ARTICLE

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Microhabitat use by the rainbowfish *Melanotaenia duboulayi* in a subtropical Australian stream

Abstract Microhabitat use and feeding behavior of the rainbowfish *Melanotaenia duboulayi* (Castelnau) were investigated in a slow-flowing stream adjacent to riparian forest in south-eastern Queensland, Australia. Fish were more abundant in vegetated areas, but did not enter dense *Vallisneria* beds, where predators were observed. In sunny conditions shoals of juveniles occurred near the water surface feeding floating material on the surface, but larger fish tended to occur at the bottom near submerged vegetation, often utilizing the overhanging aquatic plant community as a refuge and food source. In the middle of the day, juveniles and small fish seemed to show behavioral thermoregulation at the surface in the warmest site. Under cloudy conditions, however, fish of all sizes preferred deeper water. The present study suggests that in still and sunny pools thermal change caused by sunlight influences the microhabitat choice of small fish. A field experiment using a kingfisher model implies that fish swimming at the surface could escape from aerial predators in sunlit conditions by responding to moving shadows, but could not do so under cloudy conditions.

Introduction

As fish are motile, they are able to maintain a dynamic balance between the benefits of feeding and the risks of pred-

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ator exposure, by moving between habitats and by taking advantage of protection and information flow associated with shoaling (Milinski 1993). The risk-balancing trade-off usually varies with the life-stage of fish, partly because diets and susceptibility to predation vary with ontogeny, and is manifested by differences in habitat preferences between juveniles and adults of the same species (Helfman et al. 1997). Size-related depth stratification within a given species appears to be an example of such variation in habitat use: a positive correlation between body size and swimming depth is reported in some freshwater fishes (Helfman et al. 1977; Lowe-McConnell 1987). This relationship has sometimes been interpreted in terms of predation pressure: it is hypothesized that small fish prefer shallow water because of swimming predators in deep water, while large fish prefer deep water because of wading and diving predators in shallow water (Schlosser 1987; Greenberg 1991). However, other factors may be also involved. In streams, for example, when predators are absent, small fish may prefer to forage in deeper pools because of the higher costs of foraging in faster flowing riffles (Schlosser 1987; Greenberg 1991).

Cost-benefit interpretations of habitat and microhabitat use are likely to be more accurate if they take into account both physiological and ecological factors. Fish show size-related differences in physiological requirements. The optimum temperature for juvenile fish tends to be higher than that of adults, which leads small fish to select microhabitats with higher temperatures close to their growth optima (Barans and Tubb 1973; Hokanson 1977). Microhabitat selection should also vary dynamically with daily fluctuations in ambient conditions, and diel temperature fluctuations at mean temperature below the physiological optimum lead to benefits such as faster growth and expanded thermal tolerance (Hokanson 1977). Variations in related environmental factors such as light and photoperiod can also influence fish growth (Huh et al. 1976). Thus, freshwater fish should seek microhabitats that offer faster growth and protection, but the balance between these priorities should vary with life-stage.

The rainbowfish *Melanotaenia duboulayi* (Castelnau), which is a diurnal freshwater fish, is known to prefer rela-

tively warm water exposed to sunlight (Merrick 1984; Leggett and Merrick 1987). It is an Australian native fish and common in vegetated natural streams in subtropical eastern Queensland (Arthington et al. 1983; Merrick 1984; Leggett and Merrick 1987; Pusey et al. 1993; Leggett 1995; McDowall 1996). Because of recent habitat modification and the translocation of predatory native fish (Barlow et al. 1987; Arthington 1991), the numbers of the rainbowfish greatly decrease (Pusey et al. 1993; Kennard, personal communication). Brown and Warburton (1997) conducted aquarium experiments and found that the interaction between habitat structure and predation pressure appears to have led to corresponding behavioral variation in rainbowfish. Furthermore, Brown and Warburton (1999) found that different populations of *M. duboulayi* vary in their response to predator threat in an aquarium. Little is known about the habitat use and anti-predator behavior, or even feeding behavior of rainbowfish in the wild.

To investigate the pattern of microhabitat use and feeding behavior of *M. duboulayi* in the wild, we conducted snorkel observations at a pool of a natural stream in subtropical regions of Queensland, where the upper reaches are surrounded by rainforests and lower reaches are wide and open. Although streams in Queensland were often muddy because of recent deforestation and development (Arthington et al. 1983; Pusey et al. 1993), we found a clear and well-vegetated pool that had different aquatic plant communities and variable exposure to sunlight. During the present study, we witnessed predatory behavior by the azure kingfisher, *Alcedo azurea*, directed at *M. duboulayi*. To examine the behavioral responses of rainbowfish to aerial attack, we also conducted a field experiment with aerial predator models. The overall aim of the present study was to understand better how microhabitat use and swim-

ming depths vary with body size, time of day, feeding opportunities and predator threat.

Materials and methods

Study site

Snorkel observations were conducted from August to December 1998 in a shallow pool of Amamoor Creek (26°20′S; 152°35′E), a branch of the Mary River, southeastern Queensland (see Pusey et al. 1993). We set out a 32-m transect line along the water channel of the pool and made a landscape map based on snorkel observations (Fig. 1). The study site was divided into four zones equally along the transect line (Fig. 1A–D). Water depth was measured every 1 m along the line. There was a significant difference in water depth between the four zones (Table 1, Kruskal-Wallis test; $H = 16.8$, $P = 0.0007$).

Water temperature

While snorkeling, we found distinct differences in water temperature between times of day. We measured temperatures of surface water (2 cm deep) and air to the nearest 0.1°C every 30 min from 0847 to 1717 hours on 29 October (a fine day), and the distribution of sunlight was also recorded. We also measured surface water temperature at a central site of each area, mid- and bottom water temperatures at a central site of area C and surface water temperature at the warmest site, where the water was stagnated (Fig. 1). On other days, surface water temperature was mea-

Fig. 1. Landscape map of the study site and the 32-m transect line along the stream. The *right* is the lower reaches. The study site was divided into four zones (*area A–D*) equally along the transect line. The *light shading* and the *striped area* are the ribbon weed (*Vallisneria*) and the watermilfoil (*Myriophyllum*) communities, respectively. The *darkest shading* and the *solid area* indicate emergent aquatic plants and a heap of fallen leaves on the shore, respectively. *R, W* and *N* mean submerged rock, wood and nest of a catfish (*Tandanus tandanus*), respectively. Four *contours* indicate 0.5 m, 0.9 m, 1.2 m and 1.4 m deep. Basking-like behavior was observed at the *asterisked site*, where the water was stagnated
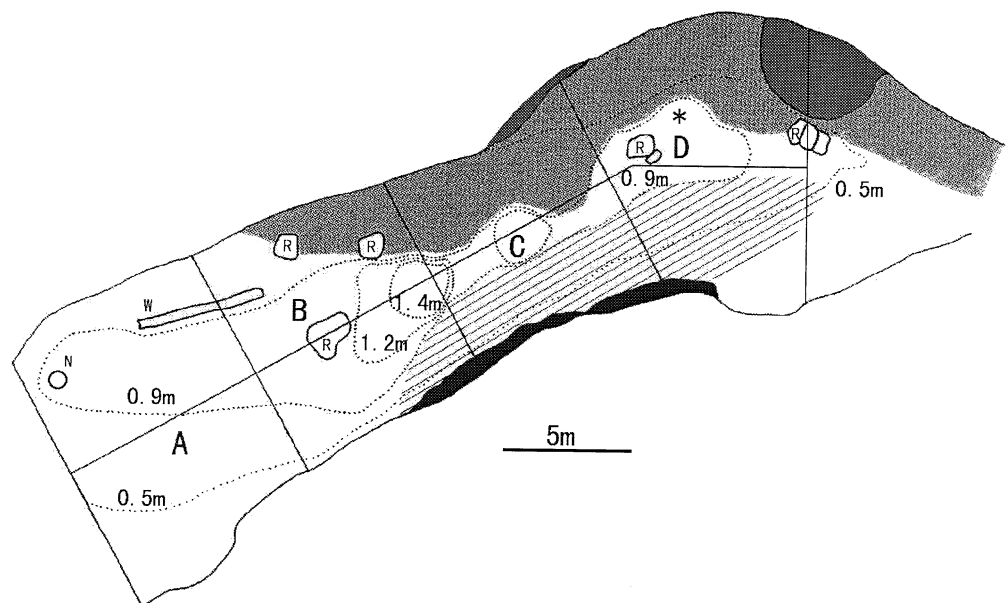
Table 1. Landscape features and surface-water temperature of areas A–D, and mid- and bottom-water temperature at area C. Temperature was measured on 29 October 1998. Standard deviations in parentheses

Features	Area A	Area B	Area C	Area D	Mid-water	Bottom-water
Time of sunlight (hours)	1200–1500	0930–1630	0900–1630	1000–1430		
Riparian vegetation type	Overhang	Normal	Normal	Normal		
Emergent vegetation cover	0	0	< 1/4	1/4		
Bottom vegetation cover	0	1/4	3/4	2/3		
Average water depth (cm, $n = 8$)	102.6 (12.3)	123.1 (14.8)	114.1 (6.6)	98.3 (9.1)		
Water temperature (°C)						
Morning (1015 hours)	20.0	20.0	20.0	20.0	19.8	19.1
Early afternoon (1340 hours)	21.0	21.0	21.0	21.4	20.8	20.7
Late afternoon (1640 hours)	21.5	21.5	21.5	21.5	21.4	21.4

sured at area C in the early afternoon when field observations were conducted.

Landscape features

Area A had overhanging riparian forest on the left bank and was the only site that was always shaded in the morning. All zones except a few spots in area A were exposed to sunlight in the early afternoon and all zones were shaded in the late afternoon. The bottom of area A was covered with sand and gravel and without aquatic vegetation. Area B had the deepest point (145 cm deep) and most of the bottom had no aquatic vegetation. The bottoms of the other areas were covered with submerged vegetation: a watermilfoil community (*Myriophyllum* sp.) on the right bank side and a ribbonweed community (*Vallisneria gigantea*) on the left bank side. In the channel in the middle, there was little vegetation. The watermilfoil was sparse (<0.6 stems/25 × 25 cm), usually reached the water surface, and overhung downstream. The ribbonweed was very dense (>25 stems/25 × 25 cm) and fully covered with epiphytic filamentous algae. Area C had the most developed submerged vegetation and was exposed to sunlight for the longest period during the day. The ribbonweed was submerged totally except in area D, where it reached the water surface in shallows less than 0.5 m deep (see Fig. 1). On the left bank side in area D, the water stagnated near the emergent vegetation. During the study period, we witnessed predatory fish species: mouth almighty *Glossamia aprion* (Richardson) ($n = 1$), spangled perch *Leiopotherapon unicolor* (Günther) ($n = 2$), long-finned eel *Anguilla reinhardtii* (Steindachner) ($n = 2$) and freshwater catfish *Tandanus tandanus* (Mitchell) ($n = 3$). Besides an individual of the catfish, which nested in area A (Fig. 1), all predatory fish were in or near (<50 cm) the dense ribbonweed.

Field observations on fish

We conducted field observations on fish from October to December 1998 (dry season). In this period, the stream was usually still (water velocity 0.04–0.05 m/sec) and clear (transparency >2 m). However, after rain, the stream always rose more than 0.5 m and became turbid: it was difficult to observe fish for several days. As a result, we were able to make field observations on 35 days (including one day under cloudy conditions). To describe habitat use by *M. duboulayi*, we carried out a census: an observer snorkeled slowly (32 m/30 min) using a stick without flippers upstream along the transect line searching for fish within a zone 1.5 m either side of the line (see Fig. 1). When an individual was seen, its size class was estimated by eye measurement [large (>55 mm standard length), medium (55–46 mm), small (45–36 mm) or juvenile (<36 mm)] as well as its position in the water column [surface (<0.2 m from the surface), bottom (<0.15 m from the bottom or the surface of dense submerged vegetation), or mid-water]. At the same time, the location and behavior of each individual was noted on the map. In August 1998, we caught 148 *M. duboulayi* by bait traps, measured their standard lengths (SL), sexed them by coloration and then released them. Based on the size distribution of *M. duboulayi*, we decided the four size classes (Fig. 2). *M. duboulayi* is sexually dimorphic: adult males are colorful with larger dorsal and anal fins pointed with black edges (Merrick 1984; Leggett and Merrick 1987).

We conducted two types of census. To record variation in microhabitat use under standard light conditions, we carried out 12 censuses in fine conditions on different days between 1230 and 1330 hours when almost all areas were exposed to sunlight. As fish seemed to escape from the observer in the first six censuses, we did not use the data for analysis. To examine how fish behavior changed with the time of day, we carried out another census on six different days at 1000–1100 hours (morning), 1330–1430 hours (early afternoon) and 1630–1700 hours (late afternoon). We avoided censusing before 1000 hours because of low water temperatures (<20°C) and after 1700 hours because of dim light conditions.

At three sites where *M. duboulayi* were always abundant, feeding behavior was observed over 5 min periods between 1230 and 1430 hours on fine days. Feeding behavior was rare and we could not follow individual fish, but the number of feeding bites (within the field of vision at a given site) during the 5-min observation period was recorded. We repeated the observation at least 3 times in a day and 54 times in total.
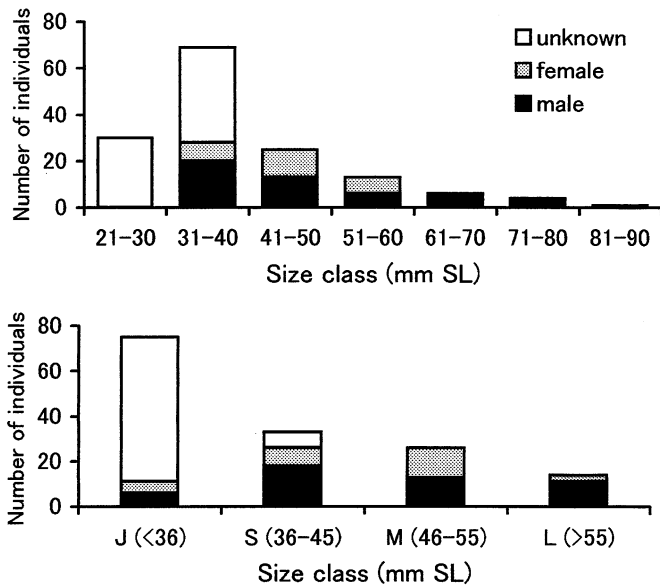
Fig. 2. Size distribution (mm in standard length) of 148 rainbowfish *Melanotaenia duboulay* caught, measured and released in the study site before the field observations were conducted. *J*, *S*, *M* and *L* were the size classes used in the present study, and mean juvenile (<36 mm SL), small (36–45), medium-sized (46–55) and large fish (>55), respectively

Fig. 3. Change of surface water temperature (2 cm deep) and air temperature at area B on a fine day

Field experiment

On 26 November (a fine day with some heavy clouds), we conducted a field experiment to record avoidance responses of *M. duboulayi* to an aerial predator, the azure kingfisher. In the deepest point in area B, fish were attracted to the surface with crushed cat food before the experiment. Like a fly fisher, one person flew the model (the stuffed azure kingfisher) that was connected to a gray plastic stick (1.5 m × 29 mm) a few centimeters above the water surface. An observer recorded fish behavior underwater. The stick without the model was used as a control. The experiment was repeated 5 times under cloudy conditions and then repeated under sunny conditions.

Results

Water temperature

The water temperature near the surface (2 cm deep) responded clearly to increases in morning air temperature in sunny conditions (Fig. 3). Temperatures at the bottom were slightly lower than those at the surface in the morning but not by the late afternoon (Table 1). In the early afternoon (1340 hours), but not at other times of day, there were some differences in water surface temperature between sites (Table 1), but these were minor (<0.5°C) compared to the range of temperature variation with water depth (<1°C) and time of day (>3°C). In the warmest site near the emergent vegetation (Fig. 1), where the water was stagnated, water surface temperature in the early afternoon was
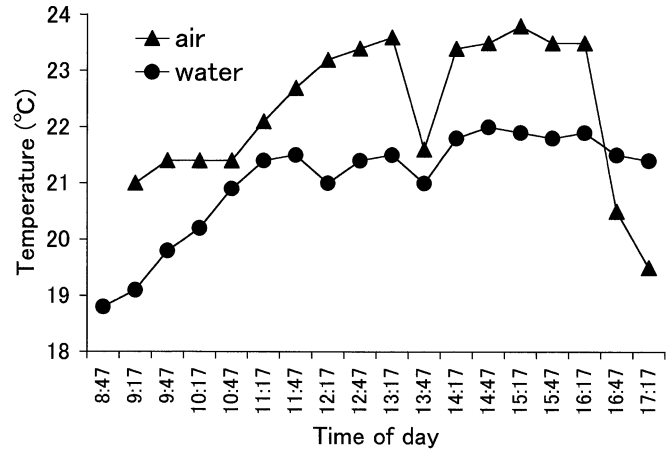
23.2°C. On sunny days, water surface temperature was 22.6°C on average (1.1 SD, $n = 27$); on one cloudy day it was 21°C ($n = 1$).

Distribution pattern in the early afternoon

M. duboulayi occurred in all areas. However, they were abundant in the vegetated zones (B–D): juveniles were especially abundant in area D (Table 2). There were significant differences among the four zones in terms of the numbers of individuals except large fish, but there were no significant differences among the dates of census (Table 2). Rainbowfish were often found in the sparse watermilfoil community, but never entered the dense ribbonweed community.

Juveniles and small fish were most abundant on the surface (Table 3), and they were often found as loose shoals. Large fish were most abundant on the bottom and never found on the surface (Table 3): they often showed courtship display at the bottom near the weed beds. For all size classes there were significant differences among the three depth strata in the numbers of individuals but not among the dates of census (Table 3). In the warmest site in area D (see Fig. 1), juveniles and small fish (>15 individuals) stayed motionlessly near the surface holding their head up without feeding. After the site was shaded, fish stayed for 10–20 min and then swam away. Large and medium-sized fish never showed such behavior.

Changes in distribution and behavior during the day

In the morning and late afternoon ($n = 6$), as well as in the early afternoon, there were significant differences among the four zones in terms of the numbers of juveniles and small fish (Freedman's test; $\chi^2 > 8.3$, $P < 0.04$ for all cases), but no significant differences among the dates of census (Freedman's test; $\chi^2 < 6.8$, $P > 0.05$ for all cases). Excluding the data of one cloudy day ($n = 5$), there were still

Table 2. Average number of individual rainbowfish *Melanotaenia duboulayi* in the early afternoon in areas A–D ($n = 6$). Standard deviations in parentheses

Size class	Area A	Area B	Area C	Area D	Friedman test			
					Areas A–D		Date of census	
					χ^2	P	χ^2	P
Juvenile	4.5 (1.71)	16.0 (2.87)	17.6 (3.15)	25.3 (4.26)	11.0	0.011	2.0	>0.05
Small	3.0 (1.34)	14.8 (4.06)	7.3 (1.70)	17.1 (1.35)	16.1	0.001	8.8	>0.05
Medium	0.8 (0.43)	6.3 (0.77)	4.8 (1.36)	8.0 (1.82)	13.3	0.003	3.7	>0.05
Large	0.2 (0.23)	2.0 (0.62)	1.5 (0.69)	1.5 (0.47)	7.7	>0.05	1.2	>0.05

Table 3. Average number of individuals at different depths in the early afternoon ($n = 6$). Standard deviations in parentheses

Size class	Depth			Friedman test			
	Surface	Mid-water	Bottom	Depth		Date of census	
				χ^2	P	χ^2	P
Juvenile	60.3 (7.29)	4.7 (2.36)	0.2 (0.33)	12.0	0.002	6.2	>0.05
Small	32.0 (7.52)	9.7 (8.11)	0.8 (0.60)	11.5	0.003	3.1	>0.05
Medium	5.7 (2.56)	9.0 (2.26)	5.3 (1.65)	6.3	0.004	2.8	>0.05
Large	0	1.8 (1.18)	4.0 (1.43)	9.6	0.008	4.2	>0.05

Table 4. Average number of juvenile and small fish at different depths in areas A–D at different times of sunny day ($n = 5$). Standard deviations in parentheses

Size class	Time of day	Area A		Area B		Area C		Area D	
		Surface	Other depths	Surface	Other depths	Surface	Other depths	Surface	Other depths
Juvenile	Morning	6.2 (4.1)	1.8 (1.4)	8.4 (5.1)	5.2 (3.7)	12.6 (6.8)	3.0 (3.7)	14.0 (4.5)	5.6 (5.8)
	Early afternoon	6.6 (4.7)	1.0 (0.7)	13.0 (9.3)	0.4 (0.5)	20.0 (9.3)	1.2 (1.6)	29.8 (7.1)	1.4 (1.1)
	Late afternoon	9.6 (4.4)	0.8 (0.8)	8.4 (7.7)	3.6 (3.0)	11.4 (6.8)	6.0 (4.5)	19.8 (7.0)	6.8 (3.6)
Small	Morning	0.6 (0.8)	3.0 (2.3)	0.6 (0.8)	6.8 (2.1)	1.8 (1.4)	6.2 (4.6)	6.4 (3.5)	7.4 (6.3)
	Early afternoon	0.4 (0.5)	3.0 (0.7)	3.6 (4.5)	6.0 (2.4)	5.2 (1.6)	6.0 (5.0)	13.0 (4.4)	5.0 (3.5)
	Late afternoon	0.4 (0.8)	1.6 (0.8)	0.4 (0.8)	8.4 (1.9)	1.2 (0.8)	9.0 (1.4)	4.6 (3.7)	6.2 (2.6)

significant differences among the four zones in the numbers of juveniles and small fish at each time of day (Freedman's test; $\chi^2 > 8.1$, $P < 0.04$ for all cases), but no significant differences among the dates of census (Freedman's test; $\chi^2 < 5.6$, $P > 0.05$ for all cases): they were abundant in the vegetated zones (B–D, Table 4).

The vertical distribution pattern did not change greatly in a day ($n = 6$, Fig. 4a–c). On sunny days ($n = 5$), however, juveniles were abundant near the surface, especially in the early afternoon in area D (Table 4): in terms of the average numbers of juveniles, interaction between times of day and depth strata was statistically significant only in area D (two-way factorial ANOVA; $F = 9.6$, $P = 0.0008$ for area D; $F < 3.2$, $P > 0.05$ for areas A–C), where there was a significant difference among all time-depth categories (one-way factorial ANOVA; $F = 19.5$, $P < 0.0001$). In area D, the average number of juveniles near the surface in the early afternoon was significantly different from that of juveniles in all other time-depth categories (Fisher's Protected LSD; $P < 0.006$ in all possible combinations), and that of juveniles near the surface in the late afternoon was also significantly different from that of juveniles in all other time-depth categories

except for that of juveniles near the surface in the morning (Fisher's Protected LSD; $P < 0.006$ in all possible combinations except the last one). In other zones, there were significant differences between depth strata (two-way factorial ANOVA; $F > 10.8$, $P < 0.003$ for areas A–C), but never between times of day in the average numbers of juveniles (two-way factorial ANOVA; $F < 0.54$, $P > 0.05$ for areas A–C). On sunny days ($n = 5$), small fish were also abundant near the surface in the early afternoon in area D (Table 4). In terms of the average numbers of small fish, interaction between times of day and depth strata was also significant only in area D (two-way factorial ANOVA; $F = 4.0$, $P = 0.03$ for area D; $F < 3.2$, $P > 0.05$ for areas A–C), where there was a significant difference among all time-depth categories (one-way factorial ANOVA; $F = 2.6$, $P = 0.048$). In area D, the average number of small fish near the surface in the early afternoon was significantly different from that of small fish in all other time-depth categories (Fisher's Protected LSD; $P < 0.04$ in all possible combinations), but there were no significant differences among other categories (Fisher's Protected LSD; $P > 0.05$). In other zones, there were significant differences in the average numbers of small fish
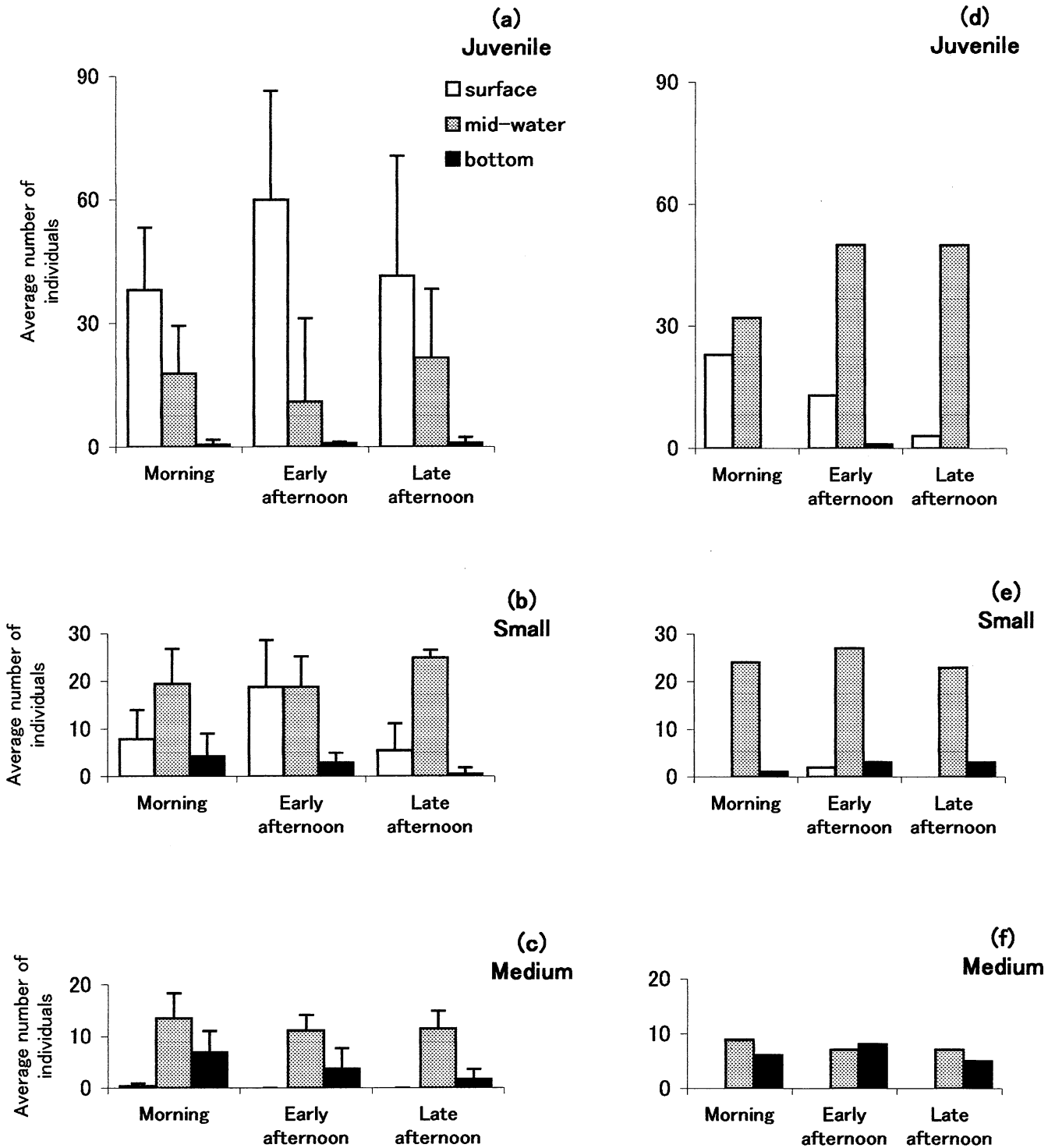
Fig. 4. Vertical distribution pattern of juvenile, small and medium-sized rainbowfish at different depths at different times of day. Mean numbers of individuals observed in six censuses at each time of day are shown with a 95% *error bar* for each size category. Numbers of fish observed on a cloudy day are also shown for each size category

between depth strata (two-way factorial ANOVA; $F > 15.4$, $P < 0.006$ for areas A–C), but never between times of day (two-way factorial ANOVA; $F < 1.31$, $P > 0.05$ for areas A–C). On the cloudy day ($n = 1$), most juveniles and small fish swam in mid-water throughout the day, even in the early afternoon (Fig. 4d, e).

Feeding behavior

We distinguished three types of foods: (1) floating material on the surface, (2) suspended material underwater, and (3) attached material on the bottom (filamentous algae or debris). Juveniles and small fish usually fed on floating

Table 5. Average number of feeding bites for three different materials during a 5-min observation period ($n = 54$). Standard deviations in parentheses

Size class	Food object			Kruskal Wallis test		Mann-Whitney U-test	
	Floating	Suspended	Attached	H	P	Z	P
Juvenile	5.44 (4.88)	0.02 (0.14)	0			−8.81	<0.00001
Small	1.33 (2.04)	0.15 (0.40)	0.02 (0.13)	48.2	<0.00001		
Medium	0.44 (0.72)	0.20 (0.49)	0.48 (1.11)	3.9	0.14		
Large	0	0	0				

material, while medium-sized fish took all types of food (Table 5). Several juveniles and small fish that swam in mid-water moved to the surface to feed. On the cloudy day, juveniles and small fish swam in mid-water, as mentioned above, but they were observed to surface to feed. Large fish never showed feeding behavior during the 5-min observation periods, though at other times we witnessed their feeding on attached material at the bottom.

Experiments on avoidance of aerial predators

Many individuals (>40), including large and medium-sized fish, gathered around food when it was placed on the surface of the water ($n = 20$). Under cloudy conditions, they showed no response to the stick with or without the kingfisher ($n = 5$ trials in each case). In sunny conditions, however, all fish showed an avoidance response to both treatments ($n = 5$ trials in each case), quickly swimming down about 10–20 cm. They all escaped from the surface waters, not only in response to the movement of the stuffed azure kingfisher, but also in response to the stick without the bird model.

Discussion

Although *M. duboulayi* were distributed throughout the pool, they tended to occur in vegetated areas that offered food and protection, as noted by Merrick (1984) and Leggett and Merrick (1987). Because of their high food densities, flow-buffering capacity and protective function, macrophyte beds tend to support relatively a high abundance and diversity of riverine fish species (West and King 1996). However, the present study revealed that macrophyte beds can differ widely in terms of their use by stream fish. *M. duboulayi* discriminated between dense *Vallisneria* and sparse *Myriophyllum*, preferring the latter possibly because fish predators were associated with the former. Small shoals of juveniles and small fish were often seen at the study site, but the dense *Vallisneria* may have hampered feeding and contact between shoal mates. In vegetated habitats, both predator and prey fish species appear to modify their behaviors in which predators improve prey capture success and prey fish minimize predation risk (Savino and

Stein 1989). A detailed assessment of the influence of plant density and growth form on the dynamics of prey fish and predators requires further study.

Juveniles and small fish of *M. duboulayi* were most abundant in area D, which was similar to area C in terms of vegetative cover, but somewhat shallower and warmer in the early afternoon. While the overall results indicated that *M. duboulayi* confirm the general predictions of the size-depth hypothesis, the data from area D are of particular interest because they showed how other factors can modify the size-depth relationship.

Rainbowfish usually inhabit still water exposed to sunlight (Arthington et al. 1983; Merrick 1984; Leggett and Merrick 1987), and at the present study site the water was still enough for the sun to warm it during the morning. The density of juveniles and small fish near the surface in the early afternoon was highest in area D, where several juveniles and small fish stayed motionless at the surface without feeding at the warmest location. Furthermore, they stayed motionless at the surface for up to 20 min after it was shaded. In the present study period, they might have exhibited behavioral thermoregulation in the warmest site, reacting to changing temperature rather than sunlight. Large fish never showed such behavior. Since the advantages associated with feeding and warmer temperatures are greater for small juveniles than for adults, behavioral strategies of the two life-stages are likely to differ. For example, juveniles fed more than adults, probably because growth is a major priority. Hokanson (1977) reported that rapid growth is aided by diel fluctuations in temperature. On the other hand, adult priorities are likely to emphasize survival for reproduction (e.g., by hiding in weed beds near the bottom) rather than feeding and growth. During our censuses, large fish never showed feeding behavior, but they often showed courtship display at the bottom near the weed beds.

In streams running through forest, fish are often dependent on allochthonous (terrestrial) food such as plant debris and aerial insects (Lowe-McConnell 1987; Pusey et al. 1995a, b; Nakano et al. 1999). In the present study, juveniles and small fish usually fed on floating material at the surface, and some of them moved to the surface to feed even when swimming in mid-water under both sunny and cloudy conditions. Medium-sized fish occasionally fed on floating material, but large fish never showed feeding at surface water. Results of our underwater observations suggest that smaller individuals are more dependent on terrestrial foods in rainbowfish.

Since larger rainbowfish are more visible and energetically more valuable, they may be targeted preferentially by avian predators such as a kingfisher. Actually, pied kingfishers *Ceryle rudis* choose larger prey individuals, so that the movement of larger fish into deeper water may aid fish survival by increasing latency to capture and other costs to the predator (Labinger et al. 1991). Smaller fish may be more willing to risk feeding at the surface, where they are vulnerable to avian predators. In fact, juveniles and small fish fed at the surface on sunny days, but they did so in shoals. Our field experiment using a stuffed kingfisher suggests that rainbowfish swimming in the surface respond to a moving object in sunny conditions, but do not in cloudy conditions. This implies that in sunlit conditions juveniles and small fish swimming in the surface can escape from an aerial predator responding to a moving shadow or the flight images. On one cloudy day, juveniles and small fish swam in mid-water. However, we do not have enough data to elucidate the reasons for their habitat use in cloudy conditions: they might have used mid-water habitat because of few foods on the water surface. Further work is required to clarify the effects of avian predators on microhabitat use by rainbowfish especially in cloudy conditions.

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