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A Radio-tracking Study on the Foraging Movements of the Dobsonfly Larva, *Protohermes grandis* (Megaloptera, Corydalidae)

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Abstract Miniature radio transmitters were used to monitor the movements of the dobsonfly larvae, *Protohermes grandis* (Thunberg) (Megaloptera, Corydalidae), in their natural habitat. The transmitter, 7×18×2 mm and 0.25 g in water, included a quartz crystal (52 MHz band) and a silver oxide battery (life of about 7 days), and was attached to the back of larval prothorax. The signal range was about 2 m and positions of larvae in stream riffles were determined using a small loop antenna. The results showed that larvae favoured a central part of riffles and spent most time there for ambushing for prey. However, they actively moved about at some nights, but never in any daytimes, probably to search for prey or suitable feeding sites. The mean movement distance per night was not clearly dependent on the degree of starvation.

Introduction

Two extreme modes of foraging in predators are ambushing and active searching for prey (Pianka, 1966; Schoener, 1971). Among insects, for general example, pit-making ant-lion larvae are ambush predators, whereas predacious lady beetles actively search their environment for prey items. However, recent detailed studies have been revealing the plasticity of foraging behaviour in response to prey availability, hunger level, predation risk, interference competition, and other environmental factors (Carter & Dixon, 1982; Formanowicz, 1982; Griffiths, 1986; Heads, 1985; Heinrich & Heinrich, 1984; Hildrew & Townsend, 1980; Inoue & Matsura, 1983; Matsura, 1981; Nakamuta, 1982; Peckarsky, 1983; Sjöström, 1985; Tanaka & Itô, 1982; Townsend & Hildrew, 1980; Walde & Davies, 1984).

These studies are conducted in the laboratory or semi-natural conditions, because it is usually difficult to observe the foraging behaviour directly under the field conditions. Especially in stream-dwelling insects, the laboratory observation or the indirect evidence from field sampling is the only method for studying the

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foraging behaviour quantitatively (PECKARSKY, 1983).

In this study, however, we developed a new radio-tracking system to apply to the stream insect, larvae of *Protohermes grandis* (THUNBERG) (Megaloptera, Corydalidae), in their natural habitat. We monitored the movements of radio-tagged larvae in the riffles of streams, and obtained quantitative data on foraging modes, feeding sites, and diel activity patterns. Some possible factors causing the alteration in foraging movements were also examined.

Although radio-telemetry and ultrasonic-telemetry have been used commonly for monitoring the behaviour of many animals, this is probably the first application to insects (STASKO & PINCOCK, 1977; AMLANER & MACDONALD, 1980; MECH, 1983).

Materials and Methods

Transmitters. A waterproof miniature radio transmitter includes a quartz crystal with a certain frequency around 52 MHz and a silver oxide battery. It has no transmitting antenna. The size of entire transmitter is approximately 7×18×2 mm. The weight in water varies among three types of transmitters; 0.28 g (Type I), 0.33 g (Type II), and 0.25 g (Type III), owing to different battery weight. Battery longevity was 8 days in Types I and II transmitters, but 7 days in Type III.

A transmitter was attached to the back of larval prothorax with a small amount of adhesive (Bond Aron Alpha®) (Fig. 1). To make sure of attachment, right and left fine wires embedded in the transmitter were tied at the ventral side of prothorax (Fig. 1 B). It was easy to fix the transmitter with adhesive and fine wire, because of the hard structure of prothorax in this larva. The front of the under-surface of the transmitter is curved to sides to fit to the dorsal prothorax, whereby no accidental slip or removal occurred on the way of tracking.

Determination of larval positions. The position of the radio-tagged larva in the riffle was determined using a small loop antenna equipped at the tip of a rod, and a multiple channel receiver (Yaesu FT-690) as shown in Fig. 2. In our system, the signal was continuously transmitted in the range of at least 2 m in radius above water surface, and it was easy to determine the center of signal range. The larva existed in water just below it, although slight aberrations (about 10 cm in radius) were unavoidable. In practice, all of twenty radio-tagged larvae could be recovered accurately after tracking.

Study sites. Radio-trackings were done on three occasions; 5–13 April 1986 at the Morito River, 17–22 May and 20–25 September 1986 at the Anado Fork. The Morito River is a small stream on the Miura Peninsula, Kanagawa Prefecture, Central Japan and the Anado Fork is a tributary of the Natori River, Miyagi Prefecture, Northeast Japan. On all occasions, a stony and knee-deep riffle was selected as a study site, and was mapped in detail.

Larvae were captured in the riffles adjacent to study sites, measured on the

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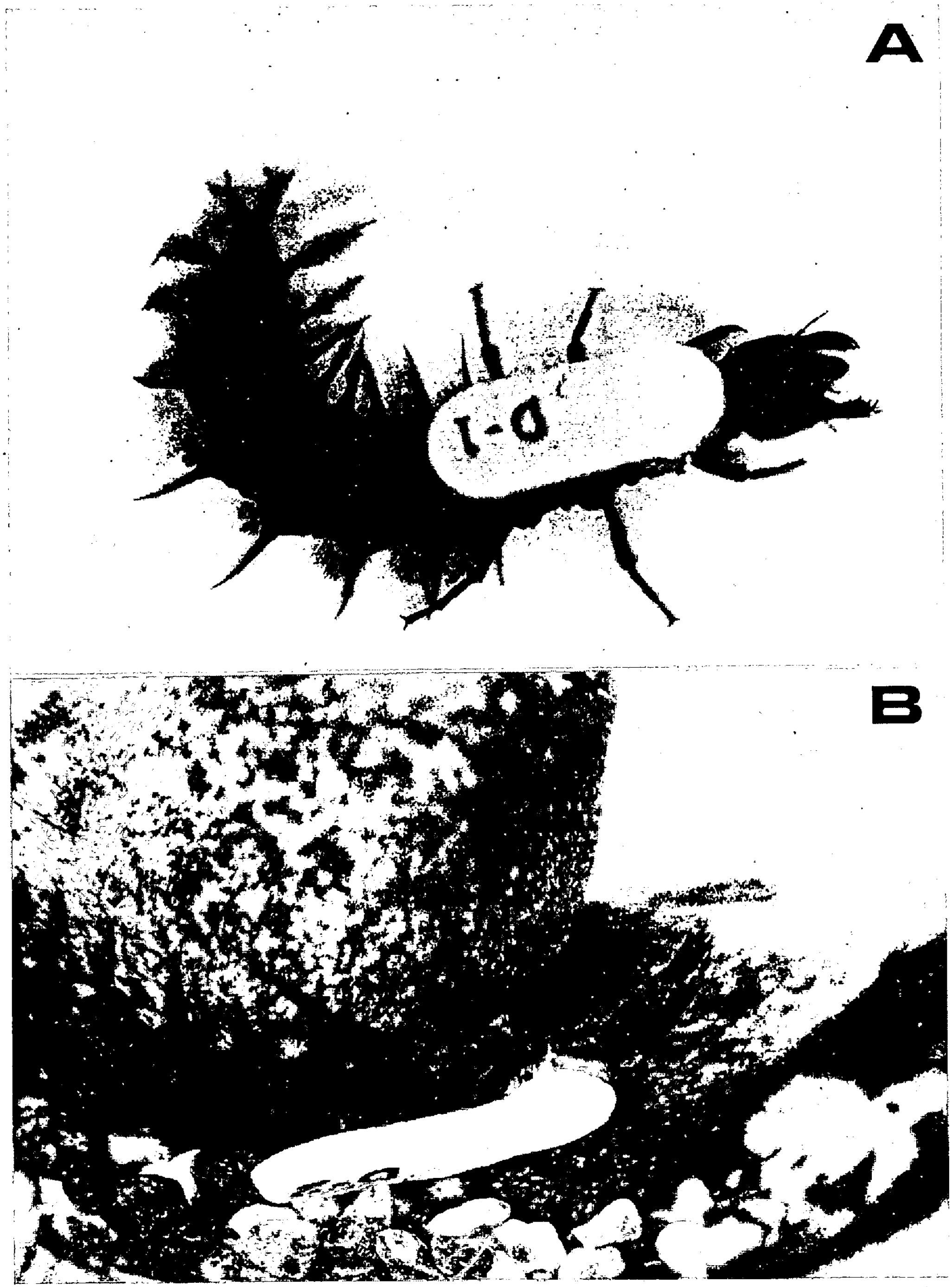

Fig. 1. A dobsonfly larva, *Protohermes grandis*, with a transmitter attached to the back of prothorax. A, Dorsal view (head capsule width, 7.20 mm). B, Lateral view.

head capsule width, and weighed. Then, transmitters were attached to them. The radio-tagged larvae were immediately released to the study riffle before sunset on that day. The number of radio-tagged larvae were 4, 10, and 6 on the respective occasions. The positions of these larvae in the riffles were plotted on maps twice

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Fig. 2. Position determination of a radio-tagged larva by using a small loop antenna equipped at the tip of a rod. The larva exists in the stream bed just below this loop antenna.

a day, at sunset and at dawn. At some nights except the day of release, time-mappings were also made at hourly intervals during the night. Water temperatures and rainfalls were recorded through the tracking period.

Fullness of foregut. After the end of tracking, all the radio-tagged larvae were recaptured at dawn. They were immediately killed in the boiling water to avoid regurgitation of gut contents. In the laboratory, the foregut contents and the larval body were separately dried at 80°C for one day, and the fullness of foregut was calculated as the dry weight ratio (%) of foregut contents to larval body mass. On 25 September, ten free-living larvae were collected at the same riffle and the same time as the radio-tagged larvae were recaptured, for comparison of foregut contents.

Effects of radio-tagging on prey handling. The handling time was measured in the laboratory to know whether or not the larvae with the transmitter suffer inconvenience for handling the prey captured. Various-sized prey items of *Chironomus* (Chironomidae), *Hydropsyche* (Hydropsychidae), and *Kamimuria* (Perlidae) were offered to two larvae which were collected on 5 November 1986 from the Nagura River, a tributary of the Yahagi River, Aichi Prefecture, and were reared at 9.5±0.2°C. Head capsule widths and live weights of them were 7.20 mm and 1.34 g, and 6.95 mm and 1.27 g, respectively. Type I transmitters were attached to them, and the time from biting the prey with mandibles until swallowing it was

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measured in the same way as HAYASHI (1985). Relationships between the handling time and the relative prey size (the ratio of prey width to the head capsule width of the predator) were compared with those in the larvae without the transmitter (HAYASHI, 1985).

Results

Radio-trackings

The fluctuation of water temperature and the duration of the rainfall are shown in Fig. 3. All the rainfalls were not so heavy as to flood the stream.

The routes of movements by respective larvae are shown in Fig. 4 through the tracking period. The larvae moved to a central part of riffles after being released in the shore. The movements to downstream were somewhat more frequent than those to upstream or across the stream.

The minimum estimate of daily movement distance (m) was determined from the change of larval positions at sunset and at the following dawn (Table 1), because any position changes did not occur in the daytime, that is, from dawn to sunset in the same day (a total number of daytime observations were 92). Although larvae seldom moved even at night, their movements occurred only at night. In the case of the Morito River, larvae were stationary in 15 of 28 night observations (53.6%)

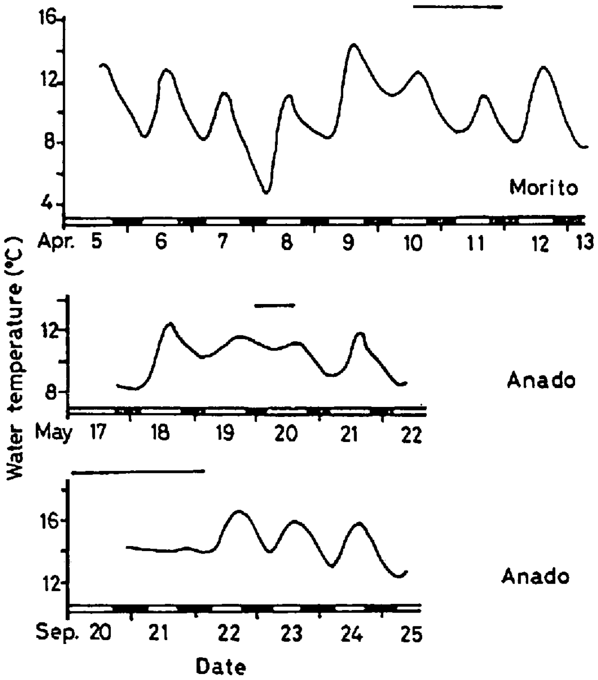

Fig. 3. Fluctuations of water temperature and durations of rainfall (horizontal bars) on three radio-tracking occasions; at the Morito River in April, at the Anado Fork in May, and also at the Anado Fork in September. Open and solid columns indicate day and night, respectively.

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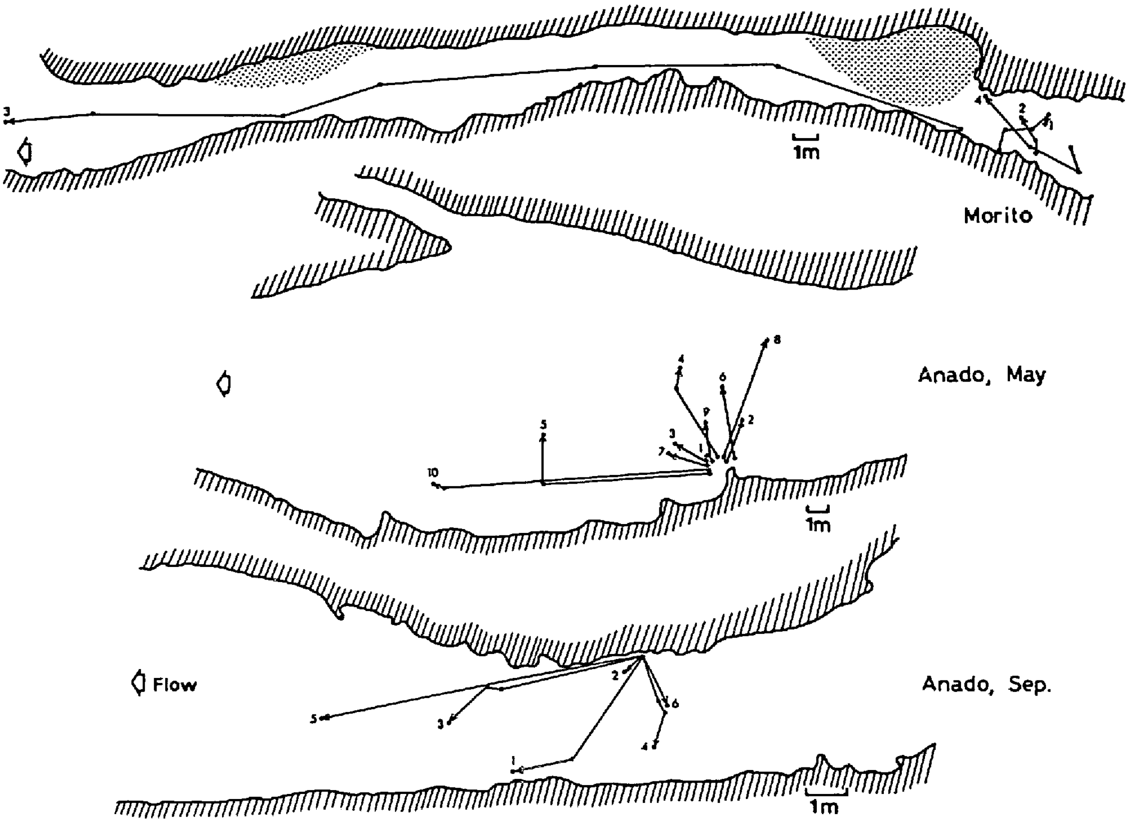

Fig. 4. Trails of movements by individual radio-tagged larvae on three occasions; at the Morito River in April, at the Anado Fork in May, and also at the Anado Fork in September. Each illustration shows the full range of one riffle downstream to the left (dotted area is part of shallow pools). Closed circles indicate positions of larvae staying during the daytime; the larvae often continued to stay at the same position for several days. Numerals represent individual larvae (the same as in Table 1) and are added to the position at which they were recovered at the end of tracking periods.

except for the night of releasing the larvae. In the Anado Fork, they were stationary in 34 of 40 nights (85.0%) in May, and 19 of 24 nights (79.2%) in September. After all, the larvae moved in only 24 of a total 92 night observations (26.1%). The mean movement distance per night in these 24 nights were 2.6 m (SD=2.5).

The time-mappings of larval movements were obtained for a total of eleven cases (Fig. 5). The larvae began to move within a few hours after the sunset and continued to move, on average, for 3.2 h (SD=2.6, n=11) at a speed of 0.88 m/h (SD=0.63, n=33; the range of water temperatures, 8–16°C). The maximum speed of move was 3.15 m/h. The movements observed at hourly intervals showed relatively smooth patterns, and the larvae never resumed the movements at the same night once after they stopped moving. Other stationary larvae were also monitored hourly at the same night, but no sign of movements was detected. This eliminated the possibility that they were apparently stationary because of homing behaviour.

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Table 1. Movement distances and conditions of twenty larvae radio-tracked at the Morito River in April (MA), at the Anado Fork in May (AM), and also at the Anado Fork in September (AS).

Larval number	Head width (mm)	Live body weight (g)	Type of transmitter[a]	Daily distance[b] (m)								Mean distance per night[c] (m)	Fullness of foregut[d] (%)	Condition factor[e] (mg/mm^3)	Load[f] (%)
				1	2	3	4	5	6	7	8				
MA- 1	6.00	0.94	I	0	0.9	1.1	0.8	0	0	0	0.3	0.44 (0.08)[g]	0.70	4.4	30
2	5.80	0.91	I	0.3	0.9	0	0	0	0	0	0	0.13 (0)	0.44	4.7	31
3	6.60	1.34	I	0	7.3	7.0	8.5	0	4.1	7.6	3.7	5.46 (3.85)	0.62	4.7	21
4	6.05	0.91	I	0.9	2.1	2.8	0	0	0	0	0	0.70 (0)	0.74	4.1	31
AM- 1	7.10	1.98	I	0	0	0	0	0				0	0.15	5.5	14
2	7.00	1.72	I	0	2.0	0	0	0				0.50	0.38	5.0	16
3	7.30	2.26	I	1.6	0	0	0	0				0	1.34	5.8	12
4	6.50	1.68	I	3.8	0.8	0	0	0				0.20	0.40	6.1	17
5	7.00	2.00	I	8.2	2.2	0	0	0				0.55	0.18	5.8	14
6	6.05	1.34	I	0	3.4	0	0	0				0.85	0.52	6.1	21
7	7.75	2.15	I	1.8	0	0	0	0				0	0.36	4.6	13
8	7.40	2.09	I	6.4	0	0	0	0				0	3.08	5.2	13
9	6.00	1.30	I	0	0	0	1.8	0				0.45	0.57	6.0	22
10	7.00	2.11	I	13.1	0.5	0	0	0				0.13	0.21	6.2	13
AS- 1	7.50	1.24	III	3.0	0	0	0	1.5				0.38	1.66	2.9	20
2	6.30	1.09	III	0.6	0	0	0	0				0	0.55	4.4	23
3	6.45	0.94	I	3.5	0.5	1.4	0	0				0.48	0.75	3.5	30
4	6.80	1.06	I	1.2	0.4	1.0	0	0				0.35	1.29	3.4	26
5	6.75	1.27	II	8.0	0	0	0	0				0	0.62	4.1	26
6	6.20	0.80	II	1.5	0	0	0	0				0	0.62	3.4	41

a) The weights in water are 0.28 g (I), 0.33 g (II) and 0.25 g (III).
b) Minimum distance moved in respective nights.
c) Excluding the day of releasing.
d) The ratio of foregut contents/body mass in dry weight.
e) Live body weight/(head capsule width)^3.
f) Transmitter weight/live body weight.
g) Mean distance moved per night for last four days.

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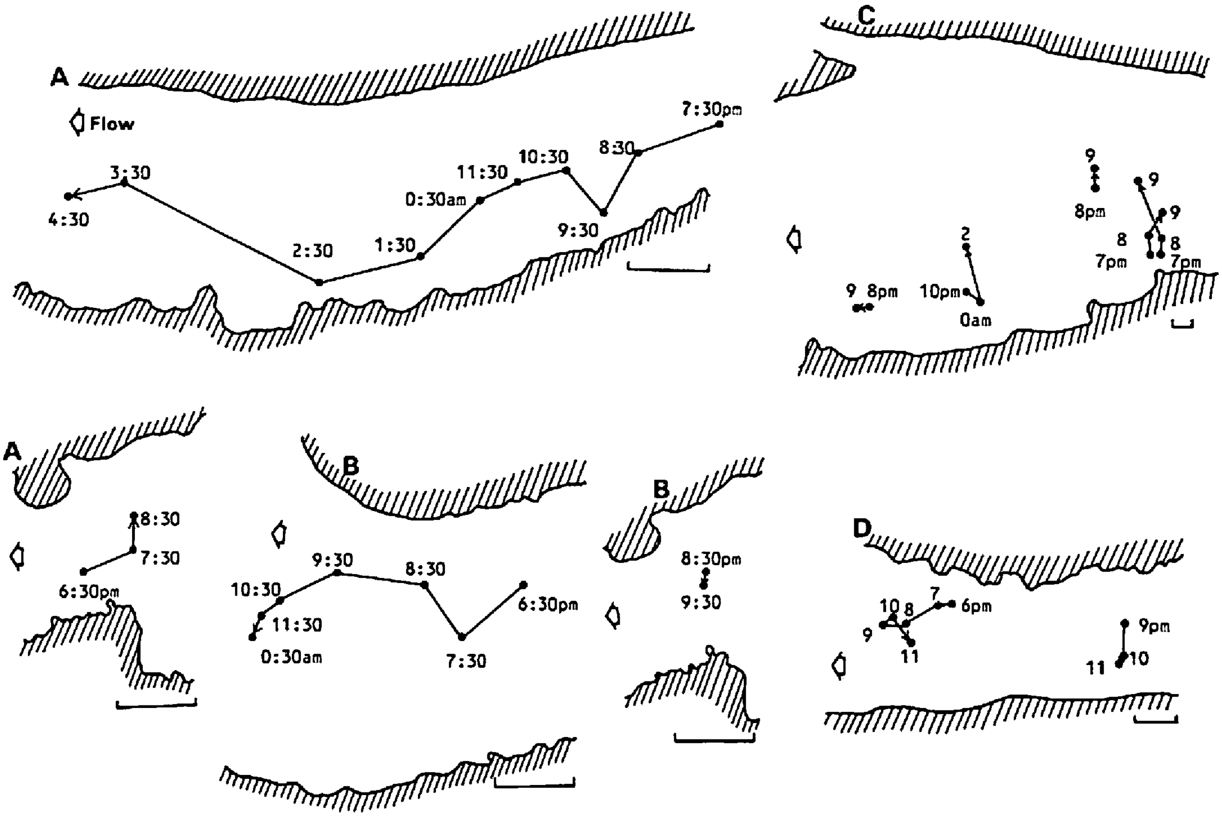

Fig. 5. Trails of radio-tagged larvae (eleven examples) which were mapped at hourly intervals (two hours intervals in one exception) during a night. —— A, At the Morito River on 8–9 April. B, At the Morito River on 12–13 April. C, At the Anado Fork on 18–19 May. D, At the Anado Fork on 22–23 September. Closed circle indicates the position of larvae at an indicated time of day. The left is downstream in all illustrations. Scales are the distance of 1 m.

Factors affecting movements

Probably the light inhibited larval movements because they never changed their positions in the daytime as mentioned above. Larvae were also stationary at most nights, whereas they moved about at some nights, which suggested the behavioural regulation by some factors other than light. Water temperature and rainfall were unlikely to concern (see Fig. 3 and Table 1).

As shown in Fig. 6 A, the movement distance per night averaged for last four days in the tracking period tended to be long in the larvae with lower foregut contents which were evaluated at the end of tracking. However, this tendency was not significant ($r=-0.09$, $P>0.05$); the larvae were often stationary in spite of starvation.

The condition factor of larvae, live body weight/(head capsule width)^3, was different among individuals and seasons owing to their life cycles. In general, this species has a 2- or 3-year larval period. They moult to the final instar larvae in autumn and grow in weight to the next early summer when they leave the stream to

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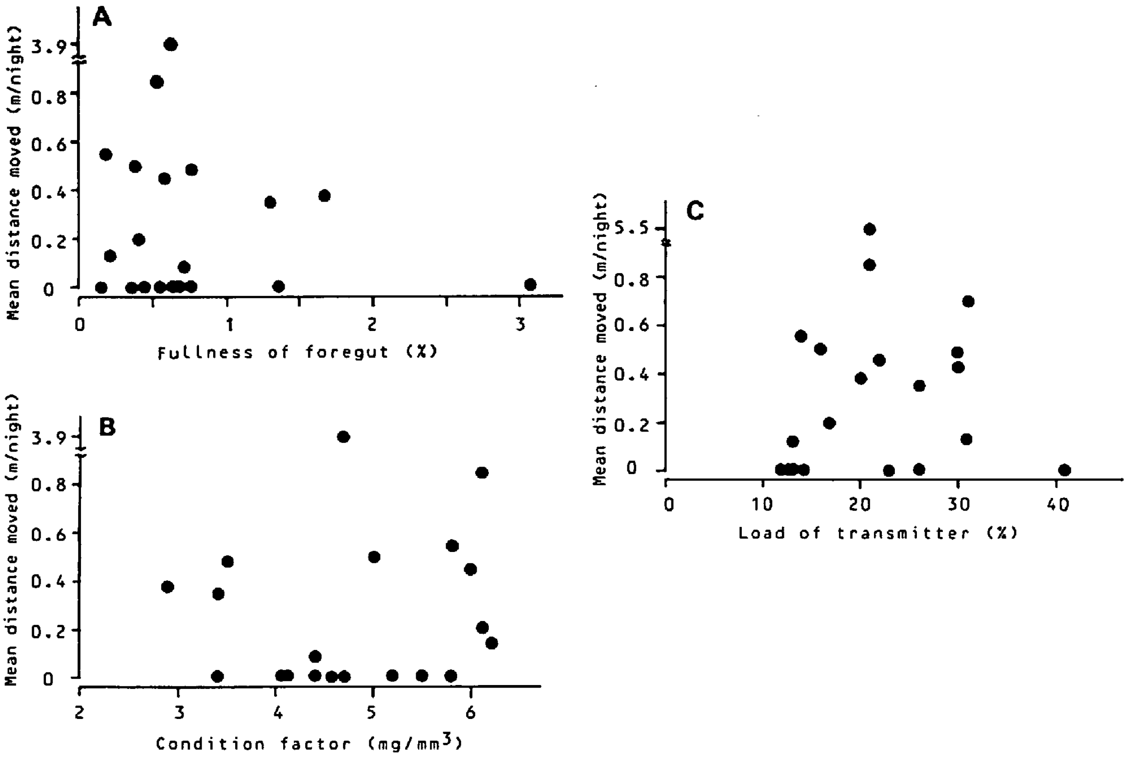

Fig. 6. Relationships between the mean distance moved per night and the fullness of foregut (A), the condition factor (B), or the load of transmitters (C) in respective radio-tagged larvae (n=20). See text for details.

pupate (Yoshida *et al.*, 1985; Hayashi & Yoshida, 1987; Hayashi, 1988). The condition factor was, therefore, lower in September than in April and May (Table 1). However, this factor was unlikely to affect the movement distance per night averaged for last four days ($r=0.03$, $P>0.05$) (Fig. 6 B).

Effects of radio-tagging on larval behaviour.

Although the ratio of the transmitter weight in water to the larval live weight (load) varied from 12% to 41% (Table 1), no tendency was obtained between the load and the mean movement distance per night excluding the night of releasing the larvae ($r=0.02$, $P>0.05$) (Fig. 6 C).

According to the observation in the aquarium, the flattened shape of the transmitter (Fig. 1) allowed the larvae to enter into a space under the stone. The tagging to the back of prothorax also allowed to bend a body, to walk, and to capture and handle the prey without any difficulties. In fact, the relationships between the handling time and the relative prey size in two radio-tagged larvae were similar to those in free larvae obtained by Hayashi (1985) (Fig. 7). The load of the transmitter in these larvae was 21% and 22%, respectively.

Figure 8 shows the fullness of foregut evaluated at the end of tracking. Large variations among larvae were observed including a control sample. On 25 Septem-

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ber, the mean values were not different significantly between the radio-tagged larvae and the controls (MANN-WHITNEY's U-test, $U=19$, $P>0.05$). The larval head capsule width was not different between both groups; 6.67 mm ($SD=0.47$, $n=6$) and 6.33 mm ($SD=0.63$, $n=10$), respectively ($t=1.14$, $0.2<P<0.3$).

Discussion

One important problem in the study using the radio-telemetry is the effects of attached instruments on the behaviour of animals. The effects for aquatic animals have been evaluated in fishes (shad, trout, salmon, bluegill, and tuna) and seabirds (penguin) (STASKO & PINCOCK, 1977; WILSON *et al.*, 1986). These animals must swim in water which is a much more viscous medium than air, and some effects were noted on swimming speed, swimming stamina, and buoyancy regulation. In general, the effects may be more critical in pelagic animals than in bottom-dwelling ones, or in swift, and especially sustained, swimmers than in sluggish movers. As shown in this paper, the foraging behaviour of *P. grandis* larvae, which dwell in the stream bed and walk slowly, was unlikely to be seriously affected by attachment of our transmitter, because 1) the movement distance per night was independent of the weight ratio of the transmitter to larval body mass, 2) the fullness of foregut did not differ significantly between radio-tagged larvae and free-ranging ones, and 3) the handling time did not differ between radio-tagged larvae and controls.

The larvae of *P. grandis* do not make a retreat with pit like ant-lion larvae or with net like caddisfly larvae. They merely hide under stones of the stream bed, which suggests that they are mobile predators. The radio-tracking, however, revealed that the larvae did not walk about the stream bed but stayed for a long time at the same site in their natural habitat. When they moved, they did only at night and never in the daytime. Even at night, they moved in only 26.1% of a total number of nights examined.

The larvae reared in the aquarium, in which they usually turned over on their back as shown in Fig. 1 B, well fed on the prey given under light conditions in the daytime. Probably in the field, they are ambushing for prey during the daytime. At night, most larvae also continue to ambush. But some begin to search for prey actively, which may lead them to move out of the space under the stone where they hide in the daytime. These larvae walked slowly (0.88 m/h on average) and seemed to seek a suitable feeding site as well as to search for prey, because they never resumed the movements at the same night once after they ceased moving. The mean duration and distance of movements per night were only 3.2 h and 2.6 m, respectively.

Several insects such as the mantis and the damselfly larvae have been known to switch their foraging modes from ambush to active search in response to hunger level (*e.g.*, INOUE & MATSURA, 1983; HEADS, 1985). Even in the ant-lions, starved larvae relocate their pits more frequently than well fed ones (HEINRICH & HEINRICH, 1984; GRIFFITHS, 1986), and in the predacious caddisfly, larvae abandon net-spinning

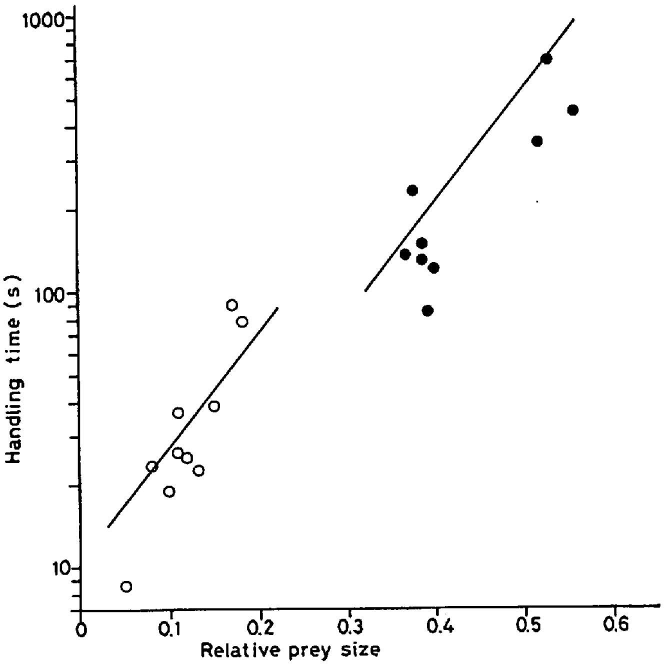

Fig. 7. Relationships between the relative prey size, i.e., the ratio of prey width to the head capsule width of predators, and the handling time for the prey of Perlidae (closed circles) and for the prey of Chironomidae and Hydropsychidae (open circles). Circles indicate the data obtained from radio-tagged larvae, and the lines are drawn from the regression equations obtained from normal larvae (the same as in HAYASHI, 1985). Water temperatures are 9.5°C in both cases.

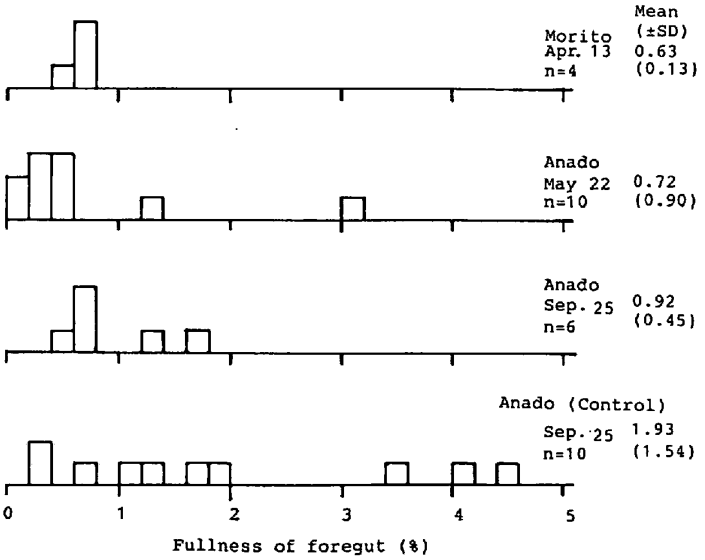

Fig. 8. Frequency distributions of the fullness of foregut evaluated for individual larvae at the end of three tracking occasions (at the Morito River in April, at the Anado Fork in May, and at the Anado Fork in September) and a control sample (at the Anado Fork on 25 September).

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sites and wander after a certain threshold time during which no prey has been captured (HILDREW & TOWNSEND, 1980; TOWNSEND & HILDREW, 1980). The larvae of *P. grandis* partly showed a similar response; the mean movement distance per night tended to be long in the larvae with lower foregut contents (Fig. 6 A).

However, they were often stationary in spite of low foregut contents. Low mobility of them is probably owing to high mobility of prey in the riffle, which is well known as the upstream movement and the drift of stream invertebrates (*e.g.*, WATERS, 1972; MÜLLER, 1974; TOWNSEND & HILDREW, 1976). In the riffle, thus, the ambush mode of foraging is successful even in starved larvae. By staying at the same position, they can also save the energy expenditure by movements.

Larval movements might be caused by other factors such as physical suitability of microhabitat and interference interactions by competitors or predators. It is impossible at present to examine these effects, but the larvae of *P. grandis* are, at least, considered to prefer the microhabitat with water current, because they usually moved to a central part of riffles after being released in the shore.

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