Historical effect in the territoriality of Ayu fish

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Keywords: fish behavior, territory formation, territory breakdown, historical effect, phase transition

Abstract

Ayu fish form algae-feeding territories in a river during a non-breeding (growing) season. We build a cost-benefit theory to describe the breakdown and formation of territory. In the early stage of a growing season, all fish hold territories at low densities. Once all territory sites are occupied, excess fish become floaters. When fish density further increases, a phase transition occurs: all the territories suddenly break down and fish form a school. In contrast, when the fish density is decreased, territories are suddenly formed from the school. Both theory and experiments demonstrate that ayu should exhibit a historical effect: the breakdown and formation processes of territory are largely different. In particular, the theory in formation process predicts a specific fish behavior: an "attempted territory holder" that tries to have a small territory emerges just before the formation of territory.

1. Introduction

Animals have evolved various behavioral strategies as an adaptation for different ecological circumstances (Krebs and Davies 1987). Territoriality and group foraging are the two different ways of adaptation (Foster 1985). Territorial behavior is a life history adaptation in the solitary state of animals (Brown and Orians 1970; Ebersole 1977; Davies and Houston 1984), while group foraging is an adaptation by forming a group (Schaller 1972; Robertson et al. 1976). In many species, mating pairs often form a breeding territory, while they forage in group during non-breeding seasons, e.g., most of migratory birds. However, it is rather rare to see a transition between territoriality and group foraging in a single (non-breeding) season.

Whether territory formation is adaptive or not can be answered by usual the cost-benefit analysis comparing the individuals with/without a territory, within a solitary state (Krebs 1971). Group foraging is also compared with solitary foraging in a species with some group foraging (Pulliam and Caraco 1984; Clark and Mangel 1986). These two different evolutionary adaptations may occur in a closely related species, e.g., fishes (Foster 1985). However, it should be extremely rare to find both territorial foraging and group foraging in a single species. The cost-benefit analyses of these behavioral strategies can provide a single framework to view the adaptive evolution of individual behavior (Stephens and Krebs 1986). We here provide such a unique case study of a fish exhibiting both territorial behavior and group foraging (school) as adaptive responses during a growing season (May to July).

Ayu (*Plecoglossus altivelis*, Osmeridae) is an endemic migratory fish in Japan (Kawanabe 1969; Miyadi 1960; Takahashi and Azuma 2006). This fish has a unique life history (Kawanabe 1969; Miyadi 1960; Iguchi 1996). Its life cycle is completed by one year. Eggs that are spawned in the downstream of a river hatch in autumn. The hatched larvae drift to a sea and feed mostly zooplankton in coastal zones. In spring, the juvenile fish migrate to the midstream (and/or upstream) of a river, where algae (diatoms) grow on the rocks of the riverbeds in rapids (swift current). Many young fish form a territory in this stage (Fig. 1). They feed on these algae from spring to fall. In fall, when ayu fish matures, they swim downstream all together. They spawn eggs and die soon afterwards. Thus, ayu is a diadromous fish, but it is strictly anadromous (Iguchi 1996).

In the midstream of a river, rapids and pools usually locate in turn (Mizuno and Kawanabe, 1981). In the early stages of a growing season (May), the feeding territory is formed in the rapids, where diatoms grow on the surfaces of rocks (Biggs and Hickey 1994; Biggs et al. 1998). In contrast, (deep) pools, without algae, are not suitable for ayu that can only feed on small amounts of drifted algae and insects. The amount of algae growing in one territory is several times more than the necessary amounts for one fish to grow to maturity (Iguchi and Abe 2002; Gill and Wolf 1975). During the growing season, many fish swim into a river and the fish density increases daily. Those that cannot hold a territory become a floater. A floater, usually staying in a pool, cannot feed well. It sometimes intrudes into a territory in the rapids and steals algae while intruding. In order to defend its own territory, the territory holder attacks a floater violently (Fig. 1). The unique “tomo-dsuri” fishing exploits such violent attacks: fishermen use a live decoy as an intruder to catch the territory holder. When the fish number in the midstream increases, all fish form a school. In contrast, when the fish number decreases, the state of fish conversely changes from school to territory. In the present paper, we estimate the fitness (Gross 1982; 1985; Tainaka et al. 2007; Tanaka et al. 2009) of an individual fish, and report a historical effect by the comparison between breakdown and formation processes of territories.

2. Model

An individual fish takes one of three strategies: territorial holder (Th), floater (Fl) and school (Sc). The optimal strategies for the energy (food) gain of an individual fish depend not only on total fish density but also on the time difference of density. We expect the breakdown and formation of a territory as illustrated in Fig. 2. First, we deal with the case that the overall density (N) increases. From the previous studies (Kawanabe 1969; Iguchi 1996; Kawanabe 1958, 1970, 1973), we assume the following three phases:

i) Th-phase

At low density, all fish can hold territories in the rapids and some territories are not occupied (Kawanabe 1973). When the density of fish increases, all incoming fish can hold a new territory in a vacant site, until all the territory sites are occupied ($N \leq N_{T\max}$). Here $N_{T\max}$ is the maximal number (density) of territories.

ii) Coexisting phase: (Th+Fl)-phase

When the population size exceeds the territory capacity ($N > N_{T\max}$), newcomers cannot hold territories. These fish become a floater staying in the pool. Hence, we suspect that a floater is not an available option, but a forced action. Each territory holder defends own territory against intruders (floaters).

iii) Sc-phase

Due to more newcomers, the number of floaters increases. Since territory intrusions by floaters become frequent, territory holders have to spend much more time in defending their own territory. They lose the time to feed on algae. When the density of fish exceeds a critical density (N_1), all the territories suddenly break down (Kawanabe 1958, 1970, 1973). For $N > N_1$, all fish form a school at once (Fig. 2).

In summary, in the increasing stage of density, the fish behavior changes as Th$\rightarrow$(Th+Fl)$\rightarrow$Sc. The total density (N) is represented by

$$\begin{cases} N = N_T & (N \le N_{T\max}) \\ N = N_T + N_F & (N_{T\max} < N \le N_1) \\ N = N_S & (N_1 < N) \end{cases} \qquad (1)$$

where N_T, N_F and N_S denote the densities of territorial holder, floater and school, respectively.

At the high density, all fish form a school. However, even when the fish density decreases less than the breakdown point N_1, territories cannot be observed. The fish schools should persist up to a very low density, until every fish can hold a territory at once. This is because the territory formation is very hard. When $N < N_1$, a fish has two options: either to attempt to make a territory or remain in a school. We call the former 'attempted territory holders' (Th*). Even if one fish attempts to hold a territory, other remaining fish become intruders. The defense against school fish is very hard, while the defense against a solitary intruder is highly effective (Iguchi 1996; Tachihara and Kimura 1992).

However, if the density becomes lower below a critical value ($N < N_2$), then territory holders can emerge at once. The formation point of territory (N_2) can be estimated by the timing when all fish can hold a territory, or when no fish are necessarily forced to be a floater. When $N < N_2$, all fish become territory holders. The formation point N_2 is much less than the breakdown point N_1, and it should be almost equal to the maximum density $N_{T\max}$ of territory. In the decreasing stage, the fish behaviors change as Sc → Th. The density of each strategy is given by

$$N = \begin{cases} N_S & N > N_2 \\ N_T & N \le N_2 \end{cases} \qquad (2)$$

There is no forced option to be a floater in the decreasing stage (Fig. 2). The attempted territory holder (Th*) can emerge for $N_1 > N > N_2$.

3. Theory

3-1. Cost-benefit theory in an increasing stage

We estimate the fitness of an individual fish for three strategies: territorial holder (Th), floater (Fl) and school (Sc). The fitness is composed of both cost and benefit, where the cost is defined by a defense cost to protect a territory, and the benefit is assumed to be the food amount each fish can eat.

When the overall density *N* is increased, the choice changes according to the following three phases:

i) Th-phase ($N \le N_{T\max}$)

When all fish have territories, the fitness of a territory holder (W_T) takes the maximum value. Let K_r be the algal food amount in the rapids, then W_T can be expressed as

$$W_T = K_r / N_{T\max} = W_{T\max} = \text{const.} \qquad (3)$$

ii) Coexisting phase ($N_{T\max} < N \le N_1$)

The territory holder bumps its body against the intruding floater repeatedly until the floater leaves its territory. Let τ_f and τ_d be the dimensionless ratios of the feeding and defense time durations of a territory holder, respectively ($\tau_f + \tau_d = 1$) (Brown 1964; Pyke 1979). The fitness of a territory holder W_T can be expressed as

$$W_T = (K_r / N_{T\max})\tau_f - c_{dF}\tau_d \qquad (4)$$

where c_{dF} is the defense cost of a fish against a floater. For simplicity, we assume τ_d is a linear function of floater density:

$$\tau_d = aN_F \qquad (5)$$

where a is a constant. Equation (5) comes from the experimental data as listed in Table 1. We find from this table that the attack frequency increases as the floater number increases.

Next, we evaluate the fitness W_F of a floater. Since the floater is the forced option, W_F is always smaller than W_T. The floater fitness is not important to determine the optimal strategy. Note the profile of W_F has the following properties: (i) if the density (N_F) of floaters is low, W_F is nearly constant. (ii) On the contrary, if N_F is high, W_F may be represented by K_p / N_F, where K_p is the food amount in the pools.

iii) Sc-phase $(N > N_1)$

Now, we evaluate the fitness W_S of a school fish for Sc-phase. Since the school fish feeds both in the rapids and pools, the fitness of a school fish is given by

$$W_S = (rK_r + K_p) / N \qquad (6)$$

where r is the feeding rate of school fish in rapids relative to a territory holder ($r < 1$). In Fig. 3, both W_F and W_T are depicted against the total density N. The breakdown point N_1 of territoriality can be determined by

$$W_S = W_T \qquad (7)$$

In the above model, to guarantee the cross point at N_1, we assume that $K_r > rK_r + K_p$. The optimal strategy is territory holder ($W_T \geq W_S$) for $N \leq N_1$, while school fish is optimal ($W_S > W_T$) for $N > N_1$ (Fig. 3).

3-2. Cost-benefit theory in a decreasing stage

At high density, the fitness W_S of school fish is same as that in the increasing stage [see Eq. (6)]. With decreasing fish density ($N < N_1$), the fitness W_S becomes smaller than W_T. Here a fish has two options: either to attempt to make a new territory or remain in a school. We specifically consider the fitness of an attempted territory holder

(W_T*). Note that there is an essential difference between increasing and decreasing stages: in the increasing stage, the intruders are floaters, while in the decreasing stage the intruders are school fish. Hence, the defense time ratio τ_d is proportional to the density of school fish.

$$\tau_d = aN_S \tag{8}$$

The fitness W_T* of an attempted territory holder can be expressed as

$$W_T* = (K_r / N_{T\max})\tau_f - c_{dS}\tau_d \tag{9}$$

where c_{dS} is the defense cost of a fish against school fish. Note that the defense cost against school fish is much larger than that of floaters, such that $c_{dS} >> c_{dF}$. This difference is very important. Below the critical density ($N < N_2$), all school fish should switch to the territory option; we have the critical point (N_2) of territory formation by

$$W_T* = W_S \tag{10}$$

When all fish can hold a territory, they become territory holder. Their fitness jumps up to the maximum value $W_{T\max}$.

3-3. Numerical estimations

We insert the empirical data into the model to estimate the expected dynamics and transition points numerically. Since an ayu fish forms a territory of ca. 1 [m^2] (Miyadi 1960; Kawanabe 1973), we set that $N_{T\max}$ = 1 [/m^2 rapids]. (We consider the fitness based on 1 m^2 rapids in a midstream of a river.) In a typical Japanese river, the midstream consists of about 55% of rapids and about 45% of pools (Kawanabe 1973). This means that 1 m^2 rapids are associated with 0.81 [m^2 pools]. The defense time (τ_d) and feeding time (τ_f) are estimated from empirical studies (Kawanabe 1969, Kawanabe 1970) as follows. Let n_f and n_d be the times (numbers: [/min]) of feeding and defense (attack), respectively, per one territory holder. The maximum number of defense in a minute is 15 times, whereas that of feeding is 30 times. Therefore, we get $\tau_d = n_d/15$ and $\tau_f = n_f/30 = 1 - n_d/15$, since $\tau_d + \tau_f = 1$. Because the times of defense (attack) n_d, increases with the number of floaters, we assume that $n_d = aN_F$. From low density ($N_F \leq 1$) experiments in pools, the attack rate is estimated that a = 1.8~6.3, on average, ca. 3.4 (Table 1). Therefore, we set a = 3.0.

The algal food amount in the rapids, K_r, is estimated 3.3 [g /day/ (m^2 rapids)] for a 20cm long fish (11 Kcal equivalent) (Kawanabe 1969). Since the defense cost c_{dF}

against a floater is estimated between 0.01 ~ 0.2 (Iguchi and Hino 1996), we set c_{dF} = 0.1. Numerically, we derive that $W_T = K_r - (K_r + c_{dF})(a/15)(N-1)$ Next, we estimate the amount of food available in pools, K_p. The average diatom dry weight for rapids and pools are 6.25 and 0.42 [g/m^2] (Miyadi 1960). Therefore, numerically, we get $K_p = [(0.42 \cdot 0.81)/6.25)]K_r = 0.054K_r$.

Now we estimate the fitness of a school fish, W_S. The relative feeding rate of fish is estimated that $r = 0.4$ from the relative sizes of territory holders and school fish (Kawanabe 1969). Therefore, we get $W_S = 0.454K_r$ (if $N \leq 1$) or $0.454K_r/N$ (if $N > 1$). Finally, we estimate the fitness W_T* of an attempted territory holder. We estimate the defense cost against school fish, $c_{dS} = 10$ (Iguchi 1996). Therefore, the defense time of an attempted territory holder is $T_d^* = (a/15)(N-1)$. Then we derive numerically that $W_T^* = K_r - (K_r + c_{dS})(a/15)(N-1)$.

4. Analysis and Results

We compare the theory with empirical data which were obtained previously. First we deal with the case that the fish density increases. The fitnesses of ayu fish against the population density are plotted in Fig. 3. When the density exceeds $N_{T\max}$, floaters emerge in the pool. Above the breakdown point ($N > N_1$), territory holders should give up the territory and switch to schooling. The breakdown point is given by N_1=5.486 [fish/m^2] in the current model.

Table 2 shows the sensitivity of the attack rates and the defense cost against floaters for their observed ranges and selected values. These results indicate that the defense costs against floaters (c_{dF}) have almost no effects on the outcomes. On the other hand, the attack rates have much more profound effects on the optimal switching points from 2 to 8 individuals. As our best estimate, we here keep the optimal switching point for a = 3 and c_{dF} = 0.1.

Table 3 shows the observation data of fish state in increasing fish density. From Table 3, territoriality is maintained for N <4.1 [fish/m^2] and schooling is seen for N >5.5 [fish/m^2]. These data mean $4.1 < N_1 < 5.5$, which are consistent with the theoretical estimation (N_1=5.486). We should also note that the estimated breakdown point is fairly robust in the estimated range of defense cost c_{dS} (=5~15).

Next, we deal with the case that the fish density decreases. At a high density, all fish form a school ($N > N_1$). In Fig. 4, the fitnesses in decreasing process are depicted against the density N. When the density decreases below N_1, a school fish attempts to have a territory. The fitness of territory holders (W_T) is not available for an attempted territory holder. Even if $N < N_1$, the fitness of attempted territory holder (W_T*) may be smaller than that of school fish (W_S). However, when $N < N_2$ ($W_T* > W_S$), all school fish should switch to the territory option.

The observation data of fish state in decreasing process are listed in Table 4. When $N > 25.0$, all fish form school. In contrast, when $N < 1.5$, all have territories. In the intermediate case, the fitness W_S is lower than W_T, but larger than W_T* ($W_T > W_S > W_T*$). Thus, few school fish attempt to have their territories, but they cannot have stable territories. The data N =5.0 in Table 4 just indicate the emergence of attempted territory holders (Th*). In this case, the territories are small and unstable and a floater never emerges. This observation agrees with the theoretical prediction at $N_2 < N < N_1$. When the density further decreases at or below N_2, then every fish can hold a territory. Hence, the fish switch to territoriality to keep a higher fitness. The critical value may be close to $N_{T\max}$. Although $N_{T\max}$ is unity for natural river, it takes a value larger than unity in experimental (rich food) condition.

5. Discussion and Conclusion

We apply a fitness theory (Gross 1982; Tainaka et al. 2007; Tanaka et al. 2009) to obtain both cost and benefit for three behavioral strategies: territory holder (Th), floater (Fl), and school fish (Sc). The empirical data (see Tables 1 and 3) show the behavior of ayu fish changes depending on its density. When the density (N) increases, the fish state changes as Th$\rightarrow$(Th+Fl)$\rightarrow$Sc (see Fig. 2 a$\rightarrow$b$\rightarrow$c). In contrast, in the decreasing process of N, the phase changes as Sc$\rightarrow$Th (Fig. 2 c$\rightarrow$a). The different phase transitions between increasing and decreasing processes denotes the historical effect (hysteresis). The breakdown point (N_1) of territory should be larger than the formation point (N_2). This is because each fish easily forms the territory in increasing stage, but the territory formation is very hard against school fish in decreasing stage. The value N_1 is determined by $W_T = W_S$ [see Eq. (7)], while N_2 is determined by $W_T{*} = W_S$ [see Eq. (10)].

Our results show the unique properties of ayu decisions along with the increase (decrease) in density. When the density increases, the decision maker is not a floater, but a territory holder (Th). When $W_T = W_S$, then the Th fish gives up the territoriality. In contrast, when the density decreases, a school fish is a decision maker: when $W_T{*} = W_S$, then the Sc fish gives up schooling. In both processes, the floater is not an option but a forced option. No fish wants to be a floater (loser)! Such a difference of transition points causes the emergence of attempted territory holder (Th*) in the decreasing process of fish density. Even if a fish tries to hold a territory (Th*), school fish ignore and swim over the territory and feed algae freely (Iguchi 1996; Tachihara and Kimura 1992). The fitness of Sc is much smaller than that of Th, but is larger than that of Th*. This is because Th* defends against school fish, while Th defends against scattered/sporadic floaters. Note that the defense against school fish is known to be very hard (Iguchi 1996; Tachihara and Kimura 1992).

The historical effect (hysteresis) is well known in physics, such as ice-water transition and magnetism. However, biological hysteresis was rare (Caraco 1980; Ronce and Kirkpatrick 2001). Caraco (1980) dealt with dynamics of avian flocks foraging in two patches, and reported the animal hysteresis. When a population size increases, the incoming birds continue to join a single crowded feeding ground, until choosing a vacant risky site becomes better than joining the already crowded patch. When the population size decreases with birds leaving the feeding grounds, the number of birds in both grounds becomes much less than the optimal flock size. The dynamics of flock sizes are shifted from the optimal flock size (a single transition point) when flock sizes are increasing or decreasing (Caraco 1980). The territoriality in ayu is another case of animal hysteresis. We show the different phase transitions as illustrated in Fig. 2. Moreover, we report a distinct property never seen in other hysteresis systems. Namely, we can see the historical effect in fish behaviors. In the decreasing process of the population size N, attempt territory holders (Th*) often appear instead of floaters.

The empirical data in increasing stage (Table 3) indicate that the breakdown point (N_1) of territoriality can be represented by $4.1 < N_1 < 5.5$. This result is consistent with the theoretical estimation (N_1=5.486). On the other hand, empirical data in decreasing stage (Table 4) suggest that $1.5 < N_2 < 5.0$. This slightly differs from our prediction ($N_2 \approx 1$). The discrepancy may come from the estimation of parameters. In particular, the number of fish which intrudes into the territory of Th* may be overestimated [see Eq. (8)]. Our model is an extremely simple cost benefit model, so that other important factors are not included, e.g., individual variations in fish traits (Katano and Iguchi 1996), interference by other fish species (Katano et al. 2000), the quality and size variations of the territories (Iguchi and Hino 1996), and the time scale of increasing/decreasing fish densities. The reproduction (regeneration) of algae after feeding may be also important, because the rate of regeneration is different between territorial feedings and school foraging (Katano et al. 2000).

Acknowledgments

We thank Fugo Takasu and Hiroya Kawanabe for valuable comments. This work was partly supported by grants-in-aids from the Ministry of Education, Culture, Sports, Science and Technology of Japan to J. Y. and to K. T.

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Tables

Table 1. The attack frequency of a territory holder against an intruder at low density in experimental running-water pools of 2 × 5 square meter in 1991 in Japan (Iguchi 1996).

TF	NT	NF	F/T	Territory size [m^2]	Attack frequency [1/min]	Attack frequency [1/min/holder]
3	2	1	0.5	3.68	2.12	4.24
				2.00	3.14	6.28
6	5	1	0.2	0.32	0.55	2.75
				0.96	0.35	1.75
				0.80	0.74	3.70
				0.40	0.60	3.00
				0.56	0.40	2.00

Entries are: TF: total fish; NT: number of territory holders; NF: floater number; F/T: the ratio of floater per a territory holder. The average attack frequency/min/holder is 3.39 times. Estimation of attack frequency is based on the 5 minutes observation of every fish per day. Attack includes against both floaters and other territory holders.

Table 2. The switching point from territory holders (T) to school (S) in relation to the attack rates (*a*) and the defense cost against floaters (c_{dF}). The unit is the number of individuals /unit area.

Defense cost against floaters	Attack cost 1.8	3	6.3
0.01	8.8	5.6	3.0
0.1	8.6	5.4	3.0
0.2	8.4	5.3	2.9

Table 3. The existence of territoriality against an increasing fish density.

Year	River or Pond	Natural or experiment	Density N [1/m^2 rapids]	State of fish	Reference
1955	Ukawa	Natural	5.5	School	[1]
1956	Ukawa	Natural	0.9	Territory	[1]
1957	Ukawa	Natural	0.3	Territory	[1]
1958	Inukai	Experiment	4.1	Territory	[1]
1987	Pond	Experiment	195.2	School	[2]
1987	Pond	Experiment	97.6	School	[2]
1989	Pond	Experiment	120.4	School	[2]
1989	Pond	Experiment	25.0	School	[2]
1991	Experimental stream		1.0	Territory	[3]
1991	Experimental stream		0.6	Territory	[3]
1999	Pond	Experiment	1250.0	School	[4]
1999	Pond	Experiment	400.0	School	[4]
1999	Pond	Experiment	100.0	School	[4]

References [1] Kawanabe 1969, [2] Iguchi and Yamaguchi 1994, [3] Iguchi 1996, and [4] Iguchi et al. 2003.

Table 4. The state of fish in an decreasing stage.

Year	River or pond	Natural or experiment	Density [1/m^{2}rapids]	State offish	Reference
1958	Inukai	Experiment	1.5	Territory	[1]
1958	Inukai	Experiment	0.5	Territory	[1]
1987	Pond	Experiment	195.2	School	[2]
1987	Pond	Experiment	97.6	School	[2]
1989	Pond	Experiment	120.4	School	[2]
1989	Pond	Experiment	25.0	School	[2]
1991	Experimental stream		5.0	School(Th*)	[3]
1991	Experimental stream		1.5	Territory	[3]
1991	Experimental stream		1.0	Territory	[3]
1991	Experimental stream		0.6	Territory	[3]
1991	Experimental stream		0.3	Territory	[3]

Th*: Attempted territory holders appear; their territories are small and unstable.

References [1] Kawanabe 1969, [2] Iguchi and Yamaguchi 1994, and [3] Iguchi 1996.

Figure Captions

Fig. 1. The territoriality in ayu. (a) Two fish check with each other at the boundary of both territories. (b) A territory holder (behind) attacks against an intruder.

Fig. 2. The breakdown and formation models of territoriality. When the fish density increases, phases (stages) change as a $\rightarrow$ b $\rightarrow$ c. Stage a: when the density is low, all fish hold a territory. Stage b: when the density increases, some fish become a floater. Stage c: when the density further increases, all the territories break down and fish swim in schools. When the fish density decreases, the change c $\rightarrow$ a occurs: when the density decreases to a low density, all the fish begin to form a territory almost simultaneously.

Fig. 3. The theoretical result with increasing of fish density. The fitnesses of a territory holder (W_T, red), a floater (W_F, blue) and a school fish (W_S, green) are depicted against the density (N). The maximum density (capacity) of territory is assumed $N_{T\max}$=1, and the transition (breakdown) point is given by N_1=5.486. The unit for fitness is

(gram diatom food)/[day(1m^2 rapids+0.81m^2 pools)]. The parameter settings are: a=3, c = 0.1, K_r=3.3, K_p=0.1782 and r=0.4.

Fig. 4. The result in decreasing stage. The fitnesses of an attempted territory holder (W_T*, solid purple line) and a school fish (W_S, solid green curve) are plotted against the density (N). For the comparison, the fitness of a territory holder (W_T, broken red line) is shown. The transition (formation) point is represented by N_2 which is much less than the breakdown point (N_1). The parameter settings are the same as in Fig. 3.

Fig. 1

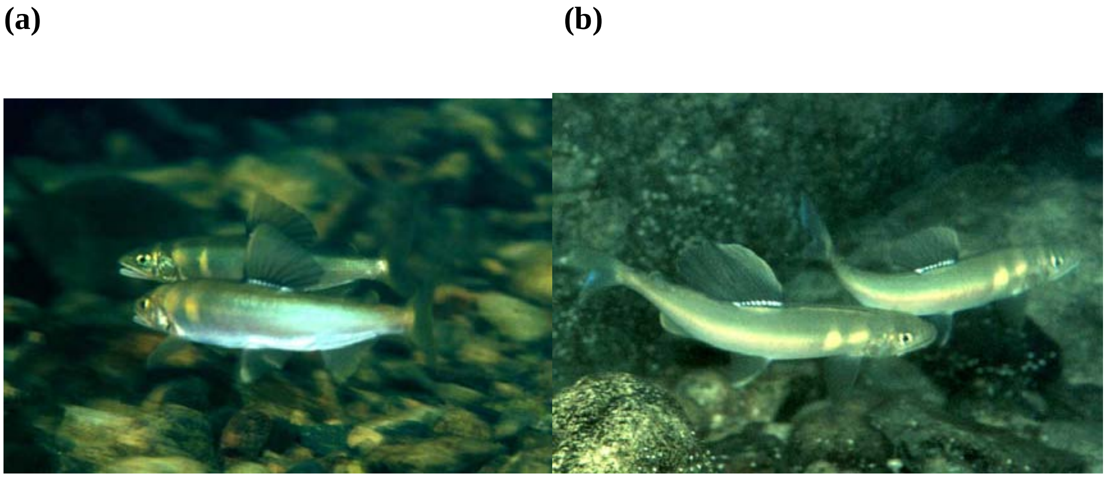


Fig. 2

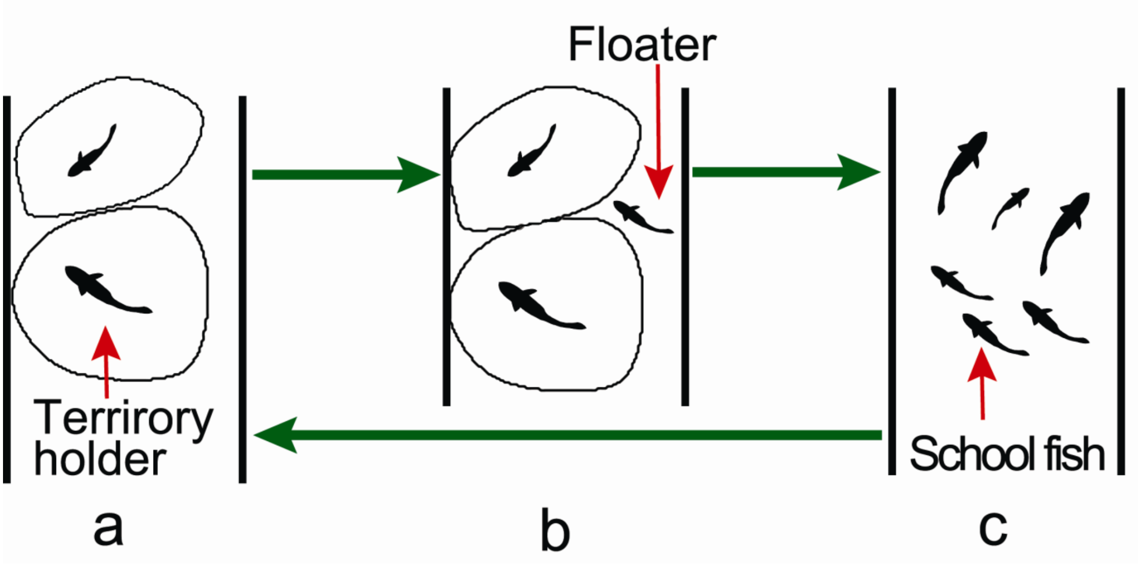


Fig. 3

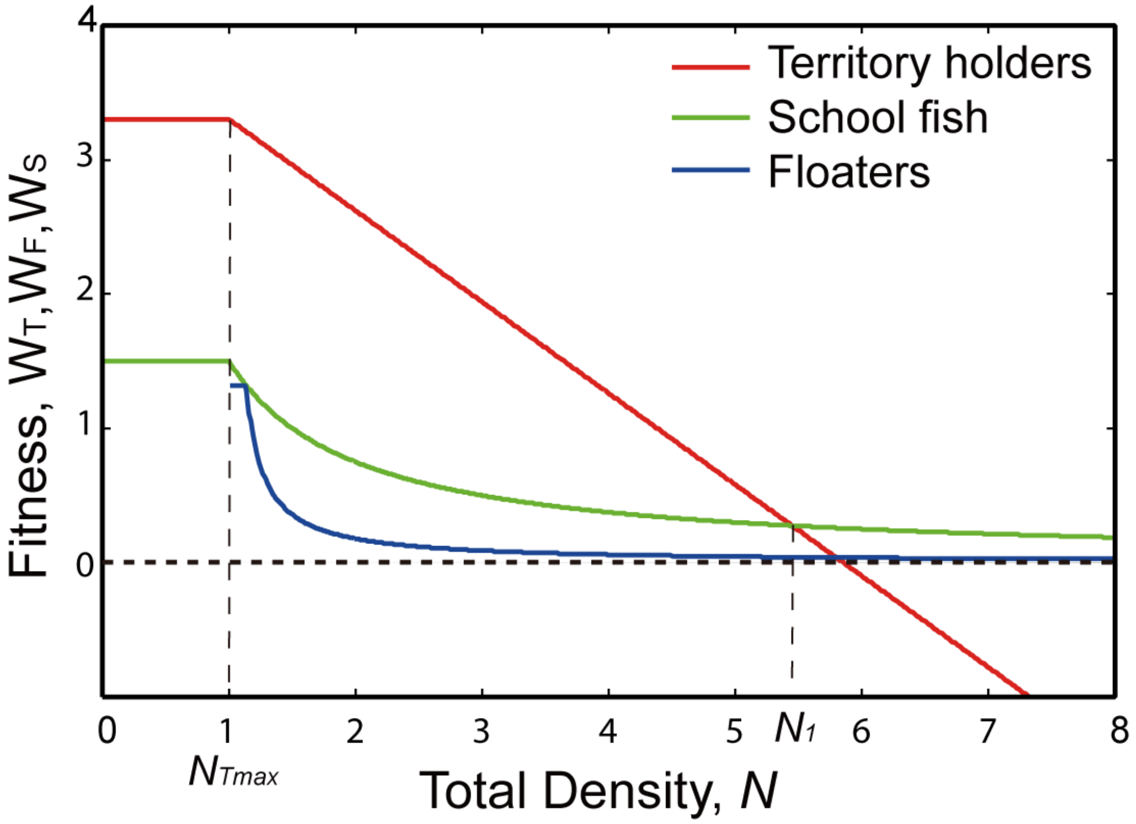
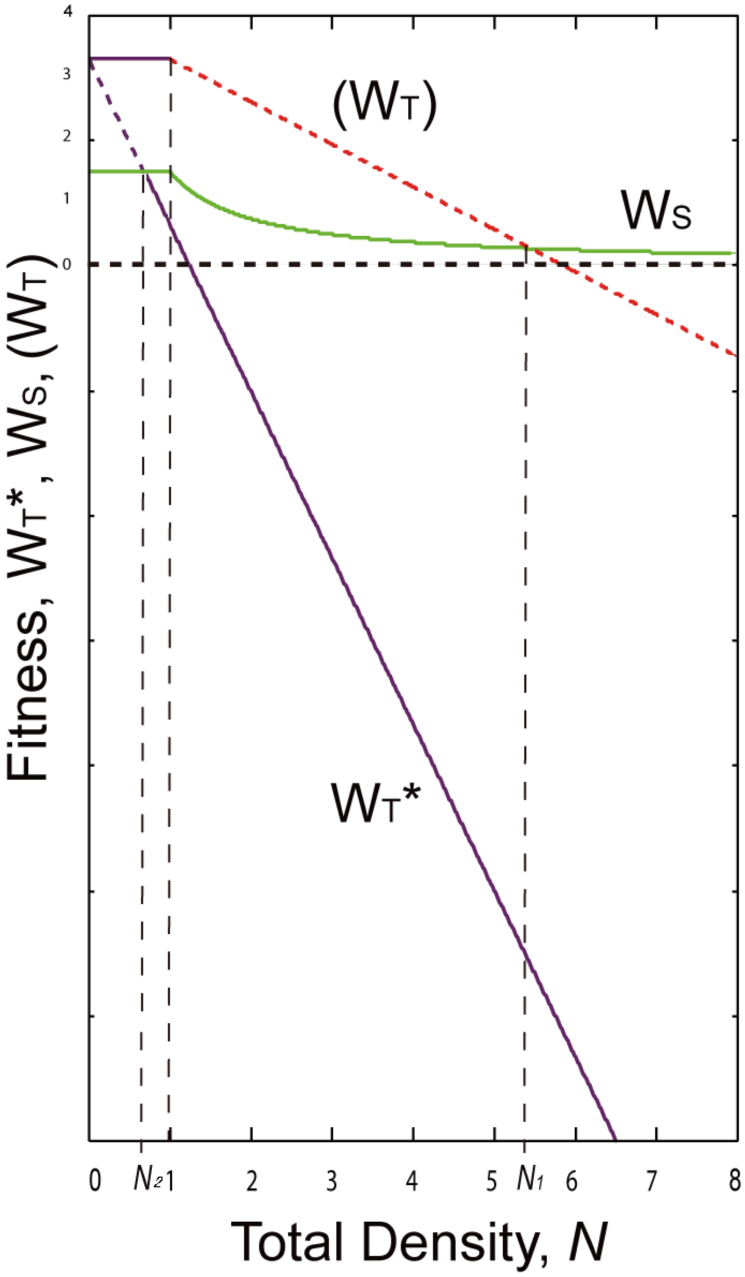

Territory holders
School fish
Floaters
Fitness, W_T, W_F, W_S
4
3
2
1
0
0
1
2
3
4
5
6
7
8
N_1
N_{Tmax}
Total Density, N

Fig. 4


4
3
2
1
0
(W_T)
W_S
W_T*
Fitness, W_T*, W_S, (W_T)
0
N_2
1
2
3
4
5
N_1
6
7
8
Total Density, N