

Research article

Polyopisthocotyloid Monogenean Infections of Amberjacks *Seriola* spp. in Japan

Kazuo Ogawa^{1*}, Sho Shirakashi² and Yutaka Fukuda³¹Meguro Parasitological Museum, Tokyo 153-0064, Japan²Aquaculture Research Institute, Kindai University, Wakayama 649-2211, Japan³Fisheries Research Division, Oita Prefectural Agriculture, Forestry and Fisheries Research Center, Oita 879-2602, Japan

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ABSTRACT—Development of *Zeuxapta seriolae* (Monogenea: Polyopisthocotylea, Heteraxinidae) collected from *Seriola dumerili* was described and compared with that of *Heteraxine heterocerca*, the same heteraxinid species from *Seriola quinqueradiata*. Based on the morphology of the two monogeneans from very young with a symmetrical body to adult, specimens retrieved from the gills of cultured and wild *Seriola* spp. (*S. quinqueradiata*, *S. dumerili* and *S. aureovittata*) collected in Japan and its adjacent areas during 1975–2019 were identified. *Heteraxine heterocerca*, previously known only from *S. quinqueradiata* and *S. dumerili*, was also recorded from *S. aureovittata*, and *Z. seriolae* hitherto known only from *S. dumerili* and *S. aureovittata*, was recorded from *S. quinqueradiata*. As a result, both *H. heterocerca* and *Z. seriolae* were confirmed from all the three *Seriola* spp. Cultured *S. quinqueradiata* and *S. aureovittata* were often infected with both *H. heterocerca* and *Z. seriolae*, whereas wild *Seriola* spp. were infected with a single species of gill monogenean. Culture seeds of foreign origin should be monitored continuously, as information on the polyopisthocotylean monogenean infections of *Seriola* species known outside Japan is quite limited.

Key words: *Heteraxine heterocerca*, *Zeuxapta seriolae*, development, mixed infection, host range

Two species of polyopisthocotyloid monogeneans, *Heteraxine heterocerca* and *Zeuxapta seriolae* (a senior synonym of *Zeuxapta japonica*; Ogawa, 2022), are known to infect the gills of three species of amberjacks *Seriola* spp. (*S. quinqueradiata*, *S. dumerili* and *S. aureovittata* (= *S. lalandi*)) cultured in Japan; the scientific name, *S. aureovittata* (Japanese name: hiramasa) follows Martinez-Takeshita *et al.* (2015)). The two monogeneans are closely related to each other, belonging to the same family, Heteraxinidae. Although these monogeneans are quite host specific, their reported hosts among wild and cultured amberjacks in Japan are different from each other. In wild, *H. heterocerca* (originally *Axine heterocerca*) and *Z. seriolae* (originally *Microcotyle seriolae*) have been recorded only from *S. quinqueradiata* and from *S. aureovittata*, respectively (Goto, 1894; Yamaguti, 1940). In contrast, among cultured amberjacks, *H. heterocerca* has been found not only from *S. quinqueradiata*, but also from *S. aureovittata* (Fukuda, 1999), and *Z. seriolae* from *S. aureovittata* and *S. dumerili* (Ogawa and Yokoyama, 1998; Fukuda, 1999). These differences in host

specificity between wild and cultured amberjacks have not been fully understood.

In Japanese amberjack farms, monogenean infections with the two heteraxinids, *H. heterocerca* and *Z. seriolae*, on the gills and two capsalids, *Benedenia seriolae* and *Neobenedenia girellae*, on the skin have caused serious damages (Hoshina, 1966; Ogawa and Yokoyama, 1998). Infections with the capsalids can be managed by treating amberjacks with freshwater or hydrogen peroxide bathing and oral administration of praziquantel (Ogawa, 2015; Ogawa and Shirakashi, 2017). On the other hand, no comparable treatment measure has been developed against heteraxinid infections until recent approval of febantel in April 2021 as an oral medication for amberjacks (Shirakashi *et al.*, 2021a, b). Basic information on the occurrences of these heteraxinids among cultured amberjacks, such as species composition on the gills of each amberjack species, needs to be provided for their effective control.

Recently, young *S. dumerili* and *S. aureovittata* have been imported from China to Japan as culture seeds (Ogawa and Fukudome, 1994), which were also infected with the above heteraxinid monogeneans. However, whether these gill parasites had originated in China or they became infected after transferred to Japan

* Corresponding author
E-mail: ogawak@kiseichu.org

remained unclear. Data on the heteraxinid infections of imported juvenile amberjacks is important for the risk assessment of Japanese aquaculture.

Morphological differentiation is essential and offers a rapid diagnosis when examining the species composition of gill monogeneans from amberjacks. Adult *H. heterocerca* and *Z. seriolae* can be easily distinguished based on their distinct asymmetrical body shape (Yamaguti, 1963). In contrast, it is unclear if such morphological differentiation is also possible in early developmental stages, which was studied for *H. heterocerca* by Ogawa and Egusa (1981) but not in detail for *Z. seriolae*.

In the present study, we described early development of *Z. seriolae* based on stained specimens and compared its morphological differences with *H. heterocerca*. After establishing how to morphologically distinguish young stages of these two species, we examined the species composition of the gill monogeneans from wild and farmed amberjacks in Japanese waters including imported ones. This study will provide a baseline data on the control of these harmful gill monogeneans infecting the three amberjacks cultured in Japan.

Materials and Methods

Development of Z. seriolae

Specimens of *Z. seriolae* were collected from heavily infected 0-year-old *S. dumerili* cultured in Kochi Prefecture. They were flattened between a cover slip and a glass slide, fixed in AFA (mixture of 70% ethanol: 20 parts, 35% formaldehyde: 1 part, acetic acid: 1 part), stained with alum carmine, dehydrated in an ethanol series, cleared in xylol, and mounted in Canada balsam. Stained specimens of *Heteraxine heterocerca* were those used previously (Ogawa and Egusa, 1981). Both *Z. seriolae* and *H. heterocerca* specimens were examined for body asymmetry, clamp size and clamp numbers using a light microscope.

Composition of gill monogeneans from three Seriola species

Gill monogeneans collected from amberjacks were listed in Table 1. A total of 39 samples, each consisting of 1 to more than 10 fish, were examined; 13 samples from *S. quinqueradiata* (marked as Sq in Table 1), 11 from *S. dumerili* (Sd), 15 from *S. aureovittata* (Sa). Host fish consisted of those cultured in Kochi, Ehime, Oita, Kagoshima and Nagasaki Prefectures, Japan (25 samples) and in Fujian Province, China (two samples), and wild ones caught in Fukuoka, Tokushima, Nagasaki, Kochi and Ishikawa Prefectures, Japan (10 samples). The status of host fish (cultured or wild) was unknown for two samples, which were imported from Korea (Sq-10) and Hong Kong (Sd-4). Parasite samples include

museum specimens collected by Dr. Kusuo Iwata, Fukuoka University, deposited in Meguro Parasitological Museum, Tokyo (MPM Coll. Nos. F0089–0097, F0101–118, F0121–0134, F0136, F0138–0141).

For morphological identification, monogeneans fixed in formalin or ethanol were examined under a stereomicroscope. When they were small, specimens were mounted between a cover slip and a glass slide and observed under a light microscope to check the number of clamps on both sides of the opisthohaptor for identification (Ogawa and Egusa, 1981). Alternatively, live specimens were fixed and stained as described before (Ogawa and Egusa, 1977; Ogawa *et al.*, 2021). Briefly, they were flattened between a cover slip and a glass slide, fixed in Schaudinn's solution (mixture of saturated aqueous solution of mercuric chloride: 200 parts, 100% ethanol: 100 parts, glacial acetic acid: 15 parts) or AFA, stained with Heidenhain's iron hematoxylin, Delafield's hematoxylin, alum carmine or aceto-carmine, dehydrated, cleared, and mounted in Canada balsam.

Results

Development of Z. seriolae

The body of *Z. seriolae* was symmetrical when the number of clamps on each side of opisthohaptor was six or less (Fig. 1A–B). Body asymmetry was first noticed when clamps on one side reached eight and nine on the other (Fig. 1C, 2A). As parasites grew, asymmetry became more apparent and one side of opisthohaptor started to become longer and the number of clamps on one side exceeded that on the other side (Fig. 1D). Larval hooks were retained until the clamps on the shorter side of opisthohaptor was 14 (Fig. 1D), and, in most cases, had been lost when the number of clamps on the shorter side reached 20 (Fig. 1E). The parasite had functional male and female genital organs when the number of clamps on the shorter side reached 30, and they were considered as young adults.

In contrast to *Z. seriolae*, asymmetry in *H. heterocerca* was first confirmed when the numbers of clamps on each side of opisthohaptor reached six and seven (Fig. 2B). Larval hooks started to disappear when the clamp number of the shorter side was seven and longer side was 10 (Fig. 2B).

Except for very early developmental stages with a symmetrical body, *Z. seriolae* could be morphologically differentiated from *H. heterocerca* by body asymmetry, number of clamps on both sides and presence/absence of larval hooks at the end of opisthohaptor. When the number of clamps on one side was 7, *Z. seriolae* was still symmetrical, while *H. heterocerca* started to become asymmetrical. Larval hooks were still retained in *Z. seriolae* when the number of clamps on the long side of opisthohaptor was up to 15, while larval hooks in *H. heterocerca* had been lost, when its number on the long

Table 1. Identification and number of gill monogeneans collected from three species of *Seriola* from Japan and adjacent areas, with data on collection dates, geographical localities, status of fish (wild or cultured) and number of fish examined. Fish age and size were given only when data were available (FL= fork length; BW=body weight).

Host fish	Collection dates	Localities	Wild/Cultured (age or size)	No. of fish	Sample Number	<i>Heteraxine heterocerca</i>	<i>Zeuxapata seriolae</i>
<i>Seriola quinqueradiata</i>	Nov & Dec 1975; Feb 1976	Shizuoka Pref.	Cultured (0-year)	>10	Sq-1	700	0
	Aug 1976	Hiroshima Pref.	Cultured (0- & 1-year)	2	Sq-2	13	0
	Nov 1977	Inland Sea	Cultured	unknown	Sq-3	5	0
	Sep & Oct 1977	Kagoshima Pref.	Cultured	unknown	Sq-4	5	0
	Oct 1977; Jul 1978	Fukuoka Pref.	Wild	2	Sq-5	2	0
	Nov 1977; Feb 1978	Kumamoto Pref.	Cultured	unknown	Sq-6	7	0
	Nov 1977	Tokushima Pref.	Wild	unknown	Sq-7	5	0
	Jan, Mar & May 1978	Nagasaki Pref.	Wild	unknown	Sq-8	13	0
	Mar 1985	Kochi Pref.	Cultured (0-year)	unknown	Sq-9	15	4
	Oct & Nov 1986	Korea*1	unknown (0-year)	>6	Sq-10	22	0
	Dec 1995	Kagoshima Pref.	Cultured (0-year)	2	Sq-11	61	13
	Sep 2019	Ehime Pref.	Cultured	unknown	Sq-12	100	0
	Nov 2019	Ishikawa Pref.	Wild (FL 39 cm)	1	Sq-13	2	0
<i>Seriola dumerili</i>	Oct 1977	Nagasaki Pref.	Wild	1	Sd-1	0	1
	Feb & Mar 1984	Kochi Pref.	Cultured (0-year)	>5	Sd-2	0	>100
	Jul 1984	Kochi Pref.	Wild (0-year)	1	Sd-3	2	0
	May 1988	Hong Kong*1	unknown	unknown	Sd-4	0	4
	Dec 1995	Kagoshima Pref.	Cultured (0-year)	3	Sd-5	0	1,765
	Jul 2006	Kagawa Pref. (China)*2	Cultured	unknown	Sd-6	1	5
	May 2007	Fujian Province, China	Cultured (0-year)	unknown	Sd-7	0	10
	Mar 2015	Kagoshima Pref.	Cultured (0-year)	4	Sd-8	0	90
	Aug 2019	Ehime Pref.	Cultured	unknown	Sd-9	0	148
	Nov 2019	Ishikawa Pref.	Wild (FL 27 cm)	1	Sd-10	2	0
	Dec 2019	Kagoshima Pref.	Cultured (0-year)	1	Sd-11	0	38
<i>Seriola aureovittata</i>	Jul 1977	Nagasaki Pref.	Cultured	1	Sa-1	6	0
	Sep & Oct 1977	Kagoshima Pref.	Cultured	2	Sa-2	2	0
	Sep 1977	Nagasaki Pref.	Wild	1	Sa-3	1	0
	Sep 1981	Nagasaki Pref.	Wild (BW 1.3 kg)	1	Sa-4	0	14
	May 1984	Nagasaki Pref.	Cultured	1	Sa-5	0	7
	Mar 1991	Oita Pref. (China)*2	Cultured (1-year)	unknown	Sa-6	0	11
	Mar 2002	Oita Pref. (China)*2	Cultured (0-year)	2	Sa-7	0	853
	Oct 2006	Fujian Province, China	Cultured (0-year)	unknown	Sa-8	0	6
	Apr 2012	Ehime Pref.	Cultured (2-years)	1	Sa-9	17	12
	Mar 2012	Oita Pref. (China)*2	Cultured (0-year)	2	Sa-10	70	0
	Mar 2013	Oita Pref.	Cultured (0-year)	3	Sa-11	47	406
	Mar 2013	Oita Pref. (China)*2	Cultured (0-year)	2	Sa-12	32	10
	Apr 2013	Oita Pref.	Cultured (0-year)	2	Sa-13	112	122
	May 2016	Nagasaki Pref. (China)*2	Cultured	unknown	Sa-14	0	22
	Nov 2019	Ishikawa Pref.	Wild (FL 54 cm)	1	Sa-15	0	4

*1: Inspected at importation

*2: Seeds from China

side of opisthaptor reached 11. In *Z. seriolae*, the number of clamps on the short side kept increasing in number, while it never exceeded 9 in *H. heterocerca*.

Composition of gill monogeneans in three species of amberjacks

1) Cultured amberjacks

Two species, *H. heterocerca* and *Z. seriolae*, were identified from the three cultured *Seriola* species, but their compositions were different among host species. *S. quinqueradiata* was infected either only with *H. heterocerca* (number of samples [n] = 6; Sq-1–4, 6, 12) or with both *H. heterocerca* and *Z. seriolae* (n = 2; Sq-9, 11) (Table 1). For the samples infected only with *H.*

heterocerca, only *S. quinqueradiata* was cultured in the sampled areas. In contrast, for those with mixed infections, *S. dumerili* were also cultured close to *S. quinqueradiata* (Sd-2, 5).

Cultured *S. dumerili* was infected either with *Z. seriolae* only (n = 6; Sd-2, 5, 7–9, 11) or with the two species (n = 1; Sd-6). *S. aureovittata* was infected either with *Z. seriolae* only (n = 5; Sa-5–8, 14), with *H. heterocerca* only (n = 3; Sa-1, 2, 10) or with the two species (n = 4; Sa-9, 11–13).

2) Wild amberjacks

Based on the nine samples, wild *S. quinqueradiata* was infected only with *H. heterocerca* (n = 4; Sq-5, 7, 8,

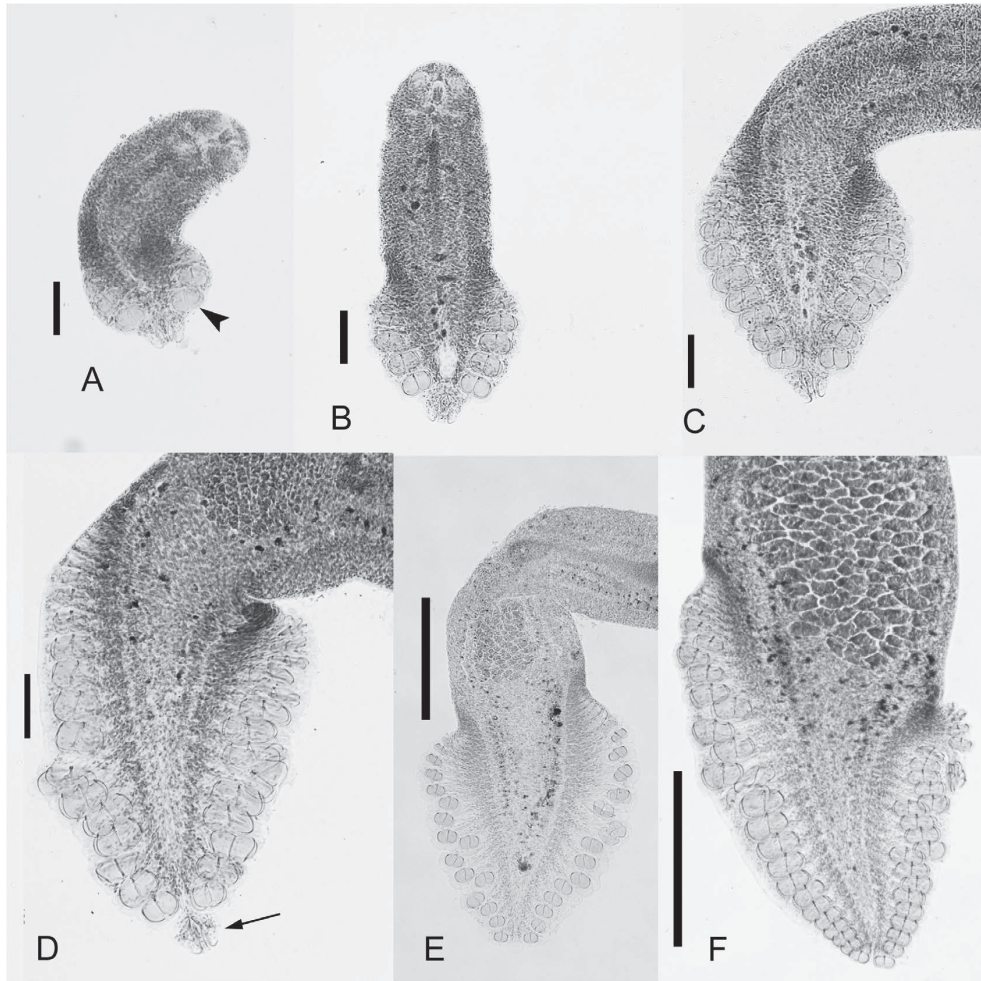


Fig. 1. Developmental stages of *Zeuxapta seriolae*. A, Youngest specimen with four clamps on each side of opisthaptor (arrow-head: posteriormost pair of clamp); B, Specimen with six clamps on each side; C, Specimen with eight clamps on one side of opisthaptor and nine clamps on the other; D, Specimen with 14 clamps on each side of opisthaptor (arrow: larval hooks); E, Specimen with 16 clamps on each side of opisthaptor; F, Specimen with 24 clamps on one side of opisthaptor and 26 on the other. Scale bars: 0.1 mm for A-D, 0.5 mm for E and F.

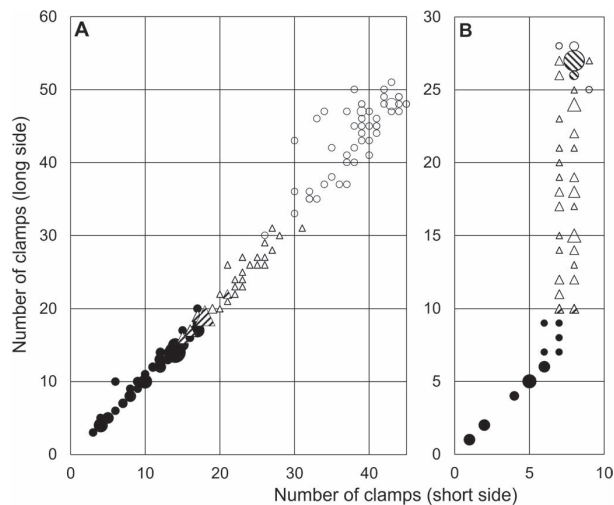


Fig. 2. Number of clamps on both sides of the opisthaptor. A, *Zeuxapta seriolae*; B, *Heteraxine heterocerca*, modified from Ogawa and Egusa (1981). X- and Y-axis represent numbers of clamps on the short and long side of the opisthaptor, respectively. Closed circle, immature form with larval anchors; open circle, mature form without larval anchors; striped circle, mature/immature form without larval anchors; open triangle, immature form without larval anchors; striped triangle, immature form with/without larval anchors. Marker sizes are shown in proportion to the number of specimens (1–7).

13), whereas wild *S. dumerili* and *S. aureovittata* were infected either with *H. heterocerca* only (n = 3; Sd-3, 10; Sa-3) or with *Z. seriolae* only (n = 2; Sd-1, Sa-15). No mixed infection was detected in any of the wild amberjacks examined.

Gill monogeneans collected from a total of 39 samples of *Seriola* spp. (13, 11 and 15 samples of *S. quinqueradiata*, *S. dumerili* and *S. aureovittata*, respectively) consisted of *H. heterocerca* and *Z. seriolae*. Both species of monogeneans were recorded from the three *Seriola* species, irrespective of cultured or wild ones.

Discussion

Based on the description of the development of *Z. seriolae* and that of *H. heterocerca* (Ogawa and Egusa, 1981), body asymmetry appeared earlier in *H. heterocerca* than in *Z. seriolae*; six and seven clamps on each side of opisthohaptor in the former vs. eight and nine in the latter. Asymmetry became more apparent with the development advanced. Diagnosis when they are still immature can be utilized for an early control of heteraxinid infections of *Seriola* spp. cultured in Japan.

Repullés *et al.* (2005)* and Tubbs *et al.* (2005) conducted experimental infection of *S. dumerili* and *S. lalandi*, respectively, with *Z. seriolae* and described the parasite development. Results of Repullés *et al.* (2005) were similar to those in this study. For example, asymmetry was first recognized when the clamp number was 11 on one side of opisthohaptor and 10 or 11 on the other in Repullés *et al.* (2005) vs. nine on one side and eight on the other in this study. Larval hooks were lost in all the specimens examined when the number of clamps on the shorter side reached 18 or 19 in Repullés *et al.* (2005) vs. 20 in this study.

Tubbs *et al.* (2005) reported temperature-dependent maturation of *Z. seriolae* and briefly described its developmental stages, which included different results from the present study. The mature specimen shown in Fig. 5 ZE in Tubbs *et al.* (2005) did not show typical morphology for *Z. seriolae*, and its opisthohaptor was rather similar to that of *Allencotyle mcintoshi*; the clamps on the shorter side much smaller in size and number than those on the longer side. Moreover, an immature specimen with larval hooks shown in Tubbs *et al.* (2005) (Fig. 5 ZB), had clearly different number of clamps on both sides of its opisthohaptor, which indicates that it was not *Z. seriolae*. In the taxonomical study of *Zeuxapta* on *Seriola lalandi* from New Zealand, Ogawa (2022) found only *Zeuxapta australica*. Assuming that the development of *Z. australica* is similar to that of *Z.*

seriolae, the immature specimen in Tubbs *et al.* (2005) was probably not *Z. australica*, either. From the five photos of Fig. 5 in Tubbs *et al.* (2005), their fish samples may have mixed infections with an unspecified *Zeuxapta* and *Al. mcintoshi*. Further examination will be needed to confirm the presence of *Al. mcintoshi* in New Zealand.

Yamaguti (1940) described a new species, *Microcotyle seriolae* collected from *S. aureovittata* at a fish market in Hyogo Prefecture in August 1939. However, the host name on the type specimen slide was written in katakana “Shiwo”. This Japanese fish name is generally used as the local name for *S. dumerili*, but not for *S. aureovittata* (Ichthyological Society of Japan, 1981). It seems likely that he mistook the host fish *S. dumerili* for *S. aureovittata*. Yamaguti (1963) reassigned it to *Zeuxapta* and renamed to *Z. japonica*, which was later synonymized with *Zeuxapta seriolae* by Rohde (1978). Thus, in Japan, *Z. seriolae* was first recorded from wild *S. dumerili*, not from *S. aureovittata*, by Yamaguti (1940), then from cultured *S. dumerili* by Ogawa and Yokoyama (1998) and subsequently from cultured *S. quinqueradiata* as well as both wild and cultured *S. aureovittata* in this study.

In the new species description, Yamaguti (1940) recognized that *Microcotyle seriolae* had considerably different numbers of clamps on both sides of the opisthohaptor, 45–47 vs. 39–42, which was contradictory to the definition of the genus *Microcotyle*. The reason why he nevertheless classified it to *Microcotyle* was that a paratype specimen had equal numbers of clamps on both sides of the opisthohaptor. Our reexamination of the paratype specimen revealed that it was already asymmetrical but not fully mature, with 25 clamps on each side of the opisthohaptor. Considering the development of *Z. seriolae* in the present study, the paratype specimen fits well with asymmetrical worms without larval hooks.

Although we had less opportunities to examine wild amberjacks (10 samples) compared to cultured ones (27 samples), the intensity of infection with gill monogeneans among wild amberjacks was generally lower than that of cultured ones. This may have been caused by relatively limited infection opportunities in the wild compared with those of cultured fish kept in much higher density. As a result, no case of mixed infection has been confirmed among wild amberjacks. Despite the low level of infection, *H. heterocerca* was confirmed for the first time from wild *S. dumerili* (Sd-9) and *S. aureovittata* (Sa-3) and from cultured *S. dumerili* (Sd-6) as mentioned above. It is interesting to note that wild *S. aureovittata* (Sa-15) was infected only with *Z. seriolae*, whereas *S. dumerili*, sampled from the same locality at the same time, harbored *H. heterocerca* (Sd-10). Reasons for the differences were not clear but may be due to paucity of surveys in wild amberjacks, and also due to the relatively low infection abundance in

* Repullés, A., F. E. Montero, F. de la Gándala, K. Ogawa and J. A. Raga (2005): Development of monogenean *Zeuxapta seriolae* on the gills of the greater amberjack (*Seriola dumerili*). Presented at 12th EAAP Conference, Copenhagen, 2005.

wild amberjacks.

Japanese *Seriola* spp. are usually infected with a single species of gill monogeneans; *S. quinqueradiata* with *H. heterocerca*, and *S. dumerili* and *S. aureovittata* with *Z. seriola* (Ogawa, 2022; Ogawa and Yokoyama, 1998; Yanagi *et al.*, 2012). In this study, *H. heterocerca* infection of both cultured and wild *S. aureovittata* were noticed for the first time (Sa-1–3). Besides, some of the samples from all the three *Seriola* spp. showed infections with both *H. heterocerca* and *Z. seriola* (Sq-9 and 11, Sd-6, Sa-9 and 11–13). In Japan, a large-scale culture of *S. dumerili* started in early 1990s, which was associated with importation of culture seeds from China (Yanagi *et al.*, 2012). The cases of *S. quinqueradiata* with mixed infection were found on the fish from Kochi Prefecture collected in 1985 (Sq-9), when *S. dumerili* culture in Japan had almost been limited in this area, using locally captured juvenile fish for culture seeds. Another case of mixed infection was found in the fish from Kagoshima Prefecture collected in 1995 (Sq-11), when *S. dumerili* of China-origin had already been intensively cultured there (Yanagi *et al.*, 2012). The two cases of mixed infections of *S. quinqueradiata* imply that *Z. seriola* infection may have originated from *S. dumerili* cultured in the same area. In contrast, no mixed infection has been recorded among *S. dumerili*, despite that *S. quinqueradiata* had been cultured nearby (Sd-2 and 5) (No information available on how *S. dumerili* were cultured for Sd-6). Species-specific susceptibility of *S. dumerili* to heteraxinid monogeneans may be higher than that of *S. quinqueradiata*. However, apparent susceptibility to certain parasite species may be affected by other factors including host age, geographical distribution of the parasites, and water temperature. Further studies will be needed to better understand host specificity of each heteraxinid species.

Other species of gill polyopisthocotyleans have been recorded from *Seriola* spp.: *Axine inada* and *Microcotyle inada* (as *Microcotyla inada*) from *S. quinqueradiata* in Japan (Ishii and Sawada, 1938), *Diplostamenides sciaenae* (as *Microcotyle hemiatrispinalis*; WoRMS, 2022) from *Seriola* sp., *Tonkinaxine homocerca* from *Seriola* sp. and *S. dumerili* and *Pseudaxine vietnamensis* (as *Pseudaxinoides vietnamensis*; WoRMS, 2022) from *S. dumerili* from Tonkin Bay, Vietnam (Lebedev *et al.*, 1970), *Paramicrocotyloides reticularis* from *S. lalandi* (as *S. grandis*) in Australia and New Zealand (Rohde, 1978; Diggles and Hutson, 2005; Hutson *et al.*, 2007), *Allencotyla mcintoshii* from *S. lalandi* (= *Seriola dorsalis* according to Martinez-Takeshita *et al.* (2015)) in USA and from *S. dumerili* in Spain (Price, 1962; Montero *et al.*, 2003) and *Z. australica* from *S. lalandi* in Australia, New Zealand and Chile (Ogawa, 2022). The first seven species can easily be distinguished morphologically from *H. heterocerca* and *Z. seriola*, unless they are in early

developmental stages: *M. inada*, *D. sciaenae*, *T. homocerca* and *Pa. reticularis* by the two symmetrical rows of clamps, *Ax. inada* by the much larger number of clamps (80–100) on the longer side of opisthohaptor, *P. vietnamensis* by the single row of clamps and *Al. mcintoshii* by the degree in asymmetry of the opisthohaptor (intermediate asymmetry between *H. heterocerca* and *Z. seriola*) and the presence of concentric crowns of spines around the genital atrium. As for *Z. australica*, mature specimens are distinguishable by the morphology of vagina; horizontally extended paired vaginal tubes in *Z. seriola* vs. short, obliquely posteriad paired extensions in *Z. australica* (Ogawa, 2022). In this study, the eight monogeneans were not confirmed in the samples from Japan, China and Korea.

In this study, we also examined *Seriola* spp. originated outside Japan. The origin of some gill monogeneans collected from *S. dumerili* and *S. aureovittata* (with asterisk2 in Table 1), which had been imported from China as culture seeds could not be determined since the fish had been maintained in Japanese waters for some time by the time of sampling. For the rest of fish samples of foreign origin (with asterisk1 in Table 1), *S. quinqueradiata* from Korea and *S. dumerili* from China that had been inspected before introduced to Japanese waters, were infected with the same heteraxinid species as in Japan, implying these monogeneans have wide geographical distribution, at least in east Asia. Culture seeds of foreign origin should be monitored continuously for pathogens including the gill monogeneans, as information on the parasite infections of these *Seriola* species is quite limited.

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