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Relation	

1 **Diel changes in the vertical distribution of larval cutlassfish *Trichiurus japonicus***

2

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12

13 Running head: Vertical distribution of cutlassfish larvae

14

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17

18

19 **Abstract**

20 *Diel vertical migration of the cutlassfish Trichiurus japonicus larvae were investigated by*  
21 *consecutive 24-h collections at 3-h intervals at a station in the central Seto Inland Sea, Japan*  
22 *in June and September. Only one larva was collected in June 2017, while 224 and 40 larvae*  
23 *were collected in September 2016 and 2017, respectively. Larvae were present only at depths*  
24 *of  $\geq 11$  m during the day, whereas they were present at depths of 1, 6, 11, and 16 m during the*  
25 *night. Migration was observed in larvae in which the swim bladder formation was completed.*  
26 *Similar pattern, namely nocturnal occurrence at shallow depths only of the developed larvae,*  
27 *was observed in another 24-h survey, suggesting that the swim bladder regulates the upward*  
28 *movement of larvae at night.*

29

30 **Key words:** developmental stage; ontogenetic change; swim bladder; Trichiuridae; vertical  
31 movement

32

33

34 INTRODUCTION

35

36 In marine fish larvae, vertical distribution governs the maintenance of geographic position  
37 (Pearre, 2003), opportunity to encounter prey (Murphy *et al.*, 2011) and escape from predators  
38 (Yamashita *et al.*, 1985; Scheuerell & Schindler, 2003); it is one of the important ecological  
39 subjects related to the growth and survival of fish larvae. The diel vertical migrations (DVM)  
40 of larvae are roughly classified into two types: one in which the larvae move up to the surface  
41 at night, and the other in which they move down to the middle or bottom at night (Neilson &  
42 Perry, 1990). The former is noted in many fishes, including the anchovy *Engraulis*  
43 *encrasicolus* (Olivar *et al.*, 2001), red seabream *Pagrus major* (Tanaka, 1985), haddock  
44 *Melanogrammus aeglefinus* (Perry & Neilson, 1988), walleye Pollock *Theragra*  
45 *chalcogramma* (Olla & Davis, 1990), and Japanese Spanish mackerel *Scomberomorus*  
46 *niphonius* (Shoji *et al.*, 1999). The latter is reported in black seabream *Acanthopagrus*  
47 *schlegelii* (Kinoshita & Tanaka, 1990), Japanese sand lance *Ammodytes japonicus* (formerly *A.*  
48 *personatus*; Yamashita *et al.*, 1985), and pinfish *Lagodon rhomboides* (Lewis & Wilkens,  
49 1971). Moreover, the day-night patterns in larval distribution varies in the same species of the  
50 pilchard *Sardina pilchardus* (Olivar *et al.*, 2001; Santos *et al.*, 2006). Thus, the patterns of  
51 larval DVM are variable and should be elucidated for deeper understandings of the early life  
52 history traits of each species.

53 The family Trichiuridae is widely distributed in oceans worldwide and includes many  
54 commercially important species. To our knowledge, no study has revealed the DVM of larvae  
55 of species belonging to this family, although some collection records of Trichiuridae larvae at  
56 various depths were observed only during the daytime (Loeb, 1979; Hayashi, 1990).

57 This study aimed to elucidate diel patterns of the vertical distribution of the larvae of  
58 *Trichiurus japonicus*, the most dominant Trichiuridae species in the western North Pacific.

59 This species had been confused with *T. lepturus*, but genetic difference between these two  
60 species was confirmed (Chakraborty *et al.*, 2006a, b). *Trichiurus japonicus* spawns from June  
61 to September (Munekiyo, 1991) or May to October (Sakamoto, 1976). In this study,  
62 consecutive day–night collections were carried out in September and June.

63

## 64 MATERIALS AND METHODS

65

### 66 **Study site and sample collection**

67

68 The vertical distribution of *T. japonicus* larvae was investigated at a sampling station during  
69 17–18 September 2015, 5–6 September 2016, 27–28 June 2017, and 20–21 September 2017.

70 This station, located near the southern coast of Hiuchi-Nada in the central Seto Inland Sea  
71 (34° 01' N; 133° 20' E; 25 m deep; Figure 1), Japan, was chosen because of the high  
72 concentration of larval fishes in this area (Shoji & Tanaka, 2005).

73 In 2015, diurnal distribution patterns were investigated at 0900 and 1000 h on 17  
74 September and at 1100 h on 18 September (Supplementary Table S1). In September 2016 and  
75 June 2017, diel distribution patterns were investigated by consecutive 24-h collections at 3-h  
76 intervals from 1500–1200 h in 2016 (eight collections in total) or from 1500–1500 h in 2017  
77 (nine collections). In September 2017, larval collections were carried out six times (1500,  
78 1800, 2100, 0000, 0600, and 0900 h). For larval collections, ring nets (called the MTD net;  
79 mouth diameter: 56 cm, mesh size: 335  $\mu\text{m}$ ; Horiki, 1981) were towed simultaneously at four  
80 depths (1, 6, 11, and 16 m) for 10 min at a speed over the water of 2 knots by the training and  
81 research vessel Toyoshiomaru (256 tons). Water volume filtered per net was estimated to be  
82  $116 \pm 36 \text{ m}^3$  (mean  $\pm$  SD,  $n = 35$ ) and  $128 \pm 51 \text{ m}^3$  ( $n = 24$ ) in June and September 2017,  
83 respectively, by using a flow meter attached to the net. Samples collected were immediately

84 preserved in 5% seawater formalin onboard.

85 Water temperature and salinity were measured at each collection by using a  
86 conductivity-temperature-depth sensor (SBE-9plus, SeaBird). The vertical structure of water  
87 temperature and salinity did not change greatly between day and night (Supplementary  
88 Figures S1, S2 & S3). Water temperature ranged from 26.0–27.4°C, 18.9–23.5°C, and  
89 25.4–26.2°C, and salinity ranged from 31.6–32.1, 31.9–33.1, and 30.1–32.3 in September  
90 2016, June 2017, and September 2017, respectively. Times of sunset were 1828 h (5  
91 September 2016), 1924 h (27 June 2017), and 1810 h (20 September 2017), and times of  
92 sunrise were 0543 h (6 September 2016), 0500 h (28 June 2017), and 0557 h (21 Sep 2017).

93 We also sorted out *T. japonicus* larvae from specimens collected in the past 24-h survey  
94 (Shoji *et al.*, 1999). In this survey, larvae were collected from four depths (0, 5, 10, and 20 m)  
95 by using a net with 1.3-m mouth opening in Hiuchi-Nada in 3–4 June 1997. Larvae including  
96 *T. japonicus* were preserved in 10% seawater formalin (Shoji *et al.*, 1999). Water volume  
97 filtered per net was estimated to be  $219 \pm 93 \text{ m}^3$  (mean  $\pm$  SD,  $n = 22$ ).

98

### 99 **Laboratory observation and data analyses**

100

101 *Trichiurus japonicus* larvae were sorted in the laboratory. The abundance of larvae at each  
102 depth was standardised to the number per 1000  $\text{m}^3$ . Because the water volume filtered by each  
103 net was not measured in 2015 and 2016, the average value in September 2017 (128  $\text{m}^3$ ) was  
104 commonly used instead.

105 Total length (TL) was measured to the nearest 0.1 mm by using a digital calliper under a  
106 microscope. The developmental stages were determined according to Munekiyo (1991) as  
107 follows (Supplementary Figure S3). No juveniles were collected.

108 Pr1 (Prelarva 1); yolksac is retained, the mouth is not opened, and the swim bladder

109 is not formed.

110 Pr2 (Prelarva 2): yolksac is retained, the mouth is opened, and the swim bladder is  
111 formed.

112 Po (Postlarva): yolk is absorbed, and three serrated dorsal spines are present on the  
113 anterior dorsal fin.

114 To test the difference in the collection depth of the larvae between day and night, the  
115 Mann-Whitney *U* test was used for the data in September 2016, September 2017, and June  
116 1997.

117 To test whether thermoclines and/or pycnoclines were formed at each survey, vertical profiles  
118 of average water temperature and average seawater density were described.

## 119 RESULTS

120

121 In 2015 and 2016, 98 and 224 *T. japonicus* larvae were collected, respectively. Their size  
122 ranged from 4.2–26.9 mm (stage: Pr1–Po) and 3.6–11.3 mm TL (stage: Pr1–Po) in 2015 and  
123 2016, respectively (Table 1). In June 2017, only one larva (5.7 mm TL, stage Pr2) was  
124 collected from the 16 m layer at 0600 h. In September 2017, 40 *T. japonicus* larvae (stage:  
125 Pr1–Po; size: 3.5–11.1 mm) were collected.

126 Larvae of *T. japonicus* were not observed at 1 and 6 m depths, but were collected at 11  
127 and 16 m depths during the daytime (0900–1100 h) in 2015 (Figure 2). Similarly, the larvae  
128 were collected only at 16 m (at 1500 and 1800 h) or at 11 and 16 m depths (at 0600, 0900, and  
129 1200 h) during the daytime in 2016 (Figure 3). In September 2017, one larva of *T. japonicus*  
130 at stage Po was collected at 6 m during the daytime (1500 h), but other individuals were  
131 collected at 11 and 16 m depths during the daytime (Figure 4). Conversely, *T. japonicus* larvae  
132 were collected from all depths during the night from 2100–0300 h in 2016 and from depths of  
133 6–16 m during the night in September 2017. However, larvae of stage Pr1 were not present in

134 samples collected from depths of 1 or 6 m irrespective of day and night in 2015 and 2016  
135 (Figures 2, 3). Similarly, the larvae of stage Pr1 were not collected from 1 m depth in 2017,  
136 although four individuals were collected from a depth of 6 m during the night (Figure 4). In  
137 September 2016, significant differences in the collection depth between day and night were  
138 observed for stages Pr2 ( $U = 2033, P < 0.001$ ) and Po ( $U = 1901.5, P < 0.001$ ), while no  
139 significant differences were observed for stage Pr1 ( $U = 54.5, P = 0.33$ ). In September 2017,  
140 no significant differences in the collection depth between day and night were observed for  
141 each stage (Pr1:  $U = 1, P = 0.62$ ; Pr2:  $U = 7, P = 0.88$ ; Po:  $U = 67, P = 0.92$ ).

142 Water temperature was higher at shallower depths except for in September 2017 (Figure  
143 5). Seawater density was lower at shallower depths. Differences in both water temperature  
144 and seawater density between 1 and 20 m depths were the greatest in June 2017. No clear  
145 thermoclines or pycnoclines were observed.

146 In 1997, 36 *T. japonicus* larvae were collected. Their size ranged 4.1–7.5 mm TL (stage:  
147 Pr1–Po). The larvae were collected from 5–20 m depths during the daytime, while some  
148 larvae except of stage Pr1 were collected from the surface layer (0 m) at the night (Figure 6).  
149 No significant difference in the collection depth between day and night was observed (Pr1:  $U$   
150  $= 6, P = 0.17$ ; Pr2:  $U = 32, P = 0.18$ ; Po: not applicable because of small sample sizes),  
151 although presence of larvae at surface was observed only during the night.

152

## 153 DISCUSSION

154

155 This is the first study to describe the vertical distribution of Trichiuridae larvae during the  
156 night and to clarify their DVM. The daytime patterns in the vertical distribution of *T.*  
157 *japonicus* larvae corresponded with those reported previously: the larvae did not appear at the  
158 surface, but were mostly found at depths of around 50 m (Okiyama, 1965; Horiki, 1981;



159 Munekiyo & Kuwahara, 1986; Hayashi, 1990).

160 The absence of stage Pr1 larvae near the surface throughout the surveys indicates that the  
161 DVM of *T. japonicus* larvae depends on the developmental stage. The formation of the swim  
162 bladder, as observed at stage Pr2, is likely related to the vertical migration, because the swim  
163 bladder plays important roles in changing the depth or acquiring neutral buoyancy (Kanwisher  
164 & Ebeling, 1957). Swim bladder inflation at night has been observed in larvae of other  
165 species, including Clupeidae (Uotani, 1973; Hoss & Phonlor, 1984; Landaeta & Castro, 2013),  
166 the red seabream *P. major* (Kitajima *et al.*, 1985), and Japanese Spanish mackerel (Shoji *et al.*,  
167 1999). Thus, the formation of the swim bladder enables the larvae to adjust their buoyancy  
168 and to move up towards the surface at night, as well as to reduce offshore advection  
169 (Landaeta & Castro, 2013). However, another possibility should be considered for the timing  
170 of swim bladder inflation. The swim bladder seemed to connect to the alimentary canal in the  
171 larvae at stages Pr2 and Po, indicating that they are physostomous, at least during larval  
172 stages. If so, the larvae has to ascend to the surface to ingest gas bubbles to inflate their swim  
173 bladder. Further observation is necessary to elucidate this.

174 The swim bladder development begins before the yolk-sac absorption in *T. japonicus*  
175 (Munekiyo, 1991). It is different from other species. For example, the swim bladder begin to  
176 inflate from the larvae after yolk-sac absorption in Pacific bluefin tuna *Thunnus orientalis*  
177 (Ina *et al.*, 2014). The yolk-sac larvae of Pacific bluefin tuna use yolk-sac and oil globule to  
178 acquire buoyancy. Similarly, Japanese Spanish mackerel larvae that complete yolk absorption  
179 show DVM, but yolk-sac larvae do not (Shoji *et al.*, 1999). The absence of DVM was also  
180 observed in preflexion (yolk-sac) larvae of many other species (Rodriguez *et al.*, 2015).  
181 Relationships between the presence/absence of DVM and the larval developmental stages in  
182 relation to yolk absorption and swim bladder formation should be further investigated in other  
183 species.

184 The stage Pr1 larvae appeared chiefly around the bottom layers, although *T. japonicus*  
185 spawns pelagic eggs. It is likely to be related to the egg distribution of this species. Eggs of  
186 early developmental stages are scarce around surface and are abundant around middle layers  
187  $\geq 10$  m depth (Horiki, 1981; Munekiyo & Kuwahara, 1986). Developed eggs are more  
188 abundant at deeper layers around 50 m compared to eggs of early developmental stages  
189 observed at a depth of 20 m (Horiki, 1981). Thus, larvae would hatched around  
190 middle-bottom layers and spend a little until their swim bladders are formed.

191 The vertical distribution of larvae is often affected by the hydrographic stratification.  
192 Thermoclines and/or pycnoclines may limit the distribution of larvae (Olivar *et al.*, 2014). In  
193 an offshore environment, larvae of some species show diel movement between above and  
194 below the pycnocline formed at depths ranging from 36–108 m, and others remained above  
195 the pycnocline (Sakuma *et al.*, 1999). However, the DVM is often not observed in well-mixed  
196 environments (Rodriguez *et al.*, 2015). Clear thermoclines or pycnoclines were absent,  
197 especially in September, in our study (Figure 5) probably because of the shallow water depth  
198 of the sampling site. Nonetheless, larval appearance at depths with relatively low seawater  
199 density during the night may reflect the DVM.

200 The ecological significance of the nocturnal migration of *T. japonicus* larvae is unclear.  
201 Since these larvae feed during the day (Munekiyo & Kuwahara, 1985), their upward  
202 movement to the surface might not likely increase their foraging success at night. One  
203 possible explanation is that inflation of the swim bladder at night reduces the energy required  
204 for maintaining a position in the water column and also reduces predation by predators  
205 responding to prey activity (Hunter & Sanchez, 1976). However, it is not yet known whether  
206 the upward movement of larvae is advantageous or not. Because not all larvae of *T. japonicus*  
207 at stages Pr2 and Po moved up to the surface, other factors such as the condition of larvae  
208 (Sclafani *et al.*, 1993) could affect the larval distribution. Further observations on the energy

209 expense or survival at various depths are necessary to elucidate the role of the vertical  
210 migration of *T. japonicus* larvae.

211

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217

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221

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- 324

325 **Table 1.** The number and body size (total length, TL) of collected larvae of *Trichiurus*  
 326 *japonicus* at each developmental stage.

<b>Developmental stage</b>	<b>N</b>	<b>TL (mm)</b>
June 1997		
Pr1	12	4.1–6.4
Pr2	15	5.2–7.5
Po	9	5.5–7.4
September 2015		
Pr1	3	4.16–4.21
Pr2	2	5.0–5.2
Po	90	4.4–26.9
September 2016		
Pr1	24	3.6–4.9
Pr2	104	4.2–5.5
Po	96	4.7–11.3
June 2017		
Pr2	1	5.7
September 2017		
Pr1	4	3.5–4.2
Pr2	13	4.0–5.6
Po	23	4.9–11.1

327

328

329



330 Figure captions

331

332 **Fig. 1.** Map of the study area in Hiuchi-Nada, the central Seto Inland Sea, Japan. Sample  
333 collections were conducted at stations shown by solid (in 2015–2017) and open (in  
334 1997) circles.

335

336 **Fig. 2.** Diurnal distribution of *Trichiurus japonicus* larvae at (A) 0900 h on 17 September, (B)  
337 1000 h on 17 September, and (C) 1100 h on 18 September 2015. The number of  
338 collected larvae per 1000 m<sup>3</sup> is shown. Developmental stages (Pr1–Po) were  
339 identified.

340

341 **Fig. 3.** Diel changes in the vertical distribution of *Trichiurus japonicus* larvae in September  
342 2016. The number of collected larvae per 1000 m<sup>3</sup> is shown. Detailed information on  
343 larval total length by year and developmental stage is shown in Table 1.  
344 Developmental stages (Pr1–Po) were identified. Open and closed bars indicate  
345 daylight (day) and dark (night) periods, respectively.

346

347 **Fig. 4.** Diel changes in the vertical distribution of *Trichiurus japonicus* larvae in September  
348 2017. The number of collected larvae per 1000 m<sup>3</sup> is shown. Detailed information on  
349 larval total length by year and developmental stage is shown in Table 1.  
350 Developmental stages (Pr1–Po) were identified. Open and closed bars indicate  
351 daylight (day) and dark (night) periods, respectively.

352

353 **Fig. 5.** Vertical profiles in average water temperature and seawater density ( $\sigma_t$ ) in (A)  
354 September 2015, (B) September 2016, (C) June 2017, and (D) September 2017. Solid

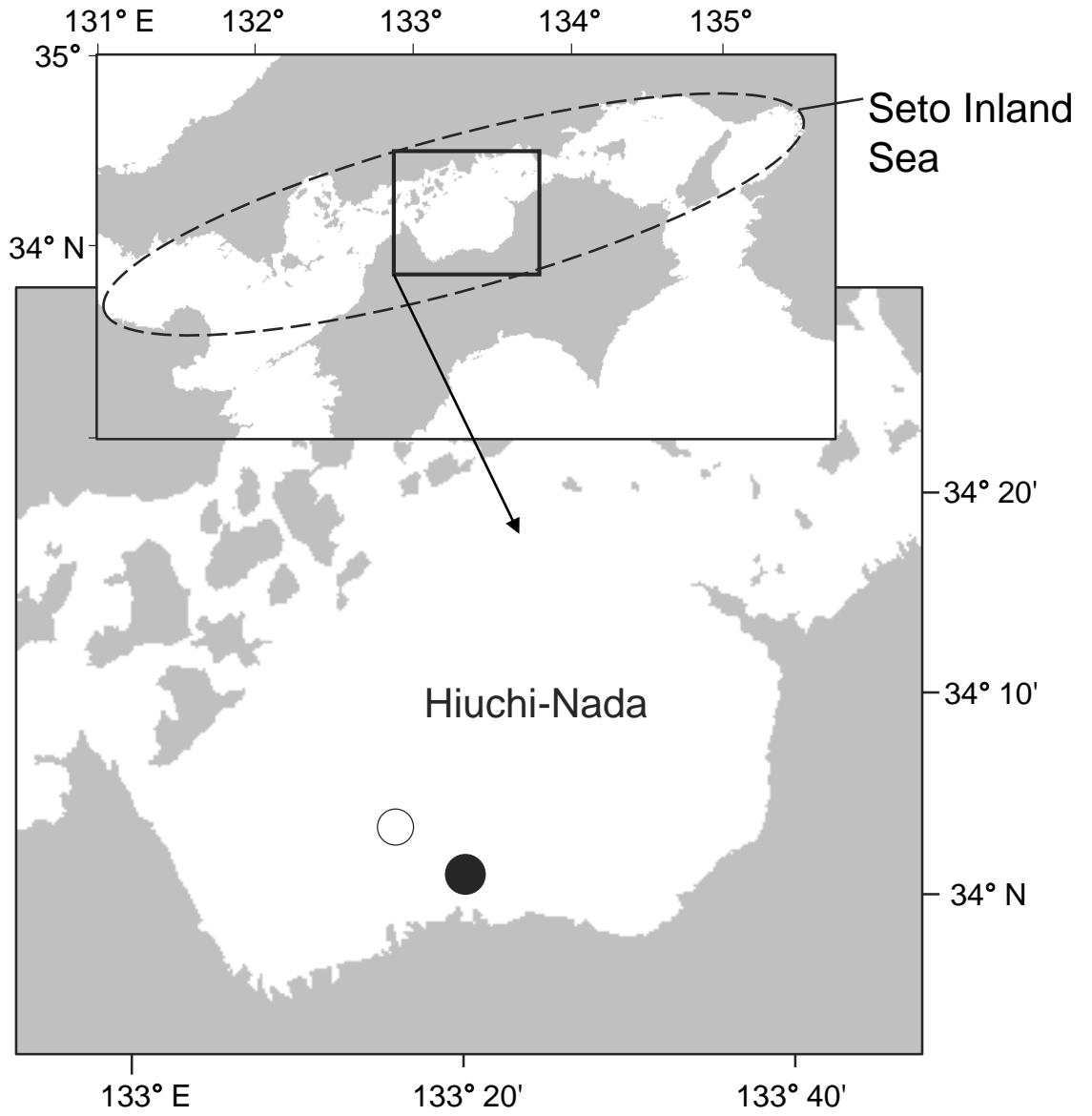
355 and dashed lines indicate water temperature and  $\sigma_t$ , respectively. Diel changes in  
356 vertical profiles in temperature and salinity are shown in the supplemental figures.

357

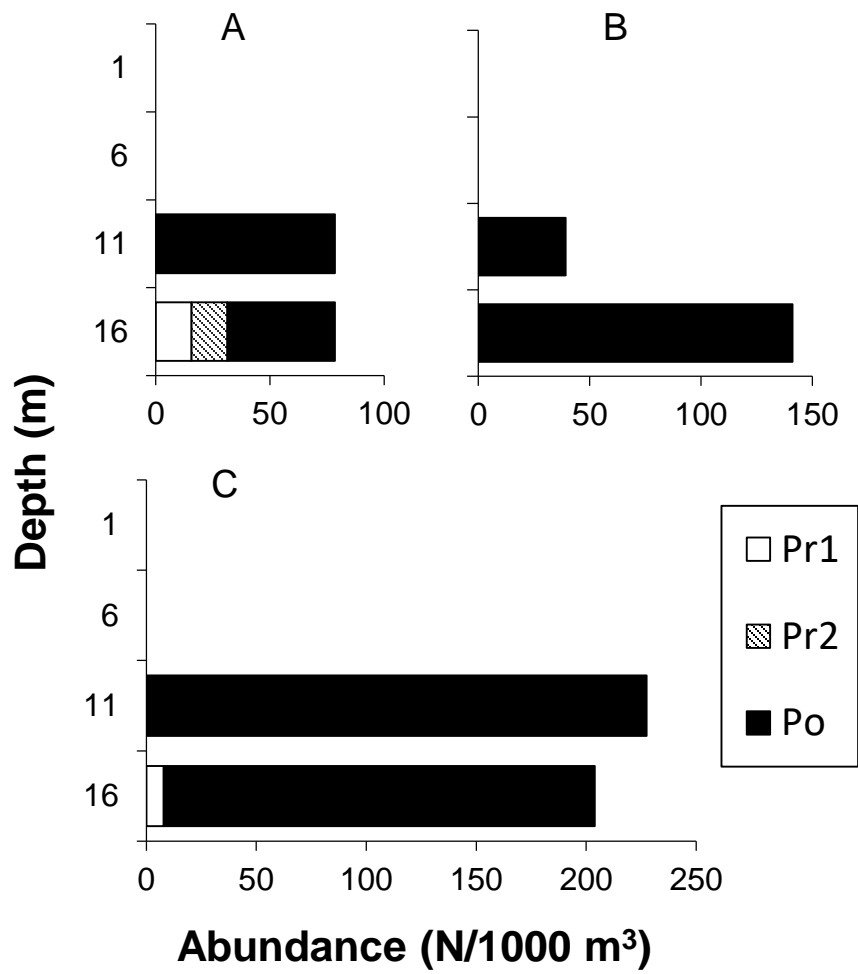
358 **Fig. 6.** Diel changes in the vertical distribution of *Trichiurus japonicus* larvae in June 1997.

359 The number of collected larvae per 1000 m<sup>3</sup> is shown. Detailed information on larval  
360 total length by year and developmental stage is shown in Table 1. Developmental  
361 stages (Pr1–Po) were identified. Open and closed bars indicate daylight (day) and dark  
362 (night) periods, respectively.

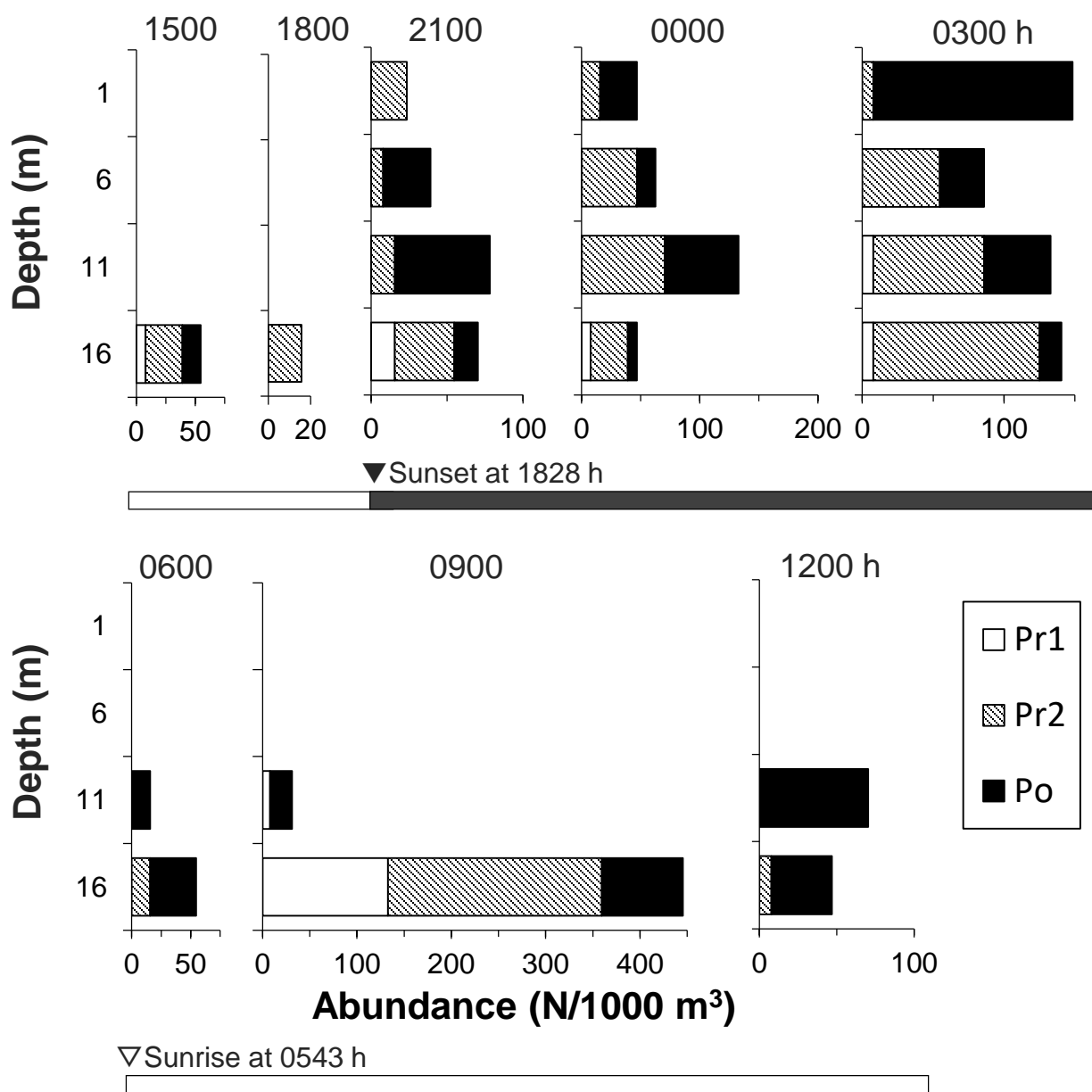
(Fig. 1)



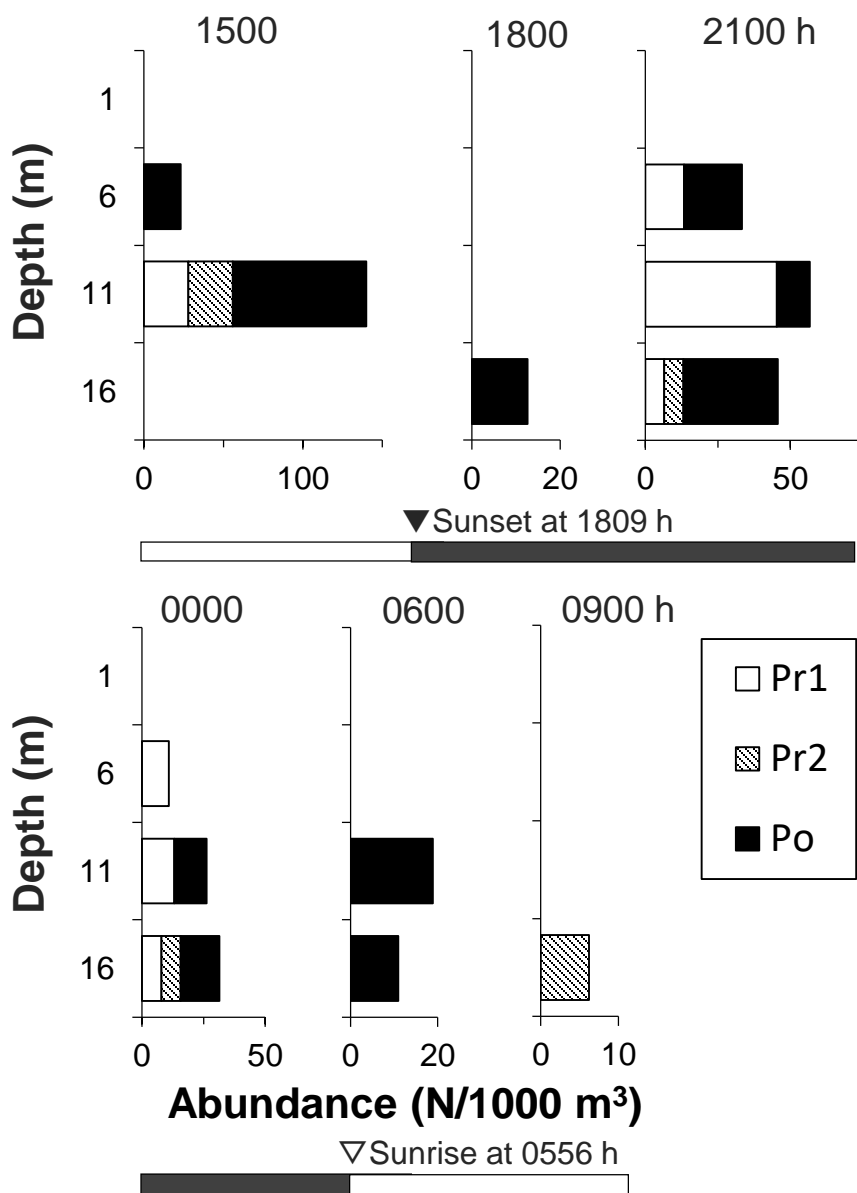
(Fig. 2)



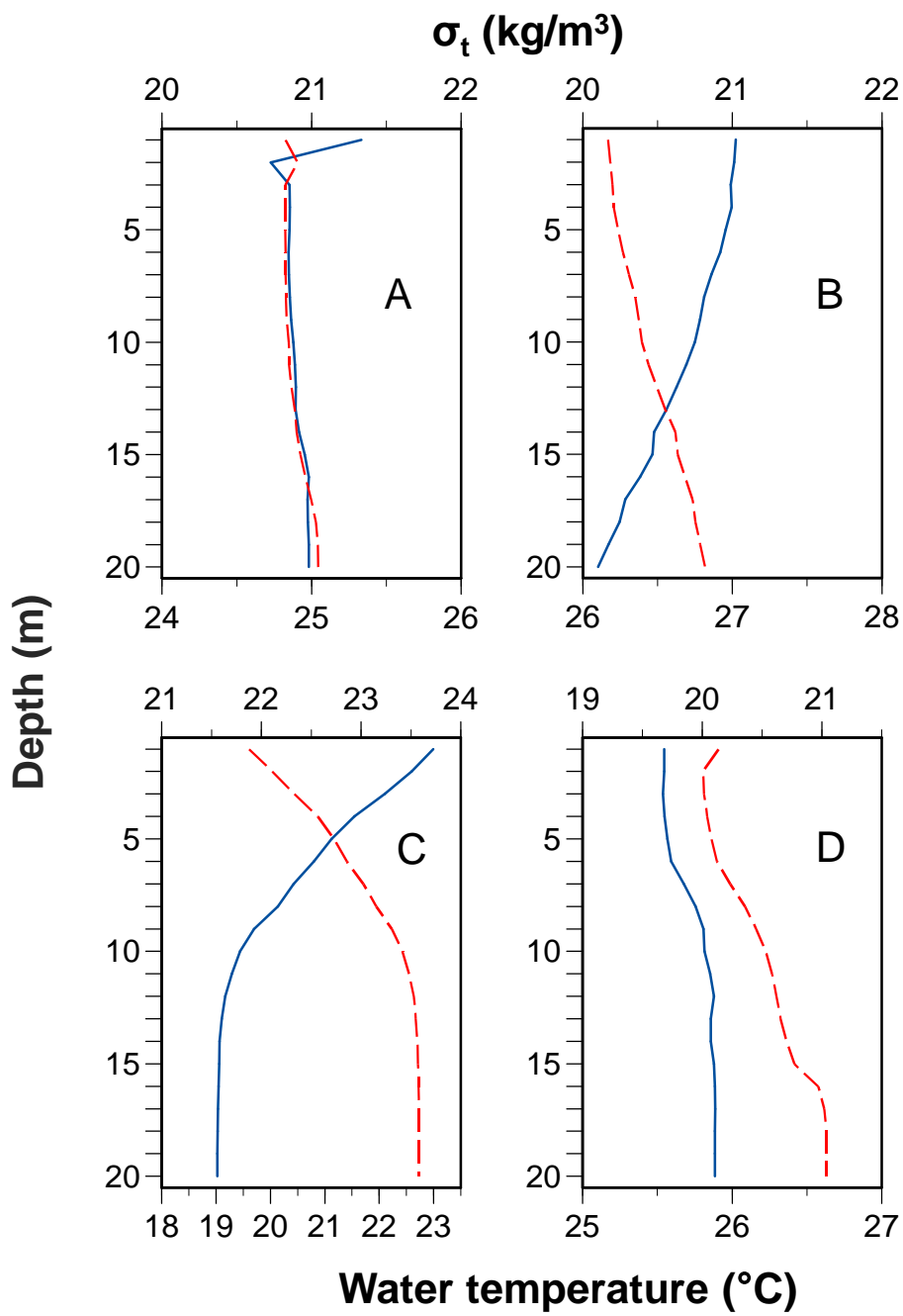
(Fig. 3)



(Fig. 4)



(Fig. 5)



(Fig. 6)

