Adaptive and plastic variation in growth and maturation of the cutlassfish *Trichiurus japonicus* in the subtropical Pacific Ocean

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Abstract—We investigated variation in growth and maturation in response to 1) spatial variation in climate and 2) exploitation of the subtropical cutlassfish *Trichiurus japonicus*, an important fishery species whose population ecology is virtually unknown. Individuals of this cutlassfish species were sampled monthly at 2 primary landing sites: Kengfang, in northeast (NE) Taiwan, and Tsukuan, in southwest (SW) Taiwan, during 2013–2015. Habitat temperatures were about 1–4°C lower at the NE site than at the SW site, and the length at age of adult fish had an inverse pattern with temperature (NE lengths >SW lengths at age). The probabilistic maturation reaction norms did not differ significantly between the 2 areas, but ages and lengths at maturation were higher for males from NE than for males from SW. Differences in asymptotic lengths (NE>SW) and growth coefficients (NE<SW), together with narrower length distribution at the SW site than at the NE site, indicate potentially different mortality between the areas (NE<SW). These results indicate plastic variation in maturation and potentially adaptive variation in growth for this species that are related to the differences in temperature and mortality between the areas, although reliable proxies for mortality are lacking. The observed life-history variation was consistent with the temperature–size rule that organisms tend to grow faster, mature earlier, and reach smaller asymptotic sizes at warmer temperatures and may indicate an adaptive divergence of cutlassfish populations.

Life-history traits (i.e., growth rate, and age and length at maturation) are key determinants of population demography and the rates of population growth (Roff, 1992; Stearns, 1992) and provide insight into the sustainability of exploited species experiencing environmental changes and fisheries exploitation (Clark, 1991; Zhou et al., 2012; Wang et al., 2014). Studies on the variation in life histories have, however, paid more attention to temperate fish species (i.e., primarily the species in the Northern Atlantic) than to subtropical or tropical species, the abundance of which is predicted to decrease significantly under the effects of climate change (Cheung et al., 2010). Consequently, it is imperative that we enhance our understanding of life-history variation for subtropical and tropical species.

Intraspecific variation in growth and maturation reflects the effects of both the physical and biological environments through a combination of phenotypic plasticity and genetic variability (Stearns, 1992; Law, 2000). For example, food availability and temperature can influence consumption and assimilation, in turn influencing an animal's energetic condition, growth rates, and maturation schedules (Saborido-Rey and Kjesbu[1]). Simultaneously, because of the heritability of life-history traits and their association with fitness attributes (i.e., fecundity and survival), physical or biological factors can potentially influence growth and maturation through adaptive processes (known as the "habitat template theory") (Southwood, 1977; Reznick et al., 1990; Arendt and Wilson, 1999). Furthermore, fishing-induced mortality also can cause plastic changes (e.g., through relaxing density-dependent processes) and adaptive genetic changes (through altering the genetic makeup of life-history traits) in growth and maturation (Law, 2000; Reznick and Ghalambor, 2005). Together, these factors can affect variation in growth and maturation for an exploited species (Carlson et al., 2007; Sharpe and Hendry, 2009; Enberg et al., 2012).

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[1] Saborido-Rey, F., and O. S. Kjesbu. 2005. Growth and maturation dynamics, 26 p. [Available from website.]

A commonly observed macroscale relationship between growth and maturation with respect to variability in temperature, known as the "temperature–size rule," is that organisms tend to grow faster, mature earlier, and reach smaller asymptotic sizes at warmer temperatures than at cooler temperatures (Atkinson, 1994; Arendt, 2011; examples for fishes: Brunel and Dickey-Collas, 2010; Matta et al., 2016). Previous research indicates that this relationship may be due to the effect of temperature on asymptotic body sizes (e.g., a greater body size at cooler temperatures), which gives rise to adaptive changes in energy allocation to reproduction and other competing needs (Berrigan and Charnov, 1994; Atkinson, 1996; Angilletta et al., 2004; Hosono, 2011). Alternatively, nonadaptive temperature effects on metabolic rates may generate the same result (e.g., Angilletta et al., 2004; Munch and Salinas, 2009).

Theoretical models and concepts, such as the reaction norm model of maturation (Stearns and Koella, 1986; Stearns, 1992), provide mechanisms for the exploration of the plastic and adaptive processes of life-history traits. By definition, the maturation reaction norms represent genetically coded traits, the changes of which are evolutionarily "optimized" through changes in mortality and growth rates (Stearns and Koella, 1986; Stearns, 1992). The probabilistic maturation reaction norm (PMRN) approach (Heino et al., 2002; Dieckmann and Heino, 2007; Heino and Dieckmann, 2008) builds on the deterministic concept of maturation reaction norms by Stearns and Koella (1986). The PMRN approach involves statistically accounting for the major sources of plastic effects due to growth and survival and quantifying the remaining variation in maturation as more likely to represent adaptive genetic variation (Heino et al., 2002). Although this approach also is criticized (e.g., Kraak, 2007), several authors have applied this method to infer potential evolutionary changes in maturation for exploited fish species (e.g., Atlantic cod [*Gadus morhua*], Olsen et al., 2005; smallmouth bass [*Micropterus dolomieu*], Dunlop et al., 2005; and lake whitefish [*Coregonus clupeaformis*], Wang et al., 2008; reviewed by Heino et al., 2015). Furthermore, a few studies have attempted to account for other sources of plastic effects in the PMRN model, such as body condition (Grift et al., 2007; Uusi-Heikkilä et al., 2011) and social cue (e.g., presence of fish of same or opposite sex; Díaz Pauli and Heino, 2013).

Cutlassfish (some of which are also known as hairtails), including several *Trichiurus* species, are an important fisheries resource in the subtropical West Pacific (He et al., 2014; Wang et al., 2017). However, reliable species identification is difficult without the use of genetic methods, and in the FAO fisheries "capture production statistics," the catches of multiple cutlassfish species are lumped into a value for one nominal species, *Trichiurus lepturus* (Hsu et al., 2009; FAO, 2014). For this reason, and because of the lack of fishery stock assessments and regular surveys, the population ecology of individual *Trichiurus* species is poorly known. Nonetheless, *T. japonicus* is likely a dominant species
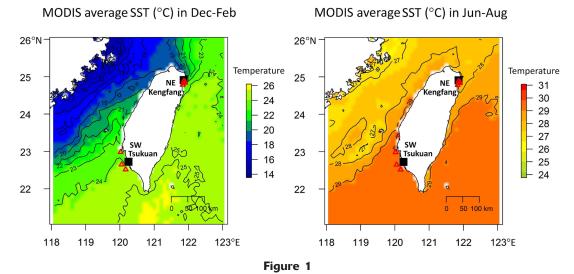
that contributes substantially to the coastal catch in this region (i.e., this species accounts for 40–100% of the total cutlassfish catch; Wang et al., 2017). Also, this cutlassfish is an important predatory fish in the subtropical Pacific and, moreover, has a year-round spawning behavior (Liu et al., 2009; Shih et al., 2011).

In this study, we focused on investigating growth and maturation patterns for *T. japonicus* along the Taiwan coast in the northwestern Pacific (Fig. 1). In Taiwan, 2 primary fishing grounds are located along the northeast (NE) and southwest (SW) coasts, and together they account for about 30% (range: 24–40%) of total annual catch of cutlassfish (based on 2003–2014 data from the Taiwan Fisheries Agency[2]). The results of a previous study indicate that these fishing grounds may represent distinct populations of *T. japonicus* (Tzeng et al., 2016). In addition, environmental and fishing conditions vary between these fishing grounds. Temperatures are lower along the NE coast than along the SW coast, in particular in winter. For example, the sea-surface temperatures (SSTs) are 19.2–24.6°C in winter (December–February) and 26.3–29.1°C in summer along the NE coast (June–August), and SSTs are 22.5–24.9°C in winter and 29.0–30.4°C in summer along the SW coast (Fig. 1) (also see Jan et al., 2002). The primary fisheries on both fishing grounds are pursued by using pair trawlers, but because of a lack of stock assessments, the fishing intensity is unknown. However, the number and size of trawlers were greater on the SW coast (282 boats, primary boat size of 50–100 metric tons) than along the NE coast (232 boats, primary boat size of 20–50 metric tons; Taiwan Fisheries Agency[3]), and therefore there is a higher exploitation pressure in the SW than on the NE coast. We hypothesize that the habitat or fisheries conditions have led to faster growth rates and earlier maturation patterns of *T. japonicus* along the SW coast than along NE coast.

Our objective was to describe growth and maturation of *T. japonicus* for the 2 fishing grounds and to infer potential adaptive-versus-plastic variation in the life-history traits of this species. Because the populations of *T. japonicus* at these 2 fishing grounds likely are distinct (Tzeng et al., 2016), some variation in adaptive traits for these populations may arise as a consequence of their genetic variability. We estimated the PMRNs to evaluate potential adaptive variation in maturation schedules and explored plastic changes in maturation schedules that are due to variations in growth. Also, we explored the covariation between growth and maturation in relation to habitat differences of the two areas.

Figure 1

Map showing locations of the ports Kengfang and Tsukuan (black squares) in Taiwan where catch of the cutlassfish *Trichiurus japonicus* was sampled during 2013–2015 and locations of areas fished by the boats based at the 2 ports (open red triangles), with average summer (June–August) and winter (December–February) sea-surface temperatures (SSTs in °C) around Taiwan. The SSTs are based on Moderate-resolution Imaging Spectroradiometer (MODIS) monthly mean SSTs for 2003–2014 (NASA Goddard Space Flight Center, Sea-viewing Wide Field-of-view Sensor [SeaWiFS] Ocean Color Data, website).

Materials and methods

Sampling

We collected immature and adult cutlassfish, including the *T. japonicus*, from the pair-trawler fisheries monthly at 2 fishing ports during 2013–2015: Kengfang (also transliterated as Gengfang) on the NE coast and Tsukuan (or Ziguan) on the SW coast of Taiwan (Fig. 1). The size of fishing boats (about 40 metric tons) and the fishing methods were similar during our sampling in these areas; for example, the nets had an array of mesh sizes descending from the opening to the codend (minimum mesh size: 2.0–2.5 cm), and the fishing depths were 100–150 m on the NE coast and 100–200 m on the SW coast (senior author, unpubl. data). The trawlers operate year-round along both coasts. However, fishing seasons for cutlassfishes varied: the fisheries along the NE coast catch cutlassfishes year-round, and the fisheries along the SW coast catch cutlassfishes mainly during autumn and early spring (September–February) and catch less in other months. Despite the differences in monthly distribution of catch between the areas, we attempted to collect samples evenly across months in both areas (Suppl. Table 1). Using a stratified random sampling design, we classified fish into 5 size categories based on body depth (defined as the vertical distance between the dorsal margin of the body and the anus, in millimeters): mini (<20 mm), small (20–25 mm), medium (25–45 mm), large (45–70 mm), and extra large (>70 mm). For each sampling trip, we randomly collected 10–20 fish for each of the small, medium, and large size categories. Fish small or large enough to fall in the mini and extra-large cat-

egories were rarely found in the catch; however, we collected these animals when they were available.

Despite the use of a standardized sampling scheme, maximum lengths and length distributions of samples of *T. japonicus* varied between the 2 areas. Maximum pre-anal lengths (i.e., the distance between the tip of upper jaw and the anterior side of anus) were 752 and 379 mm for the *T. japonicus* landed in Kengfang (NE) and Tsukuan (SW), respectively (Fig. 2). Also, mean pre-anal lengths were generally smaller in Tsukuan than in Kengfang in each year and all 3 years combined (Suppl. Table 2). Distributions of sample lengths were right-skewed in Kengfang but were approximately normal in Tsukuan (Fig. 2). We conducted additional sampling in Tsukuan to obtain large *T. japonicus* specimens, but we could not find comparable samples. Therefore, the differences in length distributions between areas probably were real and not due to sampling bias.

Because of the presence of multiple cutlassfish species in the catch of trawlers, we identified the species that composed each sample on the basis of genetic analysis; the detailed methods and results of this analysis have been published in Wang et al. (2017). For the subsequent analysis described here, we used only the specimens confirmed to be *T. japonicus*.

Biological measurements

We measured total length, pre-anal length, body depth, total weight, gonad weight, sex, and maturity state for individual fish. Because tail loss was common among the sampled fish, we used pre-anal length data to conduct the analysis. We determined sex and maturity

Table 1

Sex-specific parameters—the asymptotic length (L_∞) and the Brody growth coefficient (K) derived from the von Bertalanffy growth model (Eq. 1), the counterpart parameters, $L_{\infty,inv}$ and K_{inv}, derived from the inverse von Bertalanffy growth model (Eq. 2), and minimum length (L_{min}) and daily ages (T_{min}) of cutlassfish (*Trichiurus japonicus*). Samples were collected at 2 fishing ports, Kengfang and Tsukuan on the northeast and southwest coast of Taiwan, respectively, during 2013–2015. The 95% confidence intervals are given in parentheses.

Area	Sex	L_∞ (mm)	K (per year)	$L_{\infty,inv}$ (mm)	K_{inv} (per year)	L_{min} (mm)	T_{min} (d)
Kengfang (NE)							
	Male	370 (304–436)	0.32 (0.22–0.42)	576 (411–1275)	0.17 (0.07–0.28)	48	34
	Female	520 (407–633)	0.21 (0.15–0.27)	1094 (659–3068)	0.08 (0.03–0.15)	–	–
Tsukuan (SW)							
	Male	264 (238–290)	0.56 (0.42–0.70)	399 (337–488)	0.25 (0.18–0.34)	75	51
	Female	421 (360–482)	0.24 (0.18–0.30)	600 (477–878)	0.14 (0.09–0.20)	–	–

state of fish on the basis of visual inspection of gonads: fish with visible male or female gonads were classified as mature fish, and those with eggs present in the gonads were females (otherwise males). Fish with no visible gonads were classified as immature and of unknown sex. In addition, we collected the pair of sagittal otoliths to estimate ages of fish.

To ensure sufficient variation in lengths and ages for the subsequent growth analysis, for each area we compiled data on each group (i.e., immature fish, females, and males) by randomly selecting 5–10 fish per 20-mm size interval. Given the different ranges of pre-anal lengths of samples from Kengfang (range: 48–752 mm) and Tsukuan (75–379 mm), we selected 305 and 169 fish at the 2 areas, respectively. Further, because of a limited number of relatively small fish in the catch samples, we incorporated additional samples of small fish to conduct subsequent data analysis (no.=333 for Kengfang and no.=277 for Tsukuan).

Otolith processing and aging

There are generally no significant differences in otolith morphometrics between the left and right otoliths for a large number of fish species (Hunt, 1992; Megalofonou, 2006). Consequently, we randomly selected one of each pair of sagittal otoliths per fish, cleaned the surface of the otolith with an ultrasonic cleaning machine (Delta Sonicator DC150[4], Delta Ultrasonic Co., Ltd., Taipei, Taiwan), and air-dried and mounted it in epoxy resin blocks. We then ground the otolith resin blocks to reveal the otolith cores, using silicon carbon paper (grades 2000 or 2500).

We used the same aging techniques as those described in Shih et al. (2011): the otolith annuli were identified on the basis of the opaque bands. The first otolith annulus tended to be located at or beyond the
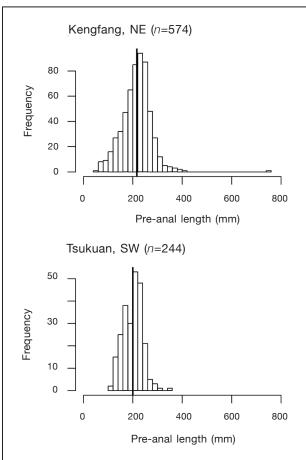

Figure 2

Length distributions of cutlassfish *Trichiurus japonicus* (males, females, and immature fish combined), sampled from the ports of (**A**) Kengfang and (**B**) Tsukuan, respectively, on the northeast (NE) and southwest (SW) coasts of Taiwan in 2013–2015. Vertical lines indicate mean lengths.

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

half distance from the core to the edge (Suppl. Fig.). Two readers counted otolith annuli under a microscope at 200–400× magnification, examining each otolith independently. The otolith age estimates were inspected to determine whether the differences in age estimates between readers were >2 years. We excluded 47 otoliths because of otolith breaks or discrepancies >2 years between the 2 readings. After these otoliths were excluded, the rate of agreement in age estimates between the 2 readers was 85.5% (i.e., the 2 readings were the same for 501 of 586 otoliths). For subsequent analyses, we used the average values of the 2 age readings. However, because *T. japonicus* spawn year-round in the waters off Taiwan, the true age can vary among fish for an age estimate.

Data analysis

Growth We compared growth of *T. japonicus* between the areas on the basis of length-at-age data and by fitting a growth model. For the length-at-age comparison, we accounted for the effects of sex and stages of maturation on lengths. Therefore, we compared lengths at a given age for immature fish, males, and females between the areas by using a 2-sample *t*-test.

Given the prolonged, year-round spawning season of *T. japonicus* (Shih et al., 2011), months of birth for these fish could vary between the areas, resulting in bias for our comparison of growth. To account for such bias, we estimated daily ages, using otoliths for age-0 fish and compared their average daily growth rates between the 2 areas (number of fish sampled [n]=24 for Kengfang and n=20 for Tsukuan). One experienced reader assessed these otoliths 3 times independently, and the data were averaged after discrepant estimates between readings were excluded (e.g., difference ≥10 d). Because daily growth increments for fish of ages ≥1 year were too dense to be counted correctly, we could not estimate daily growth rates for older fish. We calculated individual average daily growth rates as the ratio of pre-anal lengths over average daily ages. For comparison, we derived another estimate of daily growth rates by fitting a linear regression of pre-anal lengths (y axis) in relation to daily ages (x axis) with a constant intercept of 5.5 mm for each area (i.e., corresponding to the length at hatching of *T. japonicus*; Kiang[5]). The regression slopes indicate the average daily growth rates. We evaluated differences in daily growth rates between the 2 areas by comparing the explained variance of pre-anal lengths of these 2 models: the model with both area and daily ages as predictors compared with the model with daily ages as the sole predictor.

To describe ontogenetic growth, we used the von Bertalanffy growth model (von Bertalanffy, 1938). Because of apparent size dimorphism of the sexes, we fitted this model separately for males and females in

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[5] Kiang, Y.-K. 2017. Unpubl. data. National Taiwan Univ., No. 1, Sec. 4, Roosevelt Rd., Taipei, Taiwan 10617.

each area; immature fish were incorporated into samples of either sex for fitting sex-specific growth models. The von Bertalanffy growth model in terms of length is typically expressed as

$$L_t = L_\infty(1 - e^{-K(t-t_0)}),$$

where t = age, L_t is length at age t; and
L_∞ = asymptotic length;
K = the Brody growth coefficient; and
t_0 = the intercept at the horizontal axis (i.e., the hypothetical age at length 0).

Because of the lack of a biological meaning for t_0, it is common to replace it with L_0, the theoretical length at age 0. This leads to an alternative model form: $L_t=L_\infty-(L_\infty-L_0)e^{-Kt}$. This formulation is commonly applied to describe growth trajectories of elasmobranchs, given that their relatively large sizes at hatching can provide an adequate estimate of L_0 (Pardo et al., 2013). However, size at hatching is too small to be estimated accurately for many teleosts, including cutlassfish. Therefore, we substituted L_0 with L_{min}, the minimum length at catch. Accordingly, we offset all ages by t_{min}, the age corresponding with L_{min}, in the model:

$$L_t = L_\infty - (L_\infty - L_{min})e^{-K(t-t_{min})}. \quad (1)$$

The length-at-age data derived from length-stratified sampling may deviate from the true length-at-age distribution of a population. To avoid such bias and because measuring length is relatively precise and estimating age may not be, we estimated the von Bertalanffy growth parameters by using the inverse von Bertalanffy growth model, i.e., estimating age as a function of length (Vainikka et al., 2009; Mollet et al., 2013). The inverse function of Equation 1 is

$$t = t_{min} - \frac{1}{K}\ln\left(\frac{L_\infty - L_t}{L_\infty - L_{min}}\right). \quad (2)$$

The minimum lengths at catch (i.e., pre-anal lengths) of *T. japonicus* were 48 and 75 mm at Kengfang and Tsukuan (Table 1). By counting daily increments of these otoliths with 3 replicates, we estimated the mean of t_{min} to be 34 d (standard deviation [SD] 2.6) or 0.09 year and 51 d (SD 1.0) or 0.14 year at Kengfang and Tsukuan, respectively. Because a fish of length equal to L_{min} is immature and there is no reason to expect differential growth between sexes well before maturity, we assumed the same L_{min} and t_{min} for males and females. Inserting L_{min} and t_{min} into Equation 2, we used the nonlinear least squares method to estimate L_∞ and K for each sex and area. For comparison and compatibility with earlier studies, we also fitted Equation 1 to the length-at-age data.

We derived 95% confidence intervals (CIs) for the L_∞ and K estimates, using a bootstrap method (Manly, 1997). Specifically, we randomly sampled the length-at-age data with replacement to generate 1000 bootstrapped data sets, each with an equal sample size of the original data set, and then fitted Equations 1 and 2 to the bootstrapped samples. The lower and upper

bounds of the 95% CIs of L_∞ and K were respectively the 25th and 975th quantiles of the 1000-bootstrap-derived values of L_∞ and K.

Age and length at 50% maturity   Given that the maturity state is a binary variable and that probability of maturity tends to increase with length and age, we used logistic regression to estimate the age and length at which the probability of being mature is 50% (A_{50} and L_{50}). The equation that we used was

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x, \qquad (3)$$

where x = length or age; and

β_0 and β_1 are model coefficients.

A_{50} or L_{50} are the solutions of Equation 3 for p=0.5, that is, $-\beta_0/\beta_1$.

We derived the 95% CIs of A_{50} or L_{50} by using a bootstrap method (Manly, 1997). We generated 1000 bootstrapped data sets of equal sample size to those of the original data set and then fitted a logistic regression to the bootstrapped samples to derive estimates of A_{50} or L_{50}. The lower and upper bounds of the 95% CI of A_{50} or L_{50} were respectively the 25th and 975th quantiles of the 1000-bootstrap-derived values of A_{50} or L_{50}.

Probabilistic maturation reaction norms   The PMRN approach involves estimating age- and length-specific probability of maturation with the use of a logistic regression (Heino et al., 2002). Because newly mature *T. japonicus* cannot be distinguished easily from those previously mature, we followed the demographic approach developed by Barot et al. (2004a, 2004b). This method is based on calculating change in length-specific maturity over a time interval, here 1 year, aligned by the average length increment over the time interval (ΔL). Specifically, we used data for a given age, sex, and area to fit a logistic regression with maturity status as a response and length as a predictor, separately for each age group:

$$\text{logit}(O_t) = \ln\left(\frac{O_t}{1-O_t}\right) = \beta_0 + \beta_1 L_t. \qquad (4)$$

Equation 4 is equivalent to fitting Equation 3 to age-specific data.

O_t = the maturity ogive for age t;

L_t = length of fish at age t; and

β_0 and β_1 = the regression intercept and slope.

We fitted such a logit function of O_t for the ages in which both immature and mature individuals were present (i.e., t=1 and t=2 of both sexes and areas). Because of the relatively low number of age-specific samples (e.g., no.=19–58 per age-sex-location group), the logistic regression did not provide a good fit for some groups (i.e., age 1 of both sexes at Tsukuan, P=0.05–0.08). Nonetheless, we continued further analysis because these fits were reasonable on the basis of visual inspection (i.e., we accepted the model fits when the

fitting lines represented increasing probability of maturity with fish length). Then, we estimated the age-specific probability of maturing (m):

$$m(L_t) = \frac{O_t(L_t) - O_{t-1}(L_t - \Delta L)}{1 - O_{t-1}(L_t - \Delta L)}. \qquad (5)$$

Here the probability of maturing (m) is estimated as the fraction of immature fish at age t–1 that grew in length ΔL and reached maturity at age t. An underlying assumption of Equation 5 is that immature and mature fish of the same ages have the same growth and survival rates (Barot et al., 2004a, 2004b). Our data indicate that the lengths at ages 0, 1, and 2, respectively, did not vary between immature and mature fish of either sex in Kengfang but that the lengths varied between immature and mature male fish at ages 0, 1, and 2 in Tsukuan (Suppl. Table 3; this finding also is based on t-test results: P=0.01, 0.02, and 0.003 for ages 0 [n=20], 1 [n=49], and 2 [n=32], respectively). The observed differences in length at age between immature and mature fish indicate that our data violate this assumption. However, reports of previous studies have suggested that the PMRN approach was relatively robust even when this assumption is modestly violated (Barot et al., 2004a, 2004b).

The trajectory of probability of maturing generally indicates a sigmoid curve with increasing lengths. Therefore, we fitted a logistic regression with m as response and length as a predictor and estimated the length at m=0.5 (i.e., $Lp_{50,t}$):

$$\text{logit}(m(L_t)) = \beta_0 + \beta_1 \times L_t, \qquad (6)$$

with $Lp_{50,t}$ obtained as the solution of Equation 6 for $m(L_t)$=0.5.

We estimated the 95% CIs of $Lp_{50,t}$ using the bootstrap method. We generated 1000 bootstrapped data sets of age t and age t–1 (each with equal sample size of the original data set) and used these data sets to derive 1000 estimates of $Lp_{50,t}$. The lower and upper bounds of the 95% CI of $Lp_{50,t}$ were the 25th and 975th quantiles of the 1000-bootstrap-simulated values of $Lp_{50,t}$.

Randomization tests   Because parametric tests for comparing the von Bertalanffy growth coefficients (i.e., L_∞ and K) and maturation indices (i.e., A_{50}, L_{50}, and PMRNs) between the 2 sampling areas are cumbersome or unavailable, we used randomization tests (Manly, 1997; see also Barot et al., 2004b). Specifically, we permuted the data column of "area" and evaluated the between-area differences in the sex-specific estimates for each of these growth and maturation indices with 999 replicates. The sorted sequence of the 999 between-area differences of estimates approximated the range of all possible values of between-area differences for estimates under the null hypothesis (i.e., with no differences between the areas). We then evaluated the probability of the observed between-area difference for a sex-specific estimate (i.e., P-values) as $1-P(X \le D)$, where D is the observed between-area difference. We

evaluated differences in growth and maturation between sexes using similar randomization tests.

Results

Length distribution and length at age

T. japonicus sampled in Kengfang (NE) were on average larger (mean pre-anal length: 216.0 mm [SD 60.3]) than fish from Tsukuan (SW; mean pre-anal length: 200.3 mm [SD 38.8]). Length distribution for Kengfang also was broader than that found for Tsukuan (coefficient of variation (CV): 28% versus 19%; Fig. 2).

We observed an ontogenetic shift in growth variation between the 2 areas. For immature fish at ages of 0 and 1 year, mean lengths were lower in Kengfang than in Tsukuan (Fig. 3A). Subsequently, for mature fish of both sexes at ages ≤2 years, differences in lengths between the areas were not significant (Fig. 3, B and C). However, the patterns of lengths at ages between the areas were partly reversed for fish at ages ≥3 years with greater lengths at age in Kengfang than in Tsukuan (Fig. 3, B and C).

Early juvenile growth

We estimated average daily ages for 17 and 19 age-0 fish in Kengfang (NE) and Tsukuan (SW), respectively (Suppl. Table 4). Average daily ages and pre-anal lengths of fish were higher in Tsukuan than in Kengfang (Suppl. Table 4; for daily ages, $|t|$=3.56, df=21, P=0.002; for pre-anal lengths, $|t|$=2.63, df=29.9, P=0.01). However, growth of very young *T. japonicus* was similar between the areas on the basis of both estimates of daily growth rates (see Suppl. Table 4 for the ratios of pre-anal-length to daily age, $|t|$=0.41, df=17.0, P=0.68; for the regression-based daily growth rate, F=1.43, P=0.26).

Growth model

The magnitudes of area- and sex-specific estimates of L_∞ and K varied greatly between the 2 different model fits (e.g., Equations 1–2; Table 1). However, for output from both models, consistent growth patterns between the areas and sexes were observed (Table 1; Fig. 4). Generally speaking, L_∞ was higher and K lower in Kengfang (NE) than in Tsukuan (SW). Females had higher L_∞ and lower K than those of males (Table 1; Fig. 4). On the basis of randomization tests, the between-area differences in both L_∞ and K were significant for both models: for L_∞ of Equation 1, P<0.001 for males and P=0.002 for females; for L_∞ of Equation 2, P<0.001 for males and P=0.008 for females; for K of Equation 1, P<0.001 for males and P=0.003 for females; and for K of Equation 2, P<0.001 for males and P=0.003 for females (Table 1; results of randomization tests of between-sex differences in L_∞ and K are shown in Suppl. Table 5). These differences are in agreement
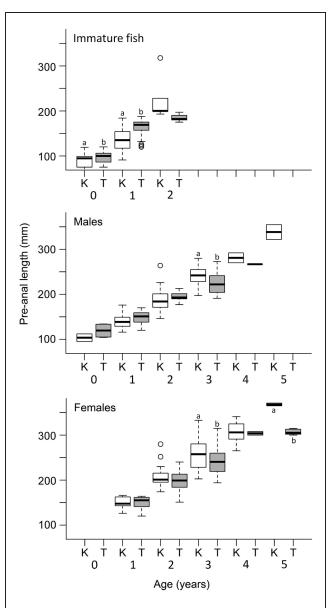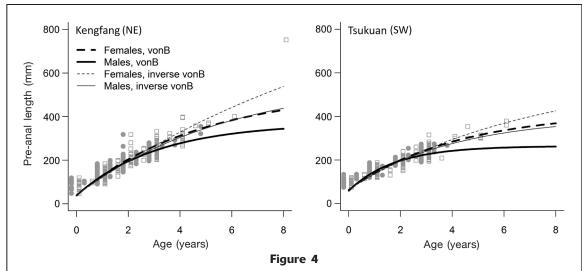

Figure 3

Length-at-age comparisons between 2 fishing areas off Taiwan near the ports of Kengfang (K, open boxes) and Tsukuan (T, gray boxes), based on sex- and maturation-state-specific data for (**A**) immature (**B**) male, and (**C**) female cutlassfish, *Trichiurus japonicus*, sampled in 2013–2015. The secondary x-axis shows the age group of fish. The letters *a* and *b* denote significant differences between the areas based on *t*-test results for immature fish at age 0 ($|t|$=2.01, df=35.9, P=0.05), immature fish at age 1 ($|t|$=4.67, df=61.4, P<0.001), males at age 3 ($|t|$=3.08, df=61.0, P=0.003), females at age 3 ($|t|$=2.29, df=91.9, P 0.02), and females at age 5 ($|t|$=15.73, df=2.7, P=0.001).

Figure 4

Sex-specific growth trajectories for populations of a cutlassfish, *Trichiurus japonicus*, near the ports of Kengfang and Tsukuan off the northeast and southwest coasts of Taiwan, derived from both the von Bertalanffy growth model (vonB, thick black lines) and the inverse model (inverse vonB, thin gray lines). For Kengfang data, one female sample with a large pre-anal length (752 mm) was excluded prior to fitting regression to enhance quality of fitting given the very high leverage and some uncertainty in the age estimate for this fish.

with the general patterns of larger length at age for older fish in Kengfang than Tsukuan (Fig. 3, B and C); however, for early ages, the larger K for *T. japonicus* in Tsukuan compensates for their lower L_∞, in agreement with length at age of immature fish being larger in Tsukuan than in Kengfang (Fig. 3A).

Age and length at 50% maturity

The estimates of A_{50} and L_{50} indicate consistent patterns between the areas and sexes: fish taken in Kengfang (NE) were older and larger at 50% maturity than those collected in Tsukuan (SW), and females reached 50% maturity at older ages and larger lengths than males (Fig. 5). Nonetheless, randomization tests revealed between-area differences in A_{50} and L_{50} were significant for males (P=0.005 and P=0.014 for A_{50} and L_{50}, respectively) but not for females (P=0.116 and P=0.066 for A_{50} and L_{50}, respectively; results of randomization tests of between-sex differences in A_{50} and L_{50} are shown in Suppl. Table 5). When data for the 2 areas were combined, ranges of A_{50} and L_{50} were 1.2–1.7 years and 153–184 mm, respectively.

Probabilistic maturation reaction norms

The PMRNs could be estimated for *T. japonicus* at ages of 1–2 years for both sexes and areas (Fig. 6), encompassing the age range during which 50% maturity was reached (Fig. 5). The 95% CIs of the sex- and area-specific midpoints of PMRNs overlapped (Fig. 6). Randomization tests showed no significant differences in these midpoints of PMRNs between sexes or areas
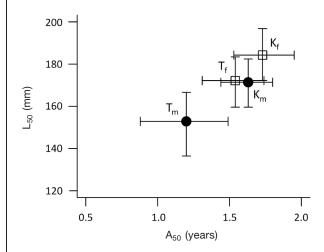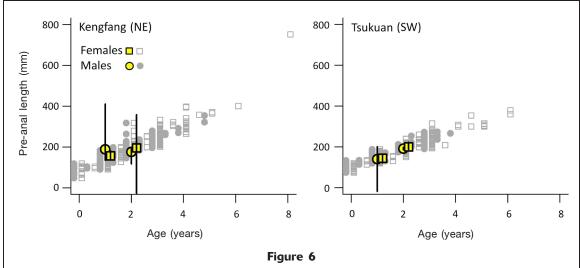

Figure 5

Estimates of length and age at 50% maturity (L_{50} and A_{50}) for populations of a cutlassfish, *Trichiurus japonicus*, sampled at the ports of Kengfang (K) and Tsukuan (T) in Taiwan in 2013–2015. Open squares indicate estimates for females (f), and black circles indicate values for males (m). Error bars indicate bootstrap-derived 95% confidence intervals.

(between-areas: P=0.24 and P=0.25 for males at ages 1 and 2, respectively; P=0.09 and P=0.44 for females at ages 1 and 2, respectively; for between-sexes randomization tests, see Suppl. Table 5).

Comparison of the midpoints of PMRNs and the

Figure 6

Estimates of probabilistic maturation reaction norms (yellow symbols) with length-at-age data (gray symbols) for populations of a cutlassfish, *Trichiurus japonicus* (females and males), sampled at the ports of Kengfang and Tsukuan on the northeast and southwest coasts of Taiwan in 2013–2015. Vertical black lines indicate bootstrap-derived 95% confidence intervals.

corresponding sex- and area-specific growth data at ages 1 and 2 revealed some phenotypic differences in maturation between the areas. As Figure 5 shows, the earliest maturation occurs in Tsukuan males (SW). In agreement with this observation, the males in Tsukuan have a relatively low PMRN midpoint, together with relatively large lengths for immature fish at age 1 (see Fig. 3A), resulting in a relatively high likelihood of maturation at that age. In contrast, for males in Kengfang (NE), the PMRN midpoint for age 1 was greater than the lengths of most age-1 individuals, resulting in a greater tendency to have delayed maturation to age 2 (Fig. 5, Fig. 6A). For female fish, between-area differences in the midpoints of PMRNs were so small (Fig. 6) that the difference in length of immature fish did not result in clear differences in maturation.

Discussion

Our study provides evidence of variation in growth and maturation patterns and potential underlying drivers of those patterns for a subtropical cutlassfish at a small spatial scale. We found that growth rates of the early stage of juvenile *T. japonicus* (first few months) were similar between areas, whereas immature fish at ages of 0–1 years grew faster in the warmer Tsukuan (SW), corresponding to the spatial gradient of temperatures. However, results for growth of adults indicate an inverse pattern and that both adult males and females tended to be larger in the colder Kengfang (NE). Further, we found that *T. japonicus* generally matured at ages 1–2 in both areas, but males in Kengfang had a tendency for delayed maturation. Because the midpoints

of PMRNs did not differ significantly between the areas, growth-related phenotypic plasticity is sufficient to explain the observed variation in maturation schedules of males. This result contrasts with those from some earlier studies in which neighboring stocks or stock components were compared (marine fish: Olsen et al., 2005; Vainikka et al., 2009; Wright et al., 2011; Mollet et al., 2013; freshwater fish: Wang et al., 2008; Morita et al., 2009). Overall, these observed patterns of differences in growth and maturation between the areas are consistent with the temperature-size rule (Angilletta et al., 2004; Arendt, 2011), where cooler temperatures led to slower prematuration growth, delayed maturation, and larger asymptotic lengths for fish. However, with the comparison of only 2 fishing grounds and limited environmental data, we cannot exclude other sources that could produce plastic variation.

Temperature-size rule involves thermal effects on growth and maturation

A negative effect of temperature on adult body size, the temperature-size rule has been reported for various organisms (Atkinson, 1994; Angilletta et al., 2004). Such an effect of temperature on variation in body size may involve multiple plastic or adaptive pathways (Angilletta et al., 2004; Ohlberger, 2013). For example, temperature may induce plastic changes in physiological rates, such as growth, metabolism, and mortality and lead to the observed variation in body size (e.g., Munch and Salinas, 2009). Simultaneously, temperature effects on the metabolic rates may induce adaptive changes. As metabolic costs increase with temperature, a thermal constraint on maximum body size may oc-

cur at warm temperatures. Consequently, selection should favor differential optimal adult body sizes with respect to the temperature differences (Berrigan and Charnov, 1994; Atkinson, 1996). Moreover, several authors suggest that the temperature-size patterns may involve changes in the reaction norms of growth and maturation (Angilletta et al., 2004; Ohlberger, 2013). In relation to these studies, our results provide a clear evidence of the covariation of growth and maturation underlying the temperature effects on adult body sizes. Additionally, we show that some variation in these life-history traits (e.g., maturation) is likely to be chiefly plastic.

Other sources of life-history variation

Potentially, other factors may also contribute to the observed life-history variation in *T. japonicus*. For example, positively size-selective fishing may induce selection for growth, favoring the genotypes associated with slower growth rates (Ricker, 1981; Conover and Munch, 2002; Reznick and Ghalambor, 2005; Wang and Höök, 2009; Enberg et al., 2012). Also, fishing-induced size truncation of adult demography (Hsieh et al., 2010) could potentially confound the patterns of differences in growth between the areas. The different length distributions (Fig. 2) indicate higher mortality for fish along the SW than along the NE coast—a finding that is consistent with the higher fishing power of the vessels operating from Tsukuan in comparison with those from Kenfang. However, because estimates of fishing mortality for cutlassfish in Taiwan were unavailable, it remains unclear whether different fishing intensity accounts for the life-history variation in cutlassfish between the areas. To enhance understanding of growth patterns for *T. japonicus*, we suggest identifying other relevant driving factors that affect growth of cutlassfish (e.g., fishing and other biological interactions).

We found that between-area variation in maturation schedules was more pronounced for males than females. In general, increasing body size tends to increase fitness more for female fish than for male fish (Bell, 1980; Gross and Sargent, 1985; Fleming and Gross, 1994). Consequently, selection may favor delayed maturation in females, compensating for the different growth rates between the areas.

Our results indicate potential adaptive variation in adult growth rates and plastic variation in maturation of *T. japonicus* between 2 areas off Taiwan. The spatial patterns of adult growth rates and maturation follow the temperature gradient, indicating that temperature variability exerts an effect on the observed life-history patterns. Also, the different adult growth rates between sexes are consistent with selection that favors sexual dimorphism with body size (Parker, 1992).

Implications for fisheries management

Adaptive and plastic variation in life-history traits are evidence of the complex effects of environmental and anthropogenic drivers on living organisms. Consequently, it is critical to understand the processes that lead to variation in life-history characteristics in order to enhance the effectiveness of natural resource management. Subtropical and tropical fishes are under much pressure from both environmental changes and fisheries exploitation (Cheung et al., 2010; Blanchard et al., 2012). Our results provide essential information on how a subtropical fish responds to these effects, information (e.g., accounting for the area-specific life-history patterns and the regulation of fishing intensity) that can be incorporated in potential management plans.

Our results indicate that there is a significant difference in growth trajectories for *T. japonicus* from the 2 primary fishing grounds in Taiwan. Such distinct growth patterns indicate the possible presence of discrete populations, and this result is in agreement with broad-scale patterns in mitochondrial DNA markers (Tzeng et al., 2016). On the other hand, we did not find significant differences in the PMRNs, which might be expected to mirror observed genetic differences. A better understanding of the spatial scales of population differentiation and the roles of genetic and plastic variation in life-history traits of this important commercial species is clearly needed.

There is increasing concern about the potential warming of ocean waters and the effects of this warming on body size of various organisms, including commercially caught fish (Sheridan and Bickford, 2011; Baudron et al., 2014). Our findings contribute to an understanding of the mechanisms underlying such warming effects through the documentation of differences in growth rates of the *T. japonicus* that experience different temperature regimes in the 2 sampling areas. Moreover, we suggest that the information on temperature–size (life-history) relationships may be useful for forecasting changes in sizes of other subtropical fish species.

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