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Effect of competitor abundance on feeding territoriality in a grazing fish, the ayu *Plecoglossus altivelis*

KEI'ICHIROH IGUCHI[1] AND TERUAKI HINO[2]

[1]*National Research Institute of Fisheries Science, Ueda Station, Komaki 1088, Ueda, Nagano 316, Japan and* [2]*Forestry and Forestry Products Research Institute, Kansai Research Center, Momoyama, Fushimi, Kyoto 612, Japan*

The grazing fish, ayu, *Plecoglossus altivelis* Temminck & Schlegel, establishes feeding territoriality during the young stage. The population density fluctuates from year to year by more than a hundredfold, but the determinant of territory size is less well known. The feeding territoriality of ayu was examined under simulated habitat conditions where fish density was manipulated and food resources were renewable. Fish competed for algae attached to the substrata and were divided into residents with territories, and floaters without territories. By experimental alteration of fish density the number of residents increased with density and territory size decreased with density. Floaters intruded into territories in a school to feed on algae, which induced overt aggression of the resident and reduced the productivity of algae growing there. Both the intruding frequency of floaters over territorial areas and their feeding pressure on algae increased at higher floater density. Floaters functioned to shift cost–benefit relationships for various territory sizes. They acted as food competitors to restrict territory size below a maximum through competitive interference. Although the growth rate of residents was inversely related to fish density, residents grew faster than floaters in each group. Under a given set of competitor abundances, economic defensibility determined territory size.

Key words: economic defensibility; energy maximizer; indeterminate growth; resource renewability.

INTRODUCTION

Food supply is fundamentally important because of energetic and nutritional requirements for maintenance, growth and reproduction (Davies 1978). Based on Brown's (1964) concept of economic defensibility, the adaptive significance of feeding territory is generally addressed within the context of costs and benefits associated with resource defence (Myers *et al.* 1979; Eberhard & Evald 1994). The dichotomy of time minimizer and energy maximizer introduced by Schoener (1968, 1971) has often been used to develop models describing how these costs and benefits vary with territory size. This distinction may define the spectrum of optimum foraging strategies (Hixon 1980). For example, time minimizers defend areas that contain a food supply adequate to their short-term energy requirements (Kodric-Brown & Brown 1978; Hart 1985). In contrast, territories of energy maximizers can be constrained below some maximum through competitive interference for increased food supply rather than direct assessment of food supply (Norton *et al.* 1982; Tricas 1989).

The 'food-maintenance' hypothesis for time minimizers predicts that territory size is adjusted as an inverse function of local food abundance, whereas the 'competitor-mediated' hypothesis for energy maximizers predicts that territory size is adjusted as an inverse function of competitor abundance (Tricas 1989). However, it must be recognized that food supply and the intensity of competition are interacting factors, and both will ultimately affect the fitness of individuals (Rubenstein 1981). Thus the independent effects of food and competitor are difficult to assess in natural systems. This paper examines the feeding territoriality of a grazing fish, formed under simulated habitat conditions.

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The ayu, *Plecoglossus altivelis* Temminck & Schlegel, is an amphidromous fish that feeds on periphyton (McDowall 1992), reproducing semelparously with an annual life span (Azuma 1964). The young establish territories and defend algae attached to the riverbed against those without territories (Kawanabe 1957). Although the population density fluctuates from year to year by more than a hundredfold (Kawanabe 1970), the determinant of territory size is less well known. We investigated spacing pattern, aggressive interaction among individuals, feeding and growth of ayu released into experimental ponds at different densities. Our study was aimed to test the competitor-mediated hypothesis of territory size.

METHODS

Fish

Young ayu about 6 months old were collected from Lake Biwa, Japan, in May 1991. Mean body size was 4.1 g (SD = 1.4, n = 50) and 71.0 mm (SD = 7.0, n = 50) standard length. Fish, until used in experiments, were stocked in an outdoor pond (1 m × 5 m × 0.5 m deep) at the National Research Institute of Fisheries Science, Ueda Station. They were fed assorted food (Kagaku Shiryo Kenkyusya Co. Ltd, Maebashi, Japan) three times per day. Based on knowledge of fish culturists in Japan, stock density was kept at more than 100 fish m^{-2} to diminish aggressive interactions between individuals.

Experimental conditions

Five identical outdoor concrete ponds (Ponds A, B, C, D and E; 2 m × 5 m × 0.3–0.5 m deep with sloped bed) were used for experiments. Water current generated by an electric pump made two types of habitat (Fig. 1), an upper shallow area with swift clockwise flow (Rapid Zone) and a lower deep area with slow anticlockwise flow (Pool Zone). Input of groundwater kept water temperature at 20–23 °C.

Algae grew freely on the pond beds, providing a renewable food for ayu. Before releasing fish, algae showed logistic growth in biomass on all six sample sites chosen at random in Pond E during July. The biomass of algae peaked 8 days after colonization then decreased. Maximum ash-free dry weight of algae at peaking was used as an index of potential food supply (Nishimura & Ando 1991). The maximum algal biomass expected from every 0.4 m × 0.4 m quadrat varied from 6.94 to 16.94 g m^{-2}, which was within the range measured in natural habitat of ayu (Furuta *et al.* 1977). On average, the Rapid Zone supplied 11.32 g m^{-2} algae at maximum, while the Pool Zone supplied 7.94 g m^{-2}.

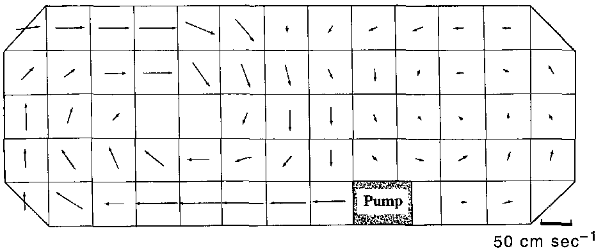

Fig. 1. Distribution of water flow in the experimental ponds. Arrows indicate direction and intensity of current.

Experimental observations

We conducted two successive experiments. The first experiment was carried out during July, except in Pond E (August), to compare the spacing pattern between groups held at different fish densities. Groups started with 3, 6, 10, 15 and 50 fish for Ponds A, B, C, D and E, respectively. These densities were within a range observed for the wild population of ayu (Kawanabe 1970). The second experiment was carried out during August to evaluate individual response to altering fish density. Individuals with territories were defined as residents and those without territories were defined as floaters. Seven and four fish were added into Ponds A and B, respectively (group size = 10). Additional fish were close to the mean body size of original members. In Pond C, two residents and four floaters were accidentally killed during removal and two new fish were introduced (group size = 6). From Pond D, three residents and six floaters were removed (group size = 6). Body weight at the start of experiments averaged 16.3 g (SD = 2.2, n = 34) in July and 25.4 g (SD = 5.6, n = 82) in August. Daily growth in body weight was expressed as specific growth rate (Busacker *et al.* 1990).

Individuals were identified by thin colored ribbon tags about 2 mm wide, sewn through the dorsal muscle. Observation of fish behavior was conducted during midday hours each day with few exceptions. Observers watched fish from 2 m high platforms at both ends of the ponds without disturbing the fish. Each fish was observed for 2 min sample periods during which position at 10 s intervals, aggressive interactions, and feeding were located with the use of 0.2 m × 0.2 m grids. However, the record at Pond E was restricted to those fish which initiated aggression because of the large number of fish. Chase (or approach), butting and circling aggression were counted as aggressive behaviour (Tachihara & Kimura 1988). A sequence of chase (or approach) and butting was regarded as a single event. Territory was marked by 0.2 m × 0.2 m grids within which a resident attacked the others. When two or more residents dominated within a 0.2 m × 0.2 m quadrat, the boundary of territories was determined proportionally by the frequency of attacks shown by each resident. Customary space of a home range, where a resident spent much time, was defined as 'core area'. Core area included the sum of quadrats containing more than 50% of all position points marked by 10 s interval observations.

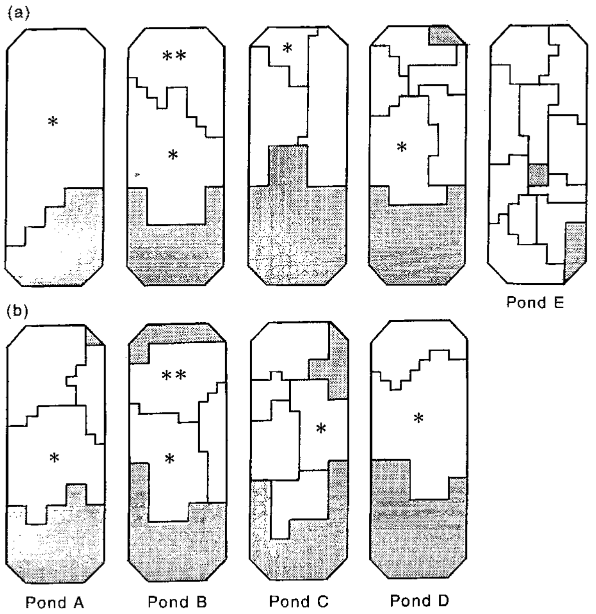

Fig. 2. (a) Distribution of territorial areas (first experiment). Fish densities are 3, 6, 10, 15 and 50 for ponds A, B, C, D and E, respectively. (b) Changes in territorial area after the alteration of fish density (second experiment). Fish densities are 10, 10, 6 and 6 for ponds A, B, C and D, respectively. Shadowed areas show space not defended. Territorial areas with asterisks are defended by the same resident in both experiments.

RESULTS

Spacing pattern and aggressive interactions

Spacing pattern varied with fish density (Fig. 2a). Initial body weights of residents averaged 17.9 g (SD = 2.0, n = 11) in July (Ponds A, B, C and D) and 28.1 g (SD = 3.5, n = 10) in August (Pond E), while those of floaters were 15.4 g (SD = 1.9, n = 23) and 22.0 g (SD = 4.2, n = 40), respectively. Relatively large individuals became residents and others behaved as floaters (Mann-Whitney U-test, $Z = 2.80$, $P < 0.01$ for July; $Z = 3.64$, $P < 0.01$ for August). Territories were established through physical contest within 4 days after introducing fish, and were spatially fixed throughout the experimental periods. Most residents held territories within the Rapid Zone. The numbers (proportion) of residents in Ponds A, B, C, D and E were 1 (33%, n = 3), 2 (33%, n = 6), 3 (30%, n = 10), 5 (33%, n = 15) and 10 (20%, n = 50), respectively. Addition and removal of fish changed the territory configuration (Fig. 2b). When fish were added to Pond A, two new territories were established and the original resident reduced the territory size by half (7.04 to 3.52 m^2). In Pond B, one new territory was established, and the two original residents reduced territory size from 4.20 to 2.68 m^2 and 3.00 to 2.44 m^2. In Pond C, four new territories were established. The original resident shifted its territory and expanded the size from 0.92 to 1.68 m^2. In Pond D, territories were reduced from five to two. One original resident expanded its territory size from 2.56 to 4.52 m^2, while the other lost the territory. The proportion of residents after altering fish density was 33% (n = 10), 33% (n = 10), 83% (n = 6) and 33% (n = 6) in Ponds A, B, C and D, respectively. On the whole, there was a positive relationship between the number of residents and the fish density (Kendall's $\tau = 0.722$, $n = 9$, $P < 0.01$).

Territory size ranged from 0.48 m^2 in Pond E in August to 7.04 m^2 in Pond A in July (mean = 1.82 m^2, SD = 1.39, $n = 34$; Fig. 3).

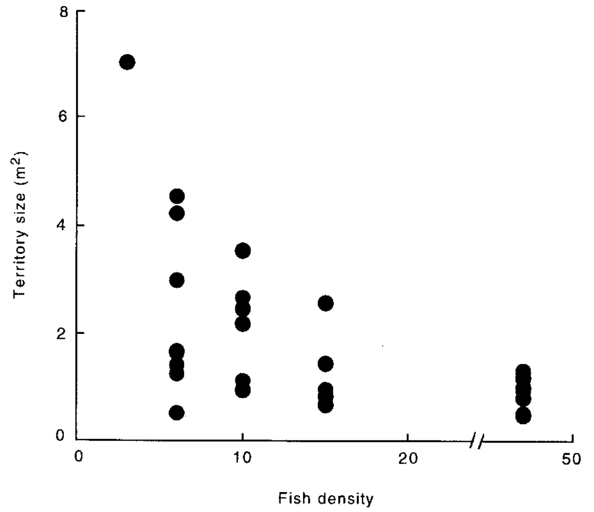

Fig. 3. Relationship between fish density and territory size.

There was an inverse correlation between fish density and the mean territory size of the fish group ($\tau = -0.722$, $n = 9$, $P < 0.01$). On average, the core area made up 30.8% of territory, and the ratio decreased with increase in territory size ($\tau = -0.458$, $n = 34$, $P < 0.01$; Fig. 4). The predicted maximum algal biomass was 10.81 g m^{-2} (SD = 1.80, $n = 34$) in the core area, while it was 10.80 g m^{-2} (SD = 1.87, $n = 34$) in the rest of the territory, showing that core area was not characterized by more food (Wilcoxon's signed rank sum test, $Z = 0.171$, NS).

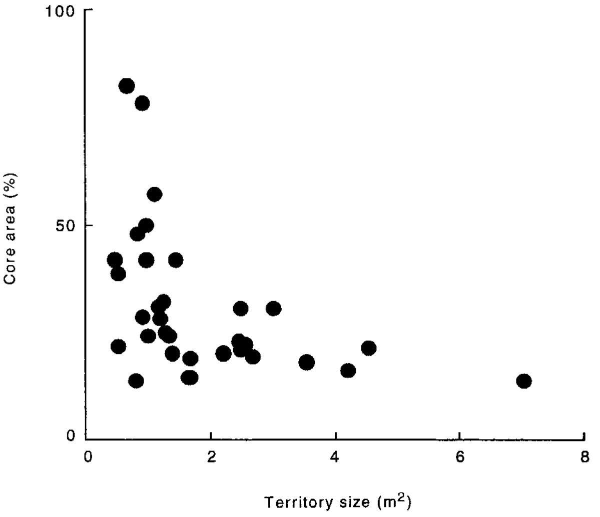

Fig. 4. Relationship between territory size and percentage of core area to the whole territorial area.

Floaters roamed over the pond in a school. Whenever they intruded into territories, residents became overtly aggressive. The intruding frequency of floaters over territorial areas varied among groups from 0.02 fish m^{-2} in Pond C in August to 1.30 fish m^{-2} in Pond D in July (mean = 0.59 fish m^{-2}, SD = 0.44, $n = 8$), which increased with the number of floaters ($\tau = 1.00$, $n = 8$, $P < 0.01$). Except in Pond C in August in which there were more residents, most of the residents attacked floaters more often than other residents, when compared to encounters expected at random (Table 1).

Residents attacked 1.6 times min^{-1} (SD = 0.9, $n = 34$). There was no significant correlation between territory size and the attack frequency ($\tau = 0.130$, $n = 34$, NS). Although the intensity of aggression differed between individuals or groups, each resident kept the attack frequency practically

Table 1 Attack frequency by a resident against floaters and other residents.

	Floaters: other residents		
	Observed	Expected	*G* value
Pond A (August)	21 : 24	112.8 : 32.2	2.87
	59 : 7	51.3 : 14.7	6.11*
	71 : 9	62.2 : 17.8	6.51*
Pond B (July)	72 : 22	75.2 : 18.8	0.65
	47 : 8	44.0 : 11.0	1.11
Pond B (August)	137 : 33	132.2 : 37.8	0.81
	63 : 15	60.7 : 17.3	0.41
	66 : 8	57.6 : 16.4	6.49*
Pond C (July)	18 : 2	15.6 : 4.4	2.00
	54 : 6	46.7 : 13.3	6.13*
	9 : 6	11.7 : 3.3	2.45
Pond C (August)	5 : 15	5.0 : 15.0	0.00
	1 : 32	6.6 : 25.4	11.01**
	1 : 16	3.4 : 13.6	2.75
	4 : 20	4.8 : 19.2	0.18
	3 : 25	5.6 : 22.4	1.75
Pond D (July)	84 : 45	92.1 : 36.9	2.31
	21 : 2	16.4 : 6.6	5.61*
	22 : 4	18.6 : 7.4	2.47
	45 : 2	33.6 : 13.4	18.63**
	78 : 11	63.6 : 25.4	13.43**
Pond D (August)	136 : 17	122.4 : 30.6	8.67**
	57 : 13	56.0 : 14.0	0.09

The observed and expected number of attacks were compared (expected number was calculated from random encounter). The difference between the observed and expected was analyzed by *G*-test.

Difference is significant at $^{*}P < 0.01$ and $^{**}P < 0.05$.

stable after the change in territory size through the alteration of fish density (Fig. 5). Floaters also fought with each other 0.2 times min^{-1} (SD = 0.2, $n = 42$), which was much lower than the attack frequency shown by residents (*U*-test, $Z = 7.06$, $P < 0.01$).

Foraging and growth

Residents foraged within their territories and took algae at 5.5 times min^{-1} (SD = 2.2, $n = 34$). There was no significant correlation between territory size and the feeding frequency of residents ($\tau = -0.116$, $n = 34$, NS). Algae within a territory was harvested by the resident 4.6 times $\text{min}^{-1}\ \text{m}^{-2}$ (SD = 3.3, $n = 34$), which was reduced with an increase in territory size ($\tau = -0.686$, $n = 34$, $P < 0.01$).

The foraging site of floaters extended over the pond involving territorial areas. Floaters took algae 5.4 times min^{-1} (SD = 2.2, $n = 42$), similar to residents (*U*-test, $Z = 0.167$, NS). The feeding pressure of floaters on algae growing in territories varied among groups from 0 times $\text{min}^{-1}\ \text{m}^{-2}$ in Pond C in August to 9.6 times $\text{min}^{-1}\ \text{m}^{-2}$ in Pond D in July (mean = 3.4 times $\text{min}^{-1}\ \text{m}^{-2}$, SD = 3.1, $n = 8$), which increased with the number of floaters ($\tau = 0.857$, $n = 8$, $P < 0.01$).

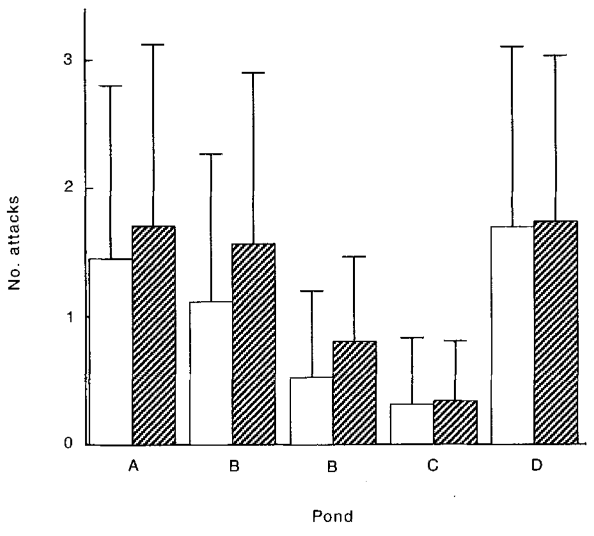

Fig. 5. Mean number of attacks (±SD) per minute observed for individuals in ponds A, B (× 2), C and D (☐) before and (▨) after the alteration of fish density. The numbers of observation times before and after the alteration of fish density are 23 and 25, respectively.

Although growth rate of fish varied between groups (Table 2), residents grew faster than floaters in each group (Wilcoxon's test, $T = 2$, $P < 0.01$). To determine explanatory variables for the growth rate of residents among the six possible variables shown in Table 3, multiple regression analysis was conducted (stepwise, $F_{in} = F_{out} = 2$). As a result, the maximum algal biomass in the core area (partial $r = 0.435$) and fish density (partial $r = -0.606$) were factored out to account for variation in growth rate among residents ($R^2 = 0.817$, $F_{2,31} = 31.19$, $P < 0.01$).

DISCUSSION

Territory size of ayu varied between individuals and changed within an individual. Fish in the first and the second experiments were allowed simultaneous and sequential settlements, respectively. Van den Assen (1967) proposed that more individuals settle when they arrive simultaneously than when they arrive sequentially. However, our data do not support his findings nor those in a study of a territorial lizard (Stamps 1992). The number of residents and their territory size are thought to be controlled by the fish density itself. An inverse function between territory size and fish density in ayu supports the competitor-mediated hypothesis of territory size, and indicates that food competitors restrict territory size below a maximum (Tricas 1989). However, the question of how territory size is determined under a given set of competitor abundances still remains.

Larger individuals acquired their territory through physical contest. This is probably due to individual differences in fighting ability correlating with body size (Beeching 1992). Aggressive behavior generally incurs costs in terms of time, energy and injuries (Blanckenhorn 1992). Injury risk is of immediate importance to an individual's fitness for animals with escalated fights (Alvarez 1993). Ayu risk higher injury because they rarely develop non-contact displays but resort to head-on butting during fighting (Iguchi 1991), suggesting that the fewer fights the better. Less interferences between neighboring residents, as is described for the wild population of ayu (Mizuno & Kawanabe 1957), are favorable to them for decreasing injury risk. However, residents have no choice but to fight against

Table 2 Mean specific growth rate (±SD, × 100) measured for residents and floaters in different fish densities

	July		August	
	Residents	Floaters	Residents	Floaters
Pond A	2.00 (1)	1.90 (2)	1.82±0.39 (3)	1.20±0.58 (7)
Pond B	2.79 (2)	2.06±0.21 (4)	1.54±0.18 (3)	1.32±0.50 (7)
Pond C	2.53±0.03 (3)	2.07±0.19 (7)	1.38±0.21 (5)	1.12 (1)
Pond D	1.81±0.38 (5)	1.60±0.40 (10)	1.39 (2)	1.50±0.61 (4)
Pond E			0.54±0.36 (10)	0.06±0.26 (40)

Figures in parentheses show sample sizes.

Table 3 Matrix of simple correlation coefficients among variables used for multiple regression analysis

	(1)	(2)	(3)	(4)	(5)	(6)
Growth rate	0.492*	0.689*	0.273	- 0.273	- 0.704*	- 0.768*
(1) Algal biomass[a] (g)		0.715*	0.140	0.230	- 0.473*	- 0.499*
(2) Algal biomass[b] (g)			0.307	- 0.023	- 0.638*	- 0.610*
(3) Feeding frequency (min^{-1})				- 0.063	- 0.101	- 0.059
(4) Attack frequency (min^{-1})					0.510	0.361*
(5) Attacked frequency (min^{-1})						- 0.768*
(6) Fish density						

[a]Maximum algal biomass in the whole territorial area. [b]Maximum algal biomass in core area. *Correlation is significant at $P < 0.05$.

intruding floaters, as they require food. Thus, the defence costs of residents expended per unit territorial area is positively related to the number of floaters.

Feeding frequency of residents was independent of territory size. Furthermore, floaters could feed as frequently as residents, although they had to utilize both territorial and non-territorial area (Pool Zone) where algal productivity was low. Feeding hierarchies within a limited space like a pond are not always essential for improved feeding opportunity if food resources occur continuously rather than discretely (McCarthy *et al.* 1992). Otherwise, the renewability of resources brings about the advantage of territory defense for ayu. Moderate harvest promotes the productivity of algae because of the logistic function of algal growth. Over-exploitation by the territorial owner itself may suppress the long-term yield of algae. In this sense, larger territories are better. Scramble consumption of algae will reduce their productivity or at worst eliminate them. However, perfect exclusion is improbable against those which invade simultaneously in a school, although it is necessary for residents to ensure sustainable yield. Thus, the taking of algae by floaters is inevitable to a certain extent, so the benefits of residents per unit territorial area are related inversely to the number of floaters.

The reproductive output of ayu correlates directly with body size (Iguchi & Yamaguchi 1994). Indeterminate growth provides no fixed goals for body size. Increased body size relative to other fish confers higher fitness. Territories observed in our experiments are actually profitable because residents can grow larger than floaters. In general, the costs of defending territory increase with territory size due to the increasing number of intruders (Davies & Houston 1984). In contrast, the benefits of occupying the area increase with size at first, but eventually reach an asymptote when resources become superabundant in relation to the animal's ability to utilize them. The relationship between costs and benefits for various territory sizes has two thresholds at which benefits equal costs. Between the two thresholds, net benefit exists and thereby territory defense is economical. Increase in floaters moves the benefit curve downward and the cost curve upward, and consequently the thresholds will decrease. The inverse function between territory size and fish density fits this prediction, indicating that economic defensibility prescribes the territory size of ayu under a given set of competitor abundance. Interestingly, attack frequencies remained nearly stable at the individual level after the change in territory size through the alteration of fish density. It is likely that each resident adjusts territory accordingly to its fighting ability, and a permissible amount of defensive effort is used as a proximate determinant of territory size (i.e. cost differs among individuals).

Ayu residents, particularly those with large territories, depended upon a core area or part of a territory rather than the whole territorial area. The role of the core area brings up a problem that surplus resources, if any, also require defense costs but bring no extra benefits to the owner. The function of less utilized space within a territory can be of three kinds which are not mutually exclusive; (i) insurance, (ii) energetic efficiency, and (iii) spite. First, environmental factors such as water quality, water temperature or current velocity affect the productivity of algae (Fukami *et al.* 1994). Residents should defend as large a territory as possible providing against unpredictable changes in environments. Resources in excess of daily assimilation will act as insurance in case algal biomass suddenly declines. The evaluation of territory size would be revised according to the time-scale over which benefits and costs are measured (Davies & Houston 1984). Second, stream fish often position themselves at fixed stations (focal points) in low velocity current yet near high velocity current (Moyle & Baltz 1985). Fausch (1984) demonstrated that juvenile salmonids select positions with focal points to achieve a positive net energy balance. These positions minimize energy expenditure for swimming and facilitate access to drifting food. Algae grow better in higher current (Tanimizu *et al.* 1981). One can propose that the preference of ayu for positions like focal points in patchy environments will make territory size large in appearance for residents with more than one profitable point. Third, an individual can increase its fitness not only by improving its own performance but by also inhibiting the performance of others (Verner 1977). Even in the presence of unutilized resources, relatively superior growth of spiteful residents is attained by preventing floaters from accessing the resources. Although theoretical studies restrict the evolution of spite, it may be possible where population size is small and the defense costs of excess resources are low (Hamilton 1970; Knowlton & Parker 1979; Parker & Knowlton 1980). A defended area that contains more resources than needed may correspond to a 'superterritory'. As Hasegawa and Tanemura (1986) suggested the evolution of spite in ayu, it may be said that optimizing to maximize net energy gain is not always the only determinant of feeding territory size. Our study does not support the classical view that ayu adheres to a territory of approximately 1 m^2 (Kawanabe 1972). Ayu is also faithful to costs and benefits of holding territory, and accordingly changes territory size.

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