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Relation	

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

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Running head: Vertical distribution of cutlassfish larvae

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Abstract

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

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

INTRODUCTION

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

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

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

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

MATERIALS AND METHODS

Study site and sample collection

The vertical distribution of *T. japonicus* larvae was investigated at a sampling station during 17–18 September 2015, 5–6 September 2016, 27–28 June 2017, and 20–21 September 2017. This station, located near the southern coast of Hiuchi-Nada in the central Seto Inland Sea (34° 01′ N; 133° 20′ E; 25 m deep; Figure 1), Japan, was chosen because of the high concentration of larval fishes in this area (Shoji & Tanaka, 2005).

In 2015, diurnal distribution patterns were investigated at 0900 and 1000 h on 17 September and at 1100 h on 18 September (Supplementary Table S1). In September 2016 and June 2017, diel distribution patterns were investigated by consecutive 24-h collections at 3-h intervals from 1500–1200 h in 2016 (eight collections in total) or from 1500–1500 h in 2017 (nine collections). In September 2017, larval collections were carried out six times (1500, 1800, 2100, 0000, 0600, and 0900 h). For larval collections, ring nets (called the MTD net; mouth diameter: 56 cm, mesh size: 335 μm; Horiki, 1981) were towed simultaneously at four depths (1, 6, 11, and 16 m) for 10 min at a speed over the water of 2 knots by the training and research vessel Toyoshiomaru (256 tons). Water volume filtered per net was estimated to be 116 ± 36 m^3 (mean ± SD, n = 35) and 128 ± 51 m^3 (n = 24) in June and September 2017, respectively, by using a flow meter attached to the net. Samples collected were immediately preserved in 5% seawater formalin onboard.

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

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

Laboratory observation and data analyses

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

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

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

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

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

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

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

RESULTS

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

Larvae of *T. japonicus* were not observed at 1 and 6 m depths, but were collected at 11 and 16 m depths during the daytime (0900–1100 h) in 2015 (Figure 2). Similarly, the larvae were collected only at 16 m (at 1500 and 1800 h) or at 11 and 16 m depths (at 0600, 0900, and 1200 h) during the daytime in 2016 (Figure 3). In September 2017, one larva of *T. japonicus* at stage Po was collected at 6 m during the daytime (1500 h), but other individuals were collected at 11 and 16 m depths during the daytime (Figure 4). Conversely, *T. japonicus* larvae were collected from all depths during the night from 2100–0300 h in 2016 and from depths of 6–16 m during the night in September 2017. However, larvae of stage Pr1 were not present in samples collected from depths of 1 or 6 m irrespective of day and night in 2015 and 2016 (Figures 2, 3). Similarly, the larvae of stage Pr1 were not collected from 1 m depth in 2017, although four individuals were collected from a depth of 6 m during the night (Figure 4). In September 2016, significant differences in the collection depth between day and night were observed for stages Pr2 (U = 2033, $P < 0.001$) and Po (U = 1901.5, $P < 0.001$), while no significant differences were observed for stage Pr1 (U = 54.5, P = 0.33). In September 2017, no significant differences in the collection depth between day and night were observed for each stage (Pr1: U = 1, P = 0.62; Pr2: U = 7, P = 0.88; Po: U = 67, P = 0.92).

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

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

DISCUSSION

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

Munekiyo & Kuwahara, 1986; Hayashi, 1990).

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

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

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

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

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

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

Developmental stage	N	TL (mm)
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

Figure captions

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

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

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

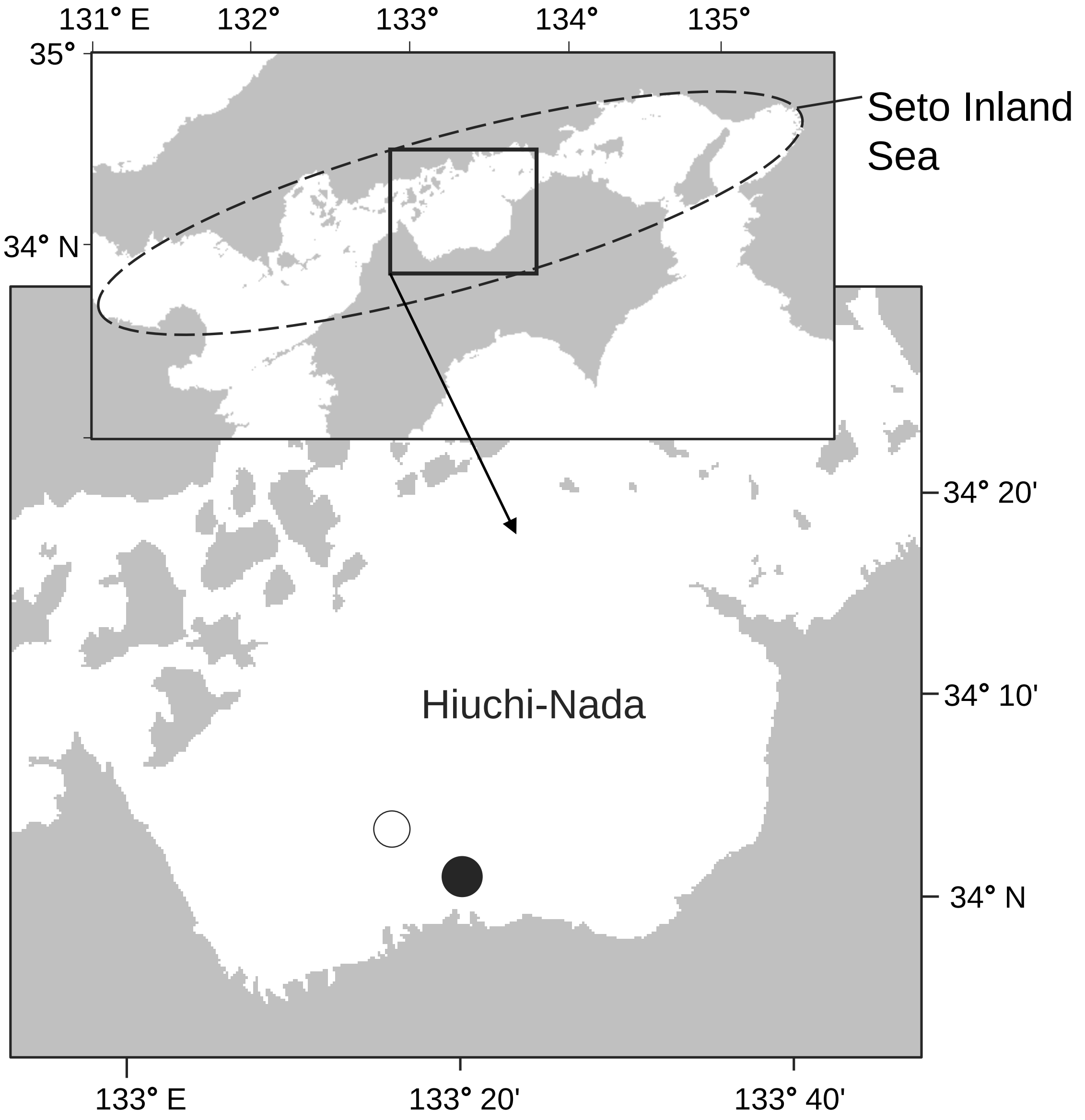
Fig. 4. Diel changes in the vertical distribution of *Trichiurus japonicus* larvae in September 2017. The number of collected larvae per 1000 m^3 is shown. Detailed information on larval total length by year and developmental stage is shown in Table 1. Developmental stages (Pr1–Po) were identified. Open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

Fig. 5. Vertical profiles in average water temperature and seawater density (σ_t) in (A) September 2015, (B) September 2016, (C) June 2017, and (D) September 2017. Solid

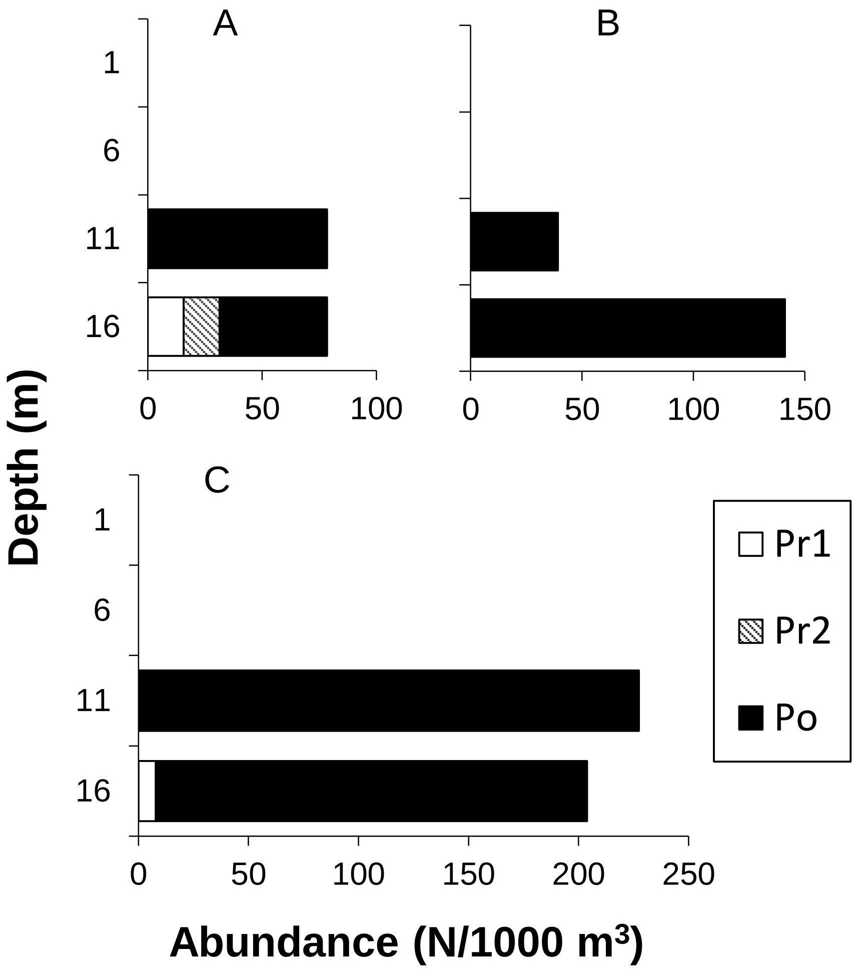
and dashed lines indicate water temperature and σ_t, respectively. Diel changes in vertical profiles in temperature and salinity are shown in the supplemental figures.

Fig. 6. Diel changes in the vertical distribution of *Trichiurus japonicus* larvae in June 1997. The number of collected larvae per 1000 m^3 is shown. Detailed information on larval total length by year and developmental stage is shown in Table 1. Developmental stages (Pr1–Po) were identified. Open and closed bars indicate daylight (day) and dark (night) periods, respectively.

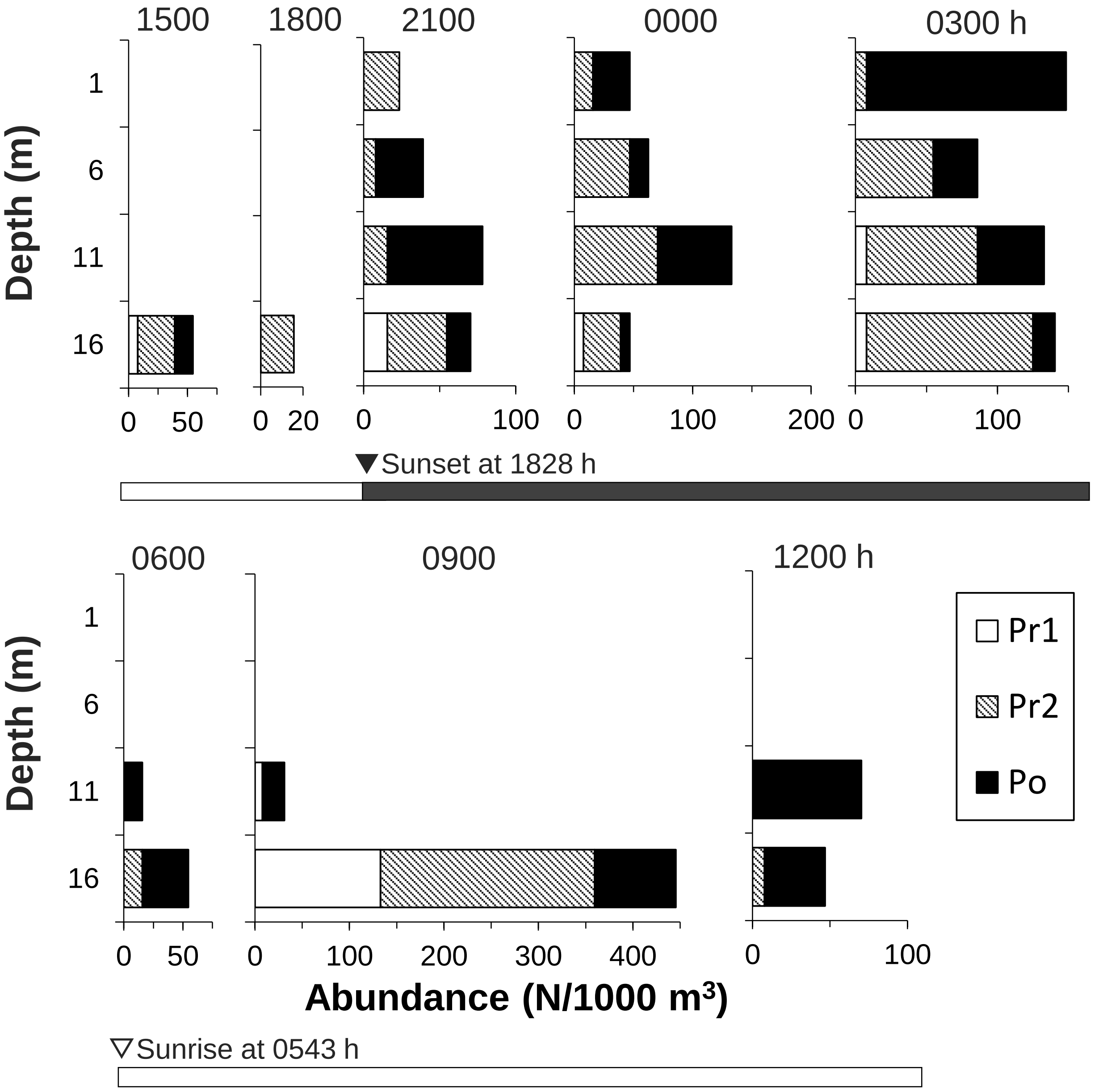
(Fig. 1)


131° E
132°
133°
134°
135°
35°
34° N
Seto Inland Sea
Hiuchi-Nada
34° 20'
34° 10'
34° N
133° E
133° 20'
133° 40'

(Fig. 2)

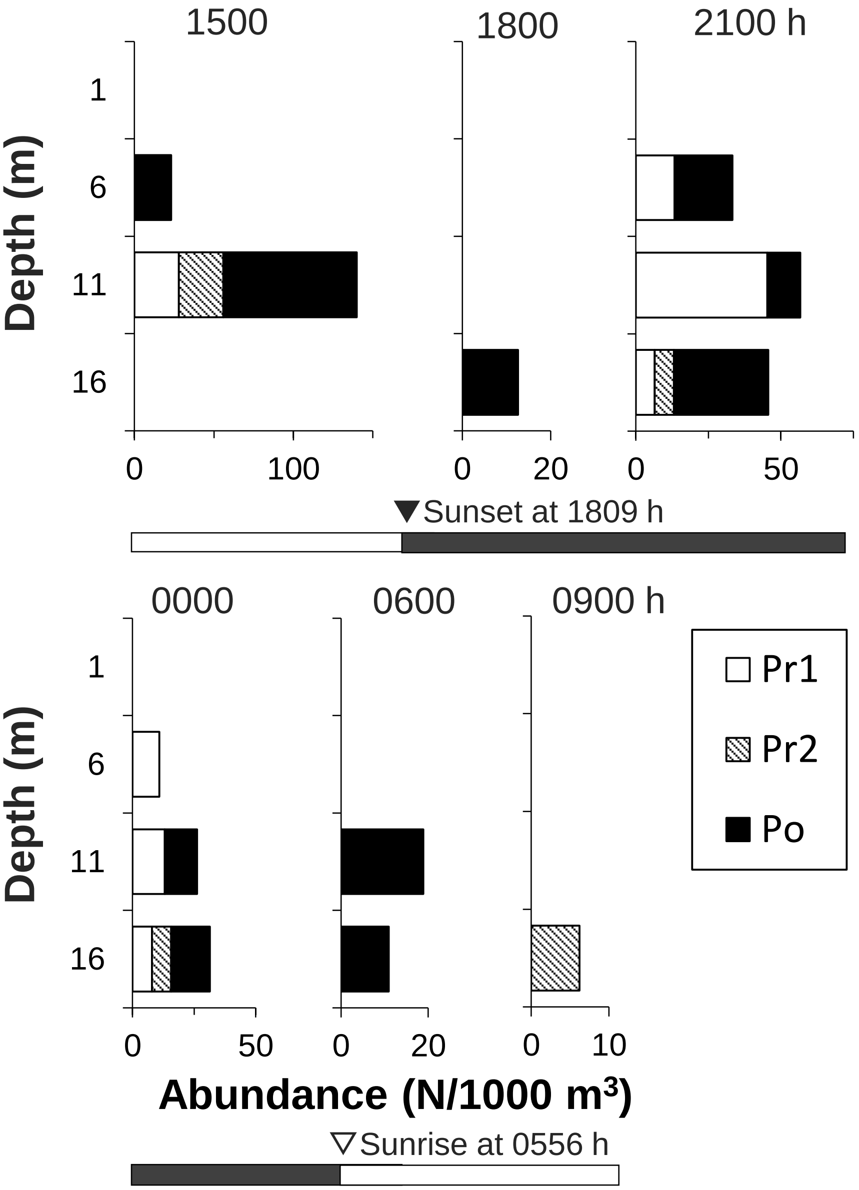

A
B
C
1
6
11
16
0
50
100
150
200
250
Depth (m)
Abundance (N/1000 m³)
□ Pr1
▨ Pr2
■ Po

(Fig. 3)



1500
1800
2100
0000
0300 h
Depth (m)
1
6
11
16
0
50
0
20
0
100
0
100
200
0
100
▼Sunset at 1828 h
0600
0900
1200 h
Depth (m)
1
6
11
16
0
50
0
100
200
300
400
0
100
Abundance (N/1000 m³)
▽Sunrise at 0543 h
□ Pr1
▨ Pr2
■ Po

(Fig. 4)


1500
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Depth (m)
1
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▼Sunset at 1809 h
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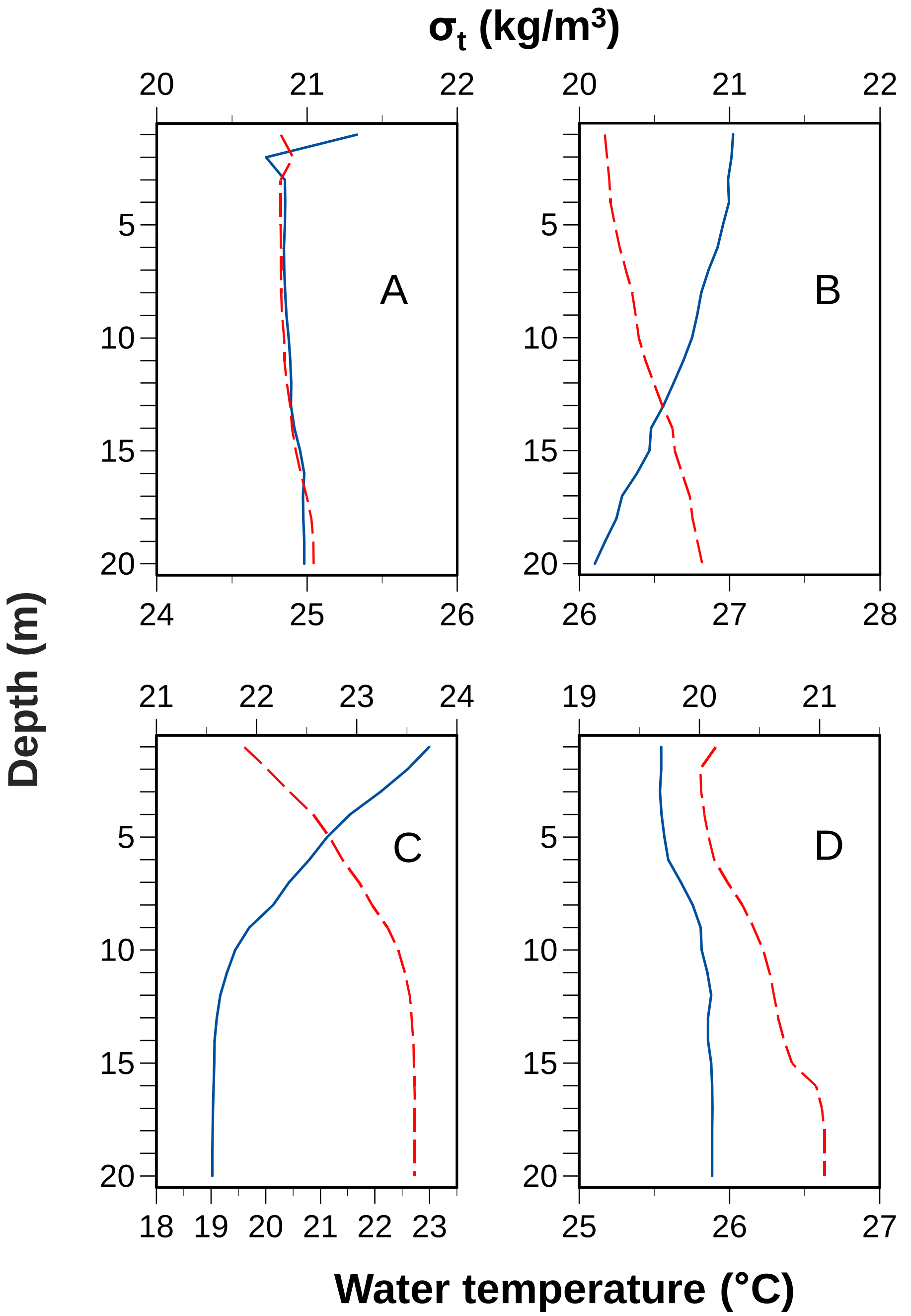
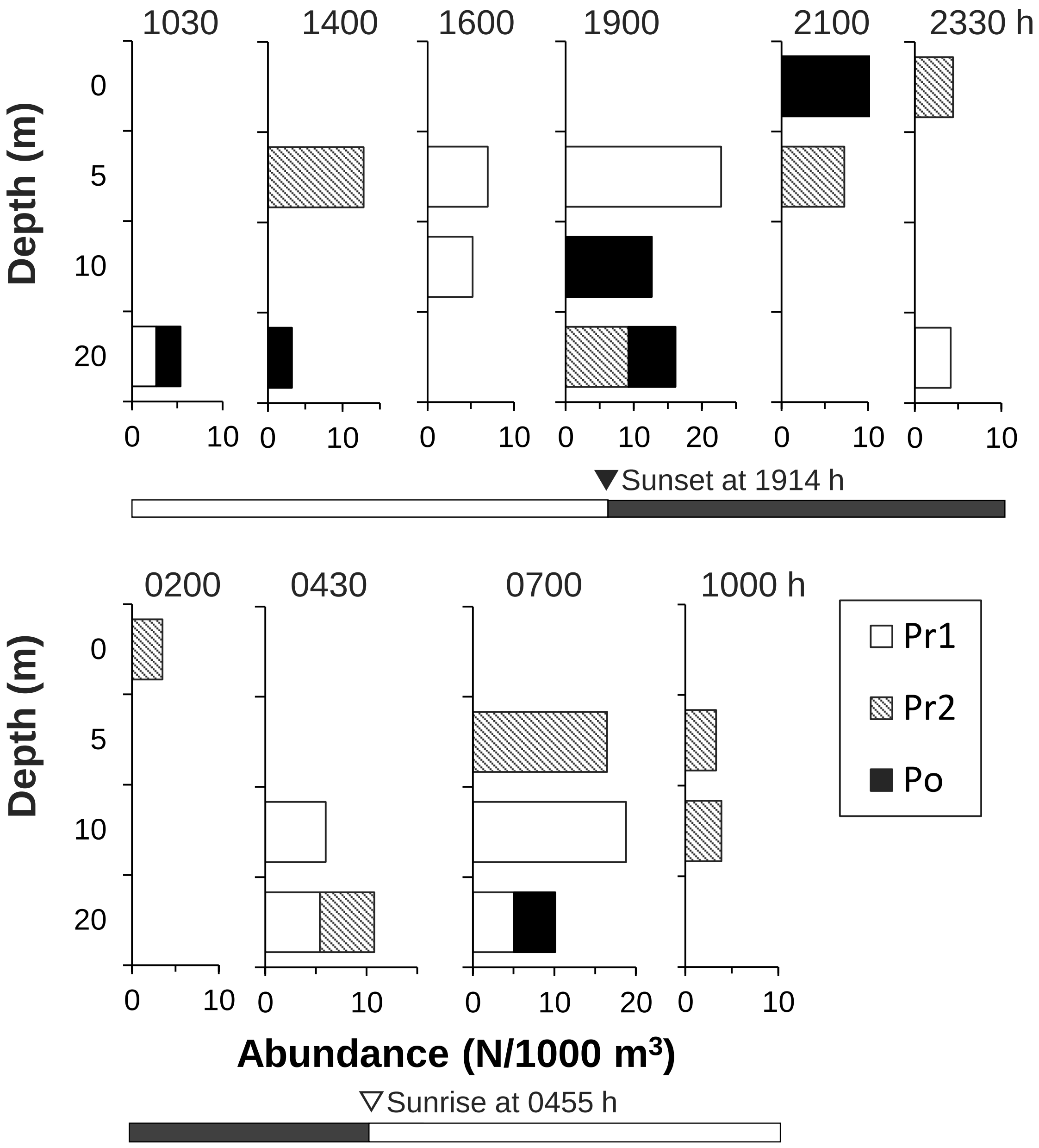
0600
0900 h
☐ Pr1
▨ Pr2
■ Po
0
50
0
20
0
10
Abundance (N/1000 m³)
▽Sunrise at 0556 h

(Fig. 5)


σt (kg/m3)
20
21
22
20
21
22
A
B
5
10
15
20
24
25
26
26
27
28
Depth (m)
21
22
23
24
19
20
21
C
D
18
19
20
21
22
23
25
26
27
Water temperature (°C)

(Fig. 6)


1030
1400
1600
1900
2100
2330 h
Depth (m)
0
5
10
20
0
10
20
▼Sunset at 1914 h
0200
0430
0700
1000 h
□ Pr1
▨ Pr2
■ Po
Abundance (N/1000 m³)
▽Sunrise at 0455 h