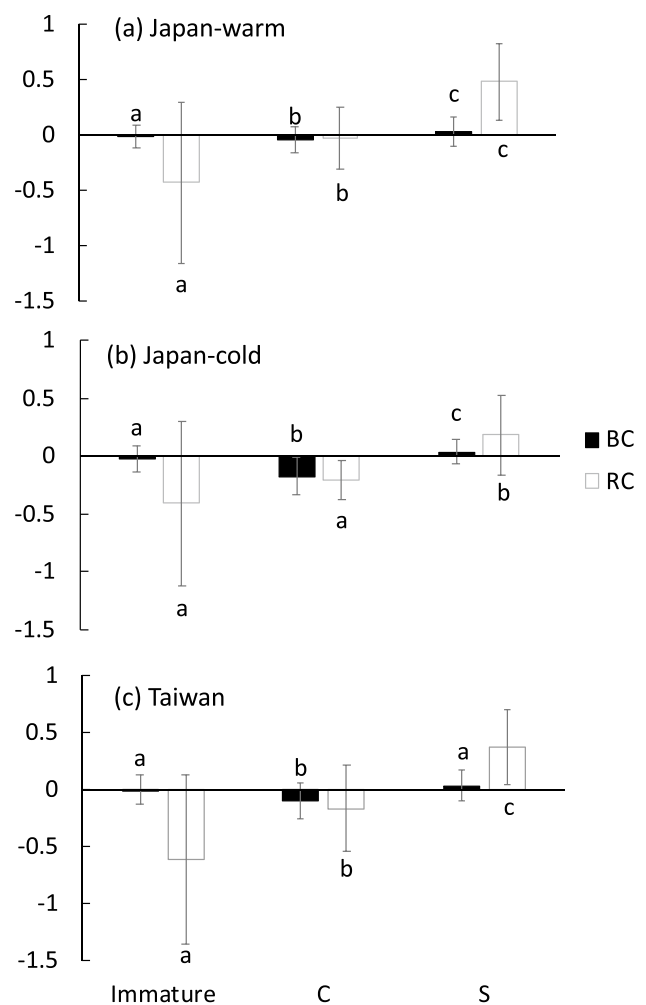
**Fig. 4** 10-Day mean statolith increment width of consorts and sneakers from different cohorts

$F = 38.18, P < 0.0001$ ), and the highest reproductive condition was observed in the Taiwan cohort (consorts:  $F = 6.87, P = 0.0013$ ; sneakers:  $F = 23.08, P < 0.0001$ ).

ML-MW residuals were positively correlated with ML-GW residuals in the Jwarm cohort (consorts:  $r = 0.665, P < 0.0001$ ; sneakers:  $r = 0.479, P < 0.0056$ ) and Taiwan cohort (consorts:  $r = 0.263, P = 0.001$ ; sneakers:  $r = 0.302, P = 0.002$ ), suggesting that individuals investing more energy in gonadal growth invested more in somatic growth as well, and vice versa; while they were negatively correlated in sneakers ( $r = -0.177, P = 0.049$ ), and there was no strong correlation in consorts of the Jcold cohort ( $r = 0.28, P = 0.25$ ).

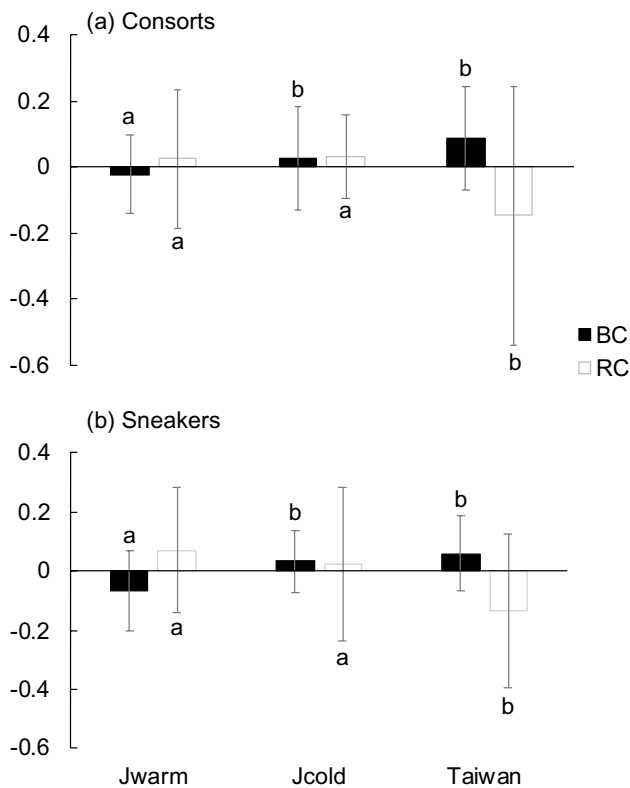
### Discussion

For short-lived species with ARTs in the temperate area, date of birth can influence ART expression, because individuals born at different periods experience different growth



**Fig. 5** Body condition (BC) and reproductive condition (RC) for males of different maturity statuses in different cohorts. *Immature* immature males, *C* consorts, *S* sneakers (for definitions of BC and RC, see “Data analysis”)

conditions before maturation (the birthdate effect: Pastres et al. 2002; Fagundes et al. 2015; Welsh et al. 2017). The high proportion of consorts appearing in the JWSG could be accounted for by the large number of consorts comprising the Jwarm cohort. Similarly, the occurrence of few consorts among the Jcold cohort led to low numbers of consorts in the JCSG. In contrast, the relatively high incidence of sneakers in the JCSG might benefit from not only those that hatched from Jcold cohort, but also the early additional recruitment of the Jwarm cohort with faster growth and of younger age, implying a strong environmental influence on the lifespan of sneakers but not consorts. The greatly overlapping hatching periods of consorts and sneakers in the Taiwan group are presumably due to the relatively stable subtropical environment off Taiwan. The birthdate effect was also considered in *Doryteuthis plei*, in which sneakers are found to be younger than consorts. However, the presence of an intermediate



**Fig. 6** Body condition (BC, black bars) and reproductive condition (RC, white bars) of consorts (a) and sneakers (b) from different cohorts. Letters above and below error bars denote statistically significant differences of BC and RC, respectively

type having characteristics of both consort and sneaker in the species did not support the hypothesis of irreversible conditional tactics (Apostólico and Marian 2018). Instead, the authors proposed that males hatching during winter may mature precociously as sneakers, but continue to grow and later become smaller consorts; whereas males that hatched during warm conditions may have delayed maturation and become the largest consorts later in life, without experiencing a sneaker stage (Apostólico and Marian 2018, 2020).

The reproductive success of an ART is influenced by its proportion in the population (Taborsky and Brockmann 2010). Squid are annual species with high phenotypic plasticity, so the ratio of each ART in the population can easily change as a result of environmental conditions. For the *U. edulis* population in Japan, the consort-to-sneaker ratio shifted between water temperature periods: that is, a consort-dominant warm period and a sneaker-dominant cold period. Water temperature cannot be the only environmental factor affecting the appearance of ARTs in males, because there was also a large bias in favor of sneakers even in the warmer Taiwan cohort (which had SST characteristics closer to those of the Jwarm cohort; see “Sampling”, above).

Social conditions such as female mate preference may explain the ratio of ARTs in different cohorts. In swordtail fish with large consorts and small sneakers, larger females have an overall preference for large males (Rios-cardenas et al. 2007; Morris et al. 2010). Therefore, when there is a larger proportion of smaller females, the mating advantage of sneakers will increase. *Uroteuthis edulis* females mature over a wider size range with larger size variation in the Jcold (range 97–323 mm, mean ML  $201.2 \pm 49.6$  mm) and Taiwan (87–294 mm, average size:  $179.4 \pm 46.6$  mm) cohorts than in the Jwarm cohort (range 101–277 mm, mean ML  $188.6 \pm 31.9$  mm) (Pang 2022, unpublished data). Hence, females may accept sneakers as mates more readily when females mature over a wide range with a larger proportion of small individuals.

In many fish species, body size is regarded as one of the main factors to determine the relative reproductive success of each ART (Ryan and Causey 1989; Bleeker et al. 2017). Body size is also a trigger to switch ARTs ontogenetically from small sneakers to large consorts (Alonzo and Warner 2000). In *H. bleekeri*, consorts and sneakers can be roughly distinguished by a body size division around ML 200–220 mm (Iwata and Sakurai 2007). However, the size range of sneakers greatly overlaps with that of consorts in Japanese cohorts of *U. edulis*, and overlaps only slightly in the Taiwan cohort. Thus, body size seems not to be an effective morphological indicator of male ARTs in *U. edulis*. The size difference between consorts and sneakers in the Taiwan cohort might be due to the early maturation of sneakers in the warm Taiwanese water, but more data are required to test this hypothesis.

Maturity has been assumed to be a polygenetic character that can be modeled as a threshold trait, where maturation is dependent on the attainment of a certain growth rate, body size, or a combination of factors (Hutchings and Myers 1994; Piché et al. 2008). Variation of size and age at maturity are common across taxa and are influenced by both genetic and environmental factors, which are often associated with ARTs (Thomaz et al. 1997; Piché et al. 2008; Berejikian et al. 2011; McKinney et al. 2020). The lack of differences in mean ML of *U. edulis* consorts among cohorts implies that there might be a body size threshold to trigger sexual maturation of consorts. Taiwanese consorts showed a younger age at maturity than Japanese consorts, which might result from the higher water temperature leading to faster growth and subsequent early maturation. However, the mean ML and age of sneakers at capture decreased with a warmer hatching environment in the present study. As observed in *U. edulis* consorts, size-dependent maturation might lead to a delay of maturation when the ambient environmental conditions are unfavorable for growth (Policansky 1983). However, size advantage is not necessary for sneakers, so



they are more flexible in terms of body size and age at maturity when responding to different environment contexts.

A growth-rate threshold has also been proposed as a factor determining male ARTs (Hutchings and Myers 1994). Individuals with a higher growth rate attain maturity earlier to adopt one reproductive tactic, while individuals with a growth rate lower than a threshold adopt another tactic (Berejikian et al. 2011). Significant genetic effects were found on growth rate at the early stage and subsequent occurrence of reproductive tactic in fish species (Berejikian et al. 2011; Wirtz-Ocana et al. 2013). In *U. edulis*, growth rate ( $G_L$  or  $G_W$ ) slightly differed among different maturity statuses in the same cohort in this study. Immature males displayed a higher growth rate in both ML ( $G_L$ ) and BW ( $G_W$ ) than consorts and sneakers in the Jcold and Taiwan cohorts, which implies that somatic growth might slow down after maturation (Arkhipkin et al. 2000; Arkhipkin and Roa-Ureta 2005). Growth rate in both ML ( $G_L$ ) and BW ( $G_W$ ) was significantly different between consorts and sneakers in each cohort, though the observed difference was small. However, comparisons of statolith increment widths between *U. edulis* consorts and sneakers in their early life stage (50–150 days) indicate that individuals achieved quite different growth rates in the early life stage, which might contribute to the determination of male ARTs. However, the early life growth of consorts was slower than that of sneakers in Japan, but the opposite occurred in Taiwan, indicating that growth of early life stages is not the sole mechanism determining ARTs but that a complex combination of many factors is probably involved.

Although the mechanism remains unclear, environments obviously influence growth rate and, consequently, choices of ARTs in *U. edulis* males. The instantaneous growth rates ML ( $G_L$ ) and BW ( $G_W$ ) are mean values across the lifetime of the squids, so it is difficult to detect any environmental influences after the attainment of maturity. Elevated temperature greatly accelerates growth rate and shortens the lifespan of many squid species (Pecl and Jackson 2008). Temperature conditions during early development play a key role in individual growth (Forsythe 2004; Moreno et al. 2007), which explains why the Taiwan cohort grew the fastest, followed by the Jwarm cohort, with the Jcold cohort showing the slowest growth for both consorts and sneakers.

Energy allocation in males with ARTs usually involves trade-offs, as energy resources and reserves are finite. The fitness of males pursuing ARTs seems to be balanced: small-size sneakers mature earlier to obtain a higher probability to reproduce, while large-size consorts achieve greater copulation success. One of the most common examples of gonado-somatic energy allocation is a trade-off between behavioral and gonadal investments (Taborsky 1994, 1998). For instance, guard (consort) males of the round goby invest highly in large body size, while sneakers

direct resources to the gonadal tissues at the expense of body size (Marentette et al. 2009). In all cohorts of *U. edulis*, sneakers invest more energy in both somatic and gonadal growth compared to consorts. After maturation, *U. edulis* consorts invest less energy in somatic growth, while sneakers continue to invest in somatic growth.

In some fish species, large males show a strong decrease in their energy reserves, which are the source of energy required for reproduction. These reserves are recharged slowly or not at all if no food is eaten during the breeding season: so these individuals are regarded as ‘capital breeders.’ In contrast, small-sized males use concurrent food intake to provide the energy for a reproductive attempt, replenishing energy faster for upcoming adoption of other mating tactics, and as such are regarded as ‘income breeders’ (Malavasi et al. 2004; von Kuerthy et al. 2015). A positive relationship between somatic growth and gonadal growth of *U. edulis* consorts implies that energy might be greatly used for conducting mating behaviors and male-male competition, sacrificing body reserves and gonadal development and probably only a small amount of food is eaten during the breeding season. In contrast to fish species, a few males intermediate between consorts and sneakers have been reported in squid species (except *D. plei*; Apostólico and Marian 2019). Additionally, the mean size and age of consorts and sneakers appear to greatly overlap in *U. edulis*, so it is unlikely that sneakers preserve energy to change from one tactic to the other. Accompanying relatively high investment in gonadal development, a positive correlation of sneaker gonado-somatic energy allocation in Jwarm and Taiwan cohorts implies that sneakers might consume food to maintain somatic growth after maturation for more sneaking opportunities through aggressive interactions (Kawase et al. 2017). Indeed, most individuals sampled during the present study had empty stomachs due to the rapid digestion in squid species (Semmens 2002), so it is difficult to support the hypothesis of gonado-somatic energy allocation patterns of *U. edulis* consorts and sneakers through estimating food intake condition from stomach weight at capture. In addition, Laskowski et al. (2020) have pointed out that a trade-off between somatic and gonadal growth tends to be found when environmental conditions are challenging and resources are depleted during the early life stages, which might explain the negative correlation between gonado-somatic energy allocations of sneakers in the Jcold cohort. The scarcity of consorts among sampled specimens in the Jcold cohort might be explained by the absence of a strong correlation with gonado-somatic energy allocation. However, the results reflect only the investment in gonadal growth in terms of gonad weight, while energy flows to mating behaviors, such as agonistic male-male competition, courtship, mating, and guarding, were not quantified in this study.

It seems that energy allocation patterns of *U. edulis* males are inherent within ARTs; however, the environment also plays a significant role in gonado-somatic energy allocation. Consorts and sneakers responded consistently to temperature influence in terms of energy allocation. Males in the Jwarm cohort showed the poorest body condition, which might be caused by experiencing a long cold water period following hatching during a warm period. In a warmer environment, such as that experienced by the Taiwan population, males would invest the least in gonadal growth. Although the mechanism of gonado-somatic allocation patterns that consorts and sneakers adopt in different temperatures cannot be completely understood from this study, *U. edulis* consorts and sneakers showed consistent responses to various temperature conditions, indicating the great impact of water temperature on the occurrence of ARTs.

Although the maturation of consorts seems to be size-dependent, and differences of growth rate between consorts and sneakers in the early life stage might be crucial to determine ARTs in *U. edulis*, this study focused on the temperature influence on male squid LHTs after their ARTs had been determined. However, there is no doubt that various factors are involved in affecting the life-history traits of *U. edulis* males observed in this study, including genetic factors, growth rate during early life stages, fluctuating water temperature and nutrition conditions experienced in the environment. Overall, sneakers showed greater flexibility of LHTs than consorts at different temperatures, and the dominance of sneakers in Taiwan might indicate that sneakers have an advantage under conditions of global warming. If so, it can be expected that the frequency of sneakers occurrence in natural populations of *U. edulis* will increase as global warming progresses.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** No conflict of interest.

**Ethical approval** This research was conducted in accordance with the Japanese Code of Conduct for Scientific Practice. All applicable international, national and institutional guidelines for sampling and experimental use of organisms for the study have been followed.

**Consent to participate** All authors consent to participate.

**Consent to publication** All authors and all institutions that provided funding and to which the authors belong consent to the publication of this study.

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