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# Difference in Size at Maturity in Annual and Overwintering Generations in the Tanaidacean *Zeuxo* sp. in Oshoro Bay, Hokkaido, Japan

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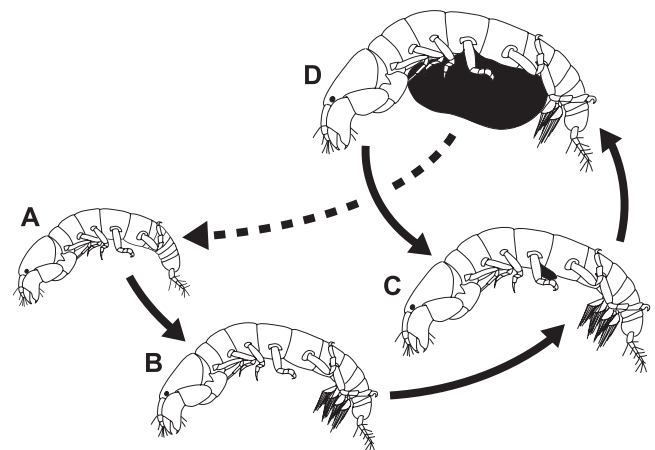
We investigated the life cycle of the tanaidid *Zeuxo* sp. 1 (Crustacea: Peracarida: Tanaidacea), which lives epiphytically in dwelling tubes on the algae *Sargassum* spp. and *Neorhodomela aculeata* in Oshoro Bay, Hokkaido, Japan. We obtained data on its population size distribution, age structure, and reproductive phenology through monthly sampling from April 2011 to June 2012. From these data, we detected an overwintering group ( $F_0$ ) that arises from mancae that are released in autumn, overwinters, reproduces the following spring, and then disappears. The overwintering group produces mancae ( $F_1$ ) that reach maturity and themselves reproduce within six weeks after release; the  $F_1$  mancae give rise to an  $F_2$  and possibly an  $F_3$  generation within a single summer. We refer to individuals that reproduce in the same summer that they were released as the ‘annual group’. Reproduction overall was restricted to the period from May to October, when the sea-surface temperature exceeded 10°C. During both years, overwintering females first became reproductive in May. Reproduction in the annual group began in June and continued through mid-October. Mancae were observed in samples from June through October. The two groups differed significantly in size at reproduction; compared to the annual group, females in the overwintering group reproduced at larger minimum and average body sizes, and males began to express enlarged chelae, a secondary sexual character, at a larger size. The difference in size at maturity may be related to the differences in water temperature during the main period of growth and maturation.

**Key words:** Tanaididae, *Sargassum*, *Neorhodomela*, population dynamics, reproductive cycle, seasonal size variation, direct development

## INTRODUCTION

Most marine benthic invertebrates produce planktonic larvae, which helps them disperse (Anger, 2006). Peracaridan crustaceans such as isopods, cumaceans, and amphipods, however, lack a planktonic larval stage (Johnson et al., 2001). Females brood eggs and hatchlings in a marsupium (= brood pouch) until the hatchlings reach the juvenile adult stage, upon which they are released. Species in the peracaridan order Tanaidacea are typically benthic, with females releasing juveniles called mancae (Fig. 1); the mancae resemble adults, but pereopod 6 and the pleopods are incompletely developed or lacking. The absence of a planktonic larval stage should lead to low and slow dispersal ability in tanaidaceans and can result in high local densities, such as the 146,000 individuals per m<sup>2</sup> reported by Delille et al. (1985). Due to their high abundance, tanaidaceans are ecologically important (Larsen et al., 2015), but their life cycles have been less well studied than those of

other peracaridans (Johnson et al., 2001; Rumbold et al., 2012). To date, only a few studies have examined their population dynamics and reproductive cycles, in the families



**Fig. 1.** Developmental stages of female *Zeuxo* sp. 1 after release from the marsupium. **(A)** Manca. **(B)** ‘Young female’, which lacks any trace of the marsupium. **(C)** ‘Preparatory female’, with the developing marsupium evident as paired precursors. **(D)** Ovigerous female. Black fill indicates the developing or developed marsupium; arrows indicate the developmental sequence; the dashed arrow indicates the release of mancae.

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† Deceased

This study was begun in 1980 by the late YH under the guidance of the late Tatsunori Itô with help in sampling from Kazuro Shinta, and then continued by KK and HK since 2011.

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Kalliapseudidae, Leptocheliidae, and Tanaididae (Rumbold et al., 2012). Several species appear to have a seasonally restricted breeding period (Fonseca and D’Incao, 2003), whereas others reproduce year-round (Aboul-dahab et al., 2001). The life cycle can vary intraspecifically along a latitudinal gradient; for example, a species can breed seasonally in subtropical populations but year-around in tropical populations (Pennafirme and Soares-Gomes, 2009).

*Zeuxo*, the most species-rich genus in the family Tanaididae, has a worldwide distribution (Larsen, 2014). Species in *Zeuxo* are often a major component of the epiphytic fauna on seaweeds and seagrasses (e.g., Esquete et al., 2011), where they interact ecologically as prey items and primary consumers. Species of *Zeuxo* occasionally occur at very high densities (e.g., more than 320,000 individuals/m<sup>2</sup>; Hayashi and Kanda, 2007), and Kakui (2015) reported the gut contents of a goby to comprise mainly a single species of *Zeuxo*. Nakaoka (2002) found that an unidentified species of *Zeuxo* consumes seagrass seeds and inhabits spathes, using them as a nursery.

*Zeuxo* sp. 1 (Supplementary Figure S1) occurs subtidally in Oshoro Bay, Hokkaido, Japan, inhabiting self-woven nests attached to seaweeds. Kito (1975) studied its seasonal fluctuation in abundance on *Sargassum* seaweeds from August 1973 to July 1974 and detected a distinct peak in September (ca. 6700 individuals/m<sup>2</sup>) but lower densities (ca. 1000 individuals/m<sup>2</sup>) in August and October; except for these three months, the density was nearly zero. Based on specimens collected from *Sargassum* seaweeds for three months (May to July, 1980), Hayakawa (1981) detected ovigerous females throughout the study period, but mancae only in June and July; in addition, he detected two body-size classes among adult individuals.

The goals of our study were to (1) elucidate the life cycle of *Zeuxo* sp. 1 in Oshoro Bay, and (2) analyze the growth patterns of the two size groups previously recognized among reproductive individuals.

## MATERIALS AND METHODS

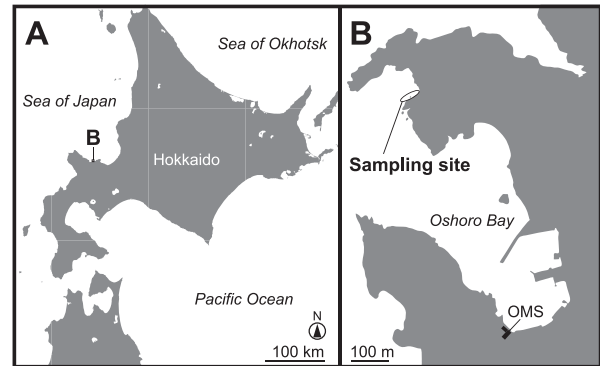
### Taxonomy

Kito (1975) identified the tanaidids he studied in Oshoro Bay as *Anatanais normani* (Richardson, 1905) (later transferred to *Zeuxo*; Sieg, 1980), although Sieg (1983) believed Kito’s (1975) species to be *Zeuxo kurilensis* (Kussakin and Tzareva, 1974). Based on morphology and habitat, all of our specimens are conspecific with the species treated by Kito (1975), but they are neither *Z. normani* nor *Z. kurilensis*. Our specimens have a slight anterior projection on the pereopod-1 coxa and only one inner plumose seta on the pleopodal endopod, whereas both these species have

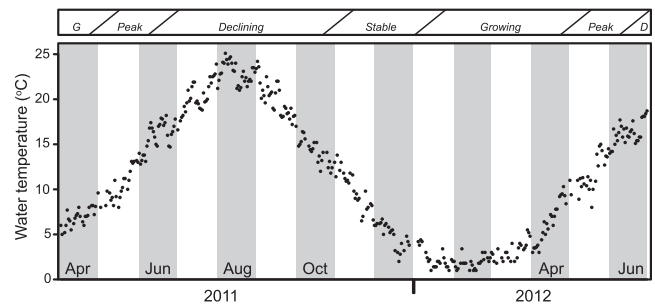
different characters (cf. Kussakin and Tzareva, 1974; Sieg, 1980). Pending identification of our specimens, this species is referred to herein as *Zeuxo* sp. 1.

### Seaweed and animal collection, and environmental data

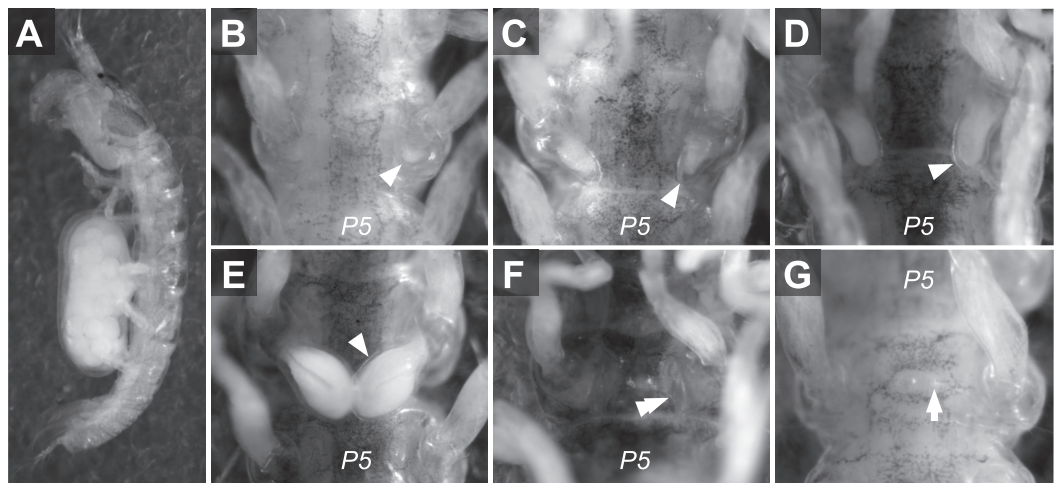
We collected *Sargassum* seaweeds (mainly *S. confusum* C. Agardh) monthly from April 2011 to June 2012 in Oshoro Bay (Fig. 2,



**Fig. 2.** Maps showing the location of the sampling site. (A) Location of Oshoro (B) in Hokkaido. (B) Sampling site in Oshoro Bay. OMS, Oshoro Marine Station.



**Fig. 3.** Daily sea-surface temperature in Oshoro Bay from April 2011 through June 2012. The bar at the top indicates the four periods in the life history of *Sargassum confusum*, after Kito (1975). Abbreviation: G, growing; D, declining.



**Fig. 4.** Sexual traits in female and male *Zeuxo* sp. 1. (A) Female with marsupium, lateral view. (B–E) Stages in development of the marsupium from paired elements (the left one indicated by arrowheads), ventral view. (F) Marsupium scars (left one with double arrowhead) in a female, ventral view. (G) Genital cones (left one with arrow) in a male, ventral view. P5, pereonite 5.

Supplementary Figure S2). The biomass of *Sargassum* spp. in Oshoro Bay changes seasonally (Kito, 1975) (Fig. 3, top), with growth from January to late April, a rapid increase from late April to early June, and a gradual decrease from June to late October. From late October to January, the biomass remains low. Amounts of seaweed sampled varied, depending on the stage of the seaweed and the density of *Zeuxo* sp. 1. As the *Sargassum* biomass decreases drastically after October and the tanaidacean densities drop to nearly zero from autumn to early spring (Kito, 1975; Hayakawa, 1981), little was known about *Zeuxo* sp. 1 in winter. During the course of our study, however, *Zeuxo* sp. 1 was found on another seaweed, *Neorhodomela aculeata* (Perestenko) Masuda, which was common low in the *Sargassum*-dominated seaweed community and occurred in moderate quantity in winter and early spring. *Neorhodomela aculeata* was collected along with *Sargassum* from November 2011 through June 2012.

Seaweeds were collected by hand from the subtidal zone and immediately put into plastic bags. The seaweeds were rinsed in tap water; after osmotic shock caused the tanaidaceans to release, the water was filtered through a plankton net (0.1 mm mesh). This process was carried out three times for each seaweed sample. Animals were fixed in 70% ethanol or Bouin's fluid, and preserved in 90% ethanol. Washed seaweeds were dried at room temperature for two days, and then weighed.

The sea-surface temperature (Fig. 3) was measured daily in front of the Oshoro Marine Station (OMS in Fig. 2) by Koji Shibazaki (administrator of OMS) and Kumiko Shibazaki. For *S. confusum* phenology (Fig. 3, top), the classification of Kito (1975) was used, although his terms 'stable season', 'growth season', 'luxuriant season', and 'withering season' have been replaced with 'stable period', 'growing period', 'peak period', and 'declining period', respectively.

#### Counting, measurements, and staging

To describe the life cycle of *Zeuxo* sp. 1 the following sex and age classes were defined:

1. *Mancae*: Post-embryonic juveniles; pereopod-6 lacking, or with fewer than six articles. Sexual characters are not yet differentiated.

2. *Post-manca individuals*: Individuals bearing pereopod-6 with six articles. Males and females are differentiated.

2.1. *Males*: Individuals having a pair of genital cones (a male trait; Fig. 4G). Two classes are recognized:

2.1.1. *Young males*: Males with chelipeds not different from

those of females.

2.1.2. *Old males*: Males with enlarged chelipeds compared to females of similar body size. Although young and old males were sometimes difficult to distinguish on an individual basis, the two groups showed different slopes in cheliped size to carapace size regressions (see below).

2.2. *Females*: Individuals lacking genital cones. We recognized three classes:

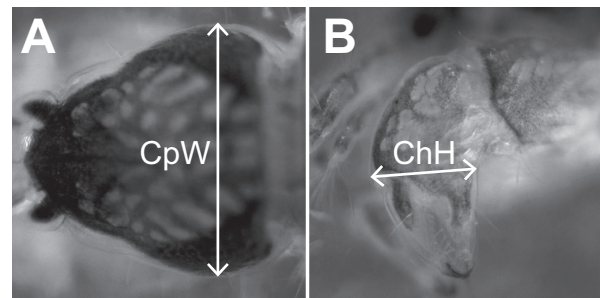
2.2.1. *Young females*: Females with neither a marsupium nor a marsupium scar.

2.2.2. *Preparatory females*: Females with a pair of developing marsupia.

2.2.3. *Reproductive females*: Females with a pair of fully developed marsupia or marsupium scars. This class included ovigerous females with eggs or hatchlings in the marsupium (Figs. 1D, 4A).

Post-manca individuals that lacked a genital cone and marsupium were treated as young females, because male traits were observable even in very small individuals (CpW < 0.20 mm). According to previous studies (e.g., Hamers and Franke, 2000; Toniollo and Masunari, 2007), tanaidid females completely lack a marsupium in the early postmarsupial stage. In our material, mancae and young females completely lacked a marsupium (Fig. 1A, B), which develops gradually via several molts (Figs. 1C, 4B–E). After the release of mancae, females lose the marsupium without a molt, leaving a marsupium scar (Fig. 4F), but may subsequently develop the marsupium again through several molts, and may spawn again.

Each sample was first checked for the presence of mancae. All



**Fig. 5.** Carapace (A) and chela (B) measurements (double-headed arrows) taken in *Zeuxo* sp. 1. CpW, carapace width; ChH, chela height.

**Table 1.** Number of *Zeuxo* sp. 1 individuals (except mancae) and the dry weight of algae sampled each month. Samples containing mancae are shown in bold.

Year	2011									2012						
	Date-Month	28-Apr	16-May	30-Jun	11-Jul	3-Aug	14-Sep	12-Oct	10-Nov	14-Dec	19-Jan	24-Feb	5-Mar	19-Apr	15-May	4-Jun
Specimens (All)	31	11	285	71	233	524	68	141	90	37	25	67	62	64	35	
Specimens (S)	31	11	<b>285</b>	<b>71</b>	<b>233</b>	<b>524</b>	<b>68</b>	13	4	4	1	0	25	47	<b>12</b>	
Dry weight (g, S)	560	216	240	70	105	95	60	50	45	41	44	37	93	186.5	201	
Specimens/100g (S)	5.5	5.1	118.8	101.4	221.9	551.6	113.3	26.0	8.9	9.8	2.3	0.0	26.9	25.2	6.0	
Specimens (N)	–	–	–	–	–	–	–	–	128	86	33	24	67	37	17	<b>23</b>
Dry weight (g, N)	–	–	–	–	–	–	–	–	25	24	20	13	32	40	27	27
Specimens/100g (N)	–	–	–	–	–	–	–	–	512.0	358.3	165.0	184.6	209.4	92.5	63.0	85.2

Abbreviation: S, *Sargassum* spp.; N, *Neorhodomela aculeata*.

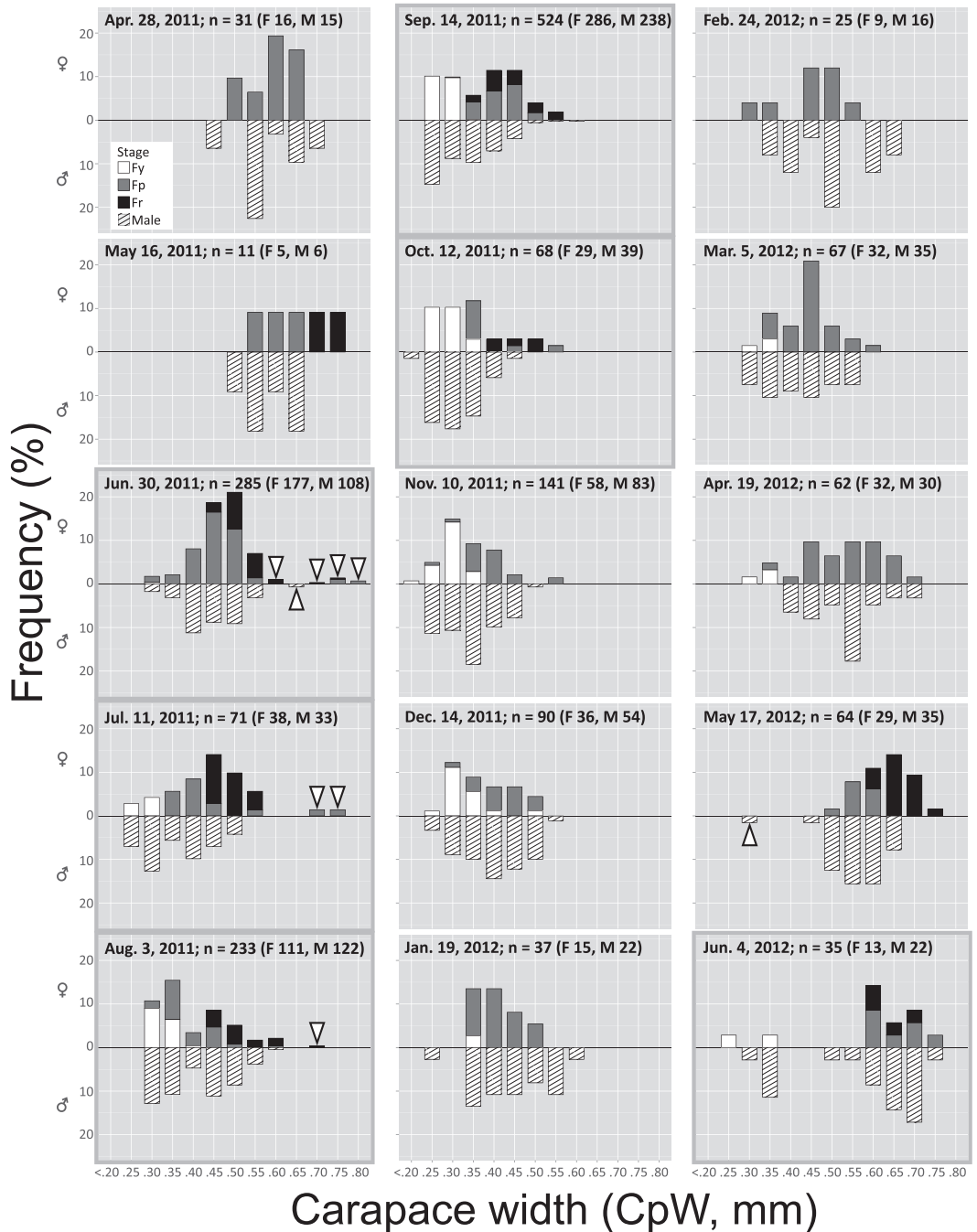
post-manca individuals then were counted, measured, sexed, and identified to stage under a Nikon SMZ 1500 stereoscopic microscope. Mancae were not counted or measured. The procedure differed for samples collected in August and September. Because these samples contained numerous mancae and small post-manca individuals, each sample was subsampled by using Motoda's (1959) plankton-sample divider (5605-F; Rigo, Tokyo, Japan), and then processed as above. The sex ratio was examined with the binominal test in R version 3.2.2 (R Core Team, 2015).

Carapace width (CpW), which correlates well with body length, was used as the body-size index (Supplementary Figure S3). The height of the chelipedal propodus (= chela height, ChH) was used to detect the smallest size of males showing secondary sexual characters (see below). CpW and ChH were measured at the widest or highest part, respectively (Fig. 5, double-headed arrows).

**Group setting and comparison of two body-size groups**

Hayakawa (1981) observed two groups of individuals in *Zeuxo* sp. 1 in summer that differed in size at reproduction and in chela size relative to body (carapace size). He speculated that these might represent individuals of larger size that reproduced in late spring and summer after overwintering (here termed the 'overwintering group'), and individuals of smaller size that reproduced during the same summer they were released as mancae (here termed the 'annual group'). We examined the differences in size at reproduction and chela development between these two groups by following the size distribution of post-manca individuals through time. For reproductive females, analysis of variance (ANOVA) was used to compare CpW between the overwintering and annual groups, and the relationship between CpW and ChH in each group was examined by linear regression. Males lack an obvious external indicator of sexual maturation; while enlargement of the chelipeds is a male secondary sexual trait

(Rumbold et al., 2014; Larsen et al., 2015; cf. Supplementary Figure S1), enlarged chelipeds do not directly indicate whether males contain mature sperm and are ready for reproduction. The relationship between CpW and ChH was analyzed for each group by using two-segment piecewise regression (Crawley, 2007), and the breakpoint was detected in the two-segment regression line with the minimal residual standard error (Crawley, 2007: p. 428). The breakpoint was defined as onset of expression of the secondary sexual trait, and males with greater CpW than the value at the breakpoint were regarded as old males. The regression lines for old males in each of the overwintering and annual groups were compared by using analy-



**Fig. 6.** Size frequency distributions of *Zeuxo* sp. 1 by month from April 2011 to June 2012. Months when mancae were collected are shaded in darker gray than the rest. White arrowheads indicate individuals regarded as in the overwintering group. Abbreviations: F, females; Fp, preparatory females; Fr, reproductive females; Fy, young females; M, males.

sis of covariance (ANCOVA).

## RESULTS

### Annual changes in the density and population structure of *Zeuxo* sp. 1

The density of *Zeuxo* on *Sargassum* spp. (Table 1) was low from mid-November to mid-May (2011) or early June (2012), increased greatly by late June, and remained high until mid-October, with highest density in September. The period of high densities coincided with the periods of highest *Sargassum* biomass, from the peak in early June through mid-October, when *Sargassum* declined. In contrast, density of *Zeuxo* on *Neorhodomela aculeata* was highest when we began sampling on that species in November 2011 and remained high to March 2012 (Table 1), with densities from mid-April to early June 2.5–14.2 times higher than densities on *Sargassum* spp. during the same period.

Figure 6 shows the size frequency distribution and population structure of *Zeuxo* sp. 1 by monthly sampling date. Data from samples collected on *Sargassum* and on *N. aculeata* were pooled. The sex ratio was biased toward females in June and September 2011 (binominal test,  $P < 0.05$ ), or toward males in November 2011 (binominal test,  $P < 0.05$ ); but not sex-biased in the whole sample (binominal test,  $P = 0.518$ ; 886 females and 858 males) or in other months (binominal test,  $P > 0.07$  in each) (Supplementary Table S1). Preparatory females (Fp) were found every month, but reproductive females (Fr) were detected only from May to October, and mancae from June to October.

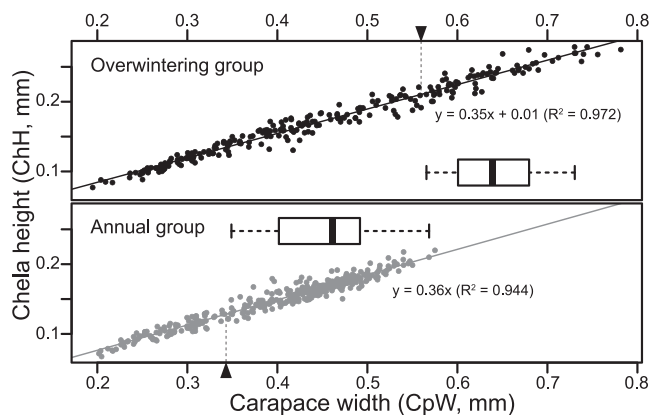
### Comparison of the overwintering and annual groups

Two size classes are evident in *Zeuxo* during the reproductive season (Fig. 6) (e.g., compare the size distribution between May and June, 2012). We consider the large size class to be an overwintering generation and the smaller size class to be individuals that were released as mancae and reached reproductive maturity the same season (see Discussion).

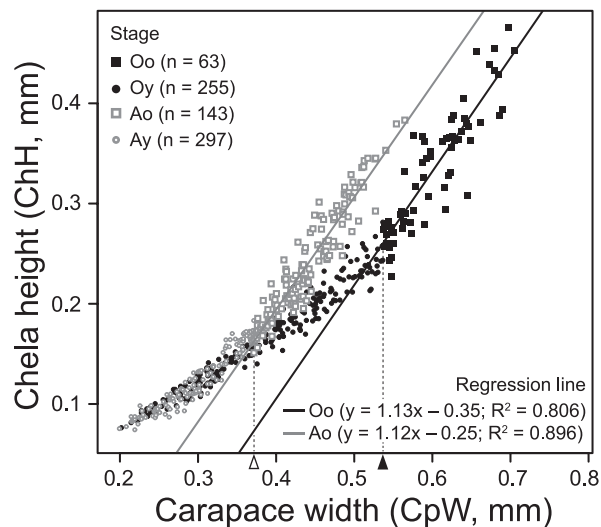
In the overwintering group were large individuals (arrowheads, Fig. 6) in June, July, and August, 2011; those with CpW greater than 0.45 mm in June 2012; and animals collected in April and May 2011, and from November 2011 to May 2012. The specimen indicated with an arrowhead in May 2012 was regarded as in the overwintering group, because no mancae were collected in this and previous months. This individual might, however, have resulted from very low-level early reproduction that gave rise to a few mancae, and thus belong in the annual group. In the annual group were individuals without arrowheads from June to August 2011, all individuals in September and October 2011, and animals with CpW less than or equal to 0.35 mm in June 2012. The October 2011 sample may actually have comprised individuals of both groups; this is because some of the smaller individuals present in the population at the time that sample was taken may have overwintered, rather than maturing and reproducing before the date the November sample was taken. However, the November sample was clearly in the overwintering group, as no reproductive females were observed that month, and the November cohort overwintered to become the group reproducing at large body size in May 2012.

Figure 7 shows the relationship between CpW and ChH for females in the two groups, with boxplots indicating the range in CpW for reproductive females. The smallest CpW of reproductive females was 0.566 mm in the overwintering group and 0.349 mm in the annual group. Overall, CpW of reproductive females was significantly larger in the overwintering group ( $n = 30$  individuals, average = 0.644 mm) than in the annual group ( $n = 168$  individuals; average = 0.454 mm) (ANOVA;  $F = 306$ ;  $P < 0.001$ ).

Figure 8 shows the relationship between CpW and ChH for males in the two groups. The breakpoints, indicative of the onset of expression of enlarged chelipeds as a secondary sexual trait, were at CpW 0.537 mm (black arrowhead) and 0.372 mm (white arrowhead), respectively.



**Fig. 7.** Relationship between carapace width and chela height for overwintering and annual females in *Zeuxo* sp. 1. The boxplots show the median and range of carapace width for reproductive females in the two groups (the boxplot whiskers extend to 1.5× the interquartile range). A dashed line and black arrowhead indicate the smallest ovigerous female observed in each group.



**Fig. 8.** Relationship between carapace width and chela height for overwintering and annual males in *Zeuxo* sp. 1. The dashed lines and black and white arrowheads indicate the breakpoints for the overwintering (0.537 mm) and annual (0.372 mm) groups, respectively. Abbreviations: Oo, Oy, old and young overwintering males; Ao, Ay, old and young annual males.

for the overwintering group and 0.372 mm (white arrowhead) for the annual group. The regression lines for old males in the two groups showed a significant difference in the intercept on the horizontal axis (ANCOVA;  $F = 215.33$ ;  $P < 0.001$ ) but not in the slope ( $F = 0.038$ ;  $P = 0.845$ ).

## DISCUSSION

### Life cycle of *Zeuxo* sp. 1 on seaweeds in Oshoro Bay

Judging from the seasonal distributions of reproductive females and mancae (Table 1, Fig. 6), *Zeuxo* sp. 1 in Oshoro Bay has an annual breeding period from May to October, when the sea-surface temperature exceeds ca. 10°C (Fig. 3). The tanaidid density on *Sargassum* spp. was high in those months, but very low at other times. Unexpectedly, we found relatively high densities of *Zeuxo* sp. 1 on *Neorhodomela aculeata*, at least during the limited sampling period from November 2011 to June 2012, during which the tanaidid density was low on *Sargassum*. We speculate that *Zeuxo* sp. 1 may utilize *N. aculeata* (and possibly other seaweeds) throughout the year, but temporally expand its habitat to *Sargassum* spp. during the breeding period, which corresponds to the period of highest biomass for *Sargassum confusum*. As *Sargassum* was much more abundant than other seaweeds during this period, a major part of *Zeuxo* reproduction probably took place on *Sargassum*. In other words, *Sargassum* is likely the major breeding habitat, with other seaweeds such as *Neorhodomela* used primarily for overwintering.

The densities of *Zeuxo* sp. 1 reported in Table 1 do not accurately reflect relative changes in biomass, because of the large seasonal changes in the *Sargassum* biomass. The real biomass of *Zeuxo* sp. 1 must be larger during the peak period and smaller during the declining period of *Sargassum* than indicated by the numbers in Table 1. Nevertheless, it seems safe to say that *Zeuxo* sp. 1 on *Sargassum* spp. increased in number of individuals and biomass from May or June to September, decreased by December, and remained at a very low level during winter and early spring.

There have been few previous studies on the life cycle and population structure of epiphytic tanaidaceans. Rumbold et al. (2012) investigated *Tanais dulongii* (Audouin, 1826) in algal beds in Argentina, where the most abundant algal species were *Ulva rigida* C. Agardh and *Corallina officinalis* Linnaeus. That study found that *T. dulongii* reproduces year-round, but did not analyze data separately for the two algal species. Nakaoka et al. (2001) documented annual changes in the density of an unidentified *Zeuxo* species on *Zostera* seagrasses in Otsuchi Bay, Japan. *Zeuxo* appeared abundantly on the seagrasses in early summer, but was rare or absent in other seasons, suggesting a habitat change by the tanaidid. There are thus indications that a seasonal habitat change may be a common feature of the life cycle in epiphytic tanaidaceans.

### Occurrence of two reproductive groups in *Zeuxo* sp. 1

We confirmed in 2011 and 2012 the occurrence of two groups in *Zeuxo* sp. 1 that reach reproductive maturity at different sizes, as Hayakawa (1981) noted, indicating this is a consistent aspect of the life cycle of *Zeuxo* sp. 1 at Oshoro. We conclude that most individuals in the overwintering group reproduce only once, as they first became reproduc-

tive in May in 2011 and 2012, and rapidly declined in abundance from June through August 2011, with no overwintering individuals remaining in mid-September 2011 (Fig. 6). However, as we observed a few preparatory females in mid-July 2011, it is conceivable that some overwintering individuals could produce two broods.

Reproductively mature annual females, i.e., individuals that matured from mancae released by overwintering females, were observed on 30 June 2011 and were probably present by mid-June. Reproductive females were present in the annual population until mid-October, a span of roughly four months, which means there was time for some of them to produce second or even third broods. This possibility made it difficult to determine whether additional generations followed the initial annual females within a single season. Considering the overwintering group as the  $F_0$  generation and their offspring as  $F_1$ , the time from the release of  $F_1$  mancae to their attaining reproductive maturity in 2011 was less than six weeks (the span from 16 May 2011, when reproductive overwintering individuals but no mancae were present, to 30 June 2011, when the annual population was already large, with about a third of females reproductive). This means that mancae present at the end of June 2011 could have matured and reproduced by mid-August, and mancae present in mid-August could have matured and reproduced by early October—in other words, the season was long enough for the production of  $F_2$  and even  $F_3$  generations. The October 2011 sample, which contained reproductive females, was collected at least a month after, and possibly up to two months after, the overwintering group had disappeared (the last individuals were observed at very low frequency on 3 August 2011). This indicates that mancae present on 12 October 2011 were at least  $F_2$  individuals and could have been  $F_3$ , although it cannot be ruled out that they resulted from second or third broods by  $F_1$  individuals. Individuals in the young and preparatory stages at the start of cold season became the overwintering group and reproduced the following year as another  $F_0$  generation. Similar size dimorphism in the reproductive season due to overlapping annual and overwintering generations has been reported in the seasonally reproducing tanaidacean *Monokalliapseudes schubarti* (Mañé-Garzón, 1949) (Fonseca and D'Incao, 2003).

Compared to the annual group, females in the overwintering group reproduce at larger minimum and average body sizes, and males begin to express enlarged chelae, a secondary sexual character, at a larger size (Figs. 7, 8). This is the first report in Tanaidacea of a size difference between generations at the onset of sexual maturation. Generally in crustaceans, both the molt increment and intermolt period are inversely proportional to temperature, with colder temperature leading to larger body size and a longer period to reach a particular stage in the life cycle, such as sexual maturity (Hartnoll, 2001). A larger size at maturity in a generation experiencing colder conditions than other generations has been reported in various crustacean groups, with examples among mysids (Matsudaira et al., 1952), decapods (Ikematsu, 1953), amphipods (Morino, 1978), and cumaceans (Duncan, 1984). The difference in size at maturity between the overwintering and annual generations in *Zeuxo* sp. 1 may thus be attributable

to seasonal differences in water temperature during development. However, other environmental factors have been proposed or tested as causal or triggering factors in seasonal size variation, including photoperiod, food availability, and predator density, as reviewed by Hashizume (1999) and Johnson et al. (2001).

Oviposition in overwintering females was suppressed until May in both 2011 and 2012, i.e., no reproductive females were observed from November to April, even though their body size exceeded the minimum size (CpW 0.566 mm; Figs. 6, 7) for reproductive females in the overwintering generation. We speculate that there is selective pressure to synchronize the onset of oviposition in these females with the peak abundance of *Sargassum* seaweeds, the putative primary breeding habitat. Further studies will be necessary to clarify many aspects of the life cycle in *Zeuxo* sp. 1.

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### COMPETING INTERESTS

The authors have no competing interests to declare.

### AUTHOR CONTRIBUTIONS

KK, YH and HK designed research. KK performed research. KK and HK wrote the paper.

### SUPPLEMENTARY MATERIALS

Supplementary materials for this article are available online (URL: <http://www.bioone.org/doi/suppl/10.2108/zs160134>).

**Supplementary Figure S1.** *Zeuxo* sp. 1, fixed specimens, illustrating overwintering and annual groups, in lateral view.

**Supplementary Figure S2.** Sampling site in August and January.

**Supplementary Figure S3.** Relationship between body length and carapace width in *Zeuxo* sp. 1.

**Supplementary Table S1.** Sex ratio of *Zeuxo* sp. 1 in each monthly sample.

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