The multi-scale aggregative response of cormorants to the mass stocking of fish in rivers

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Abstract. In Japanese rivers, there is a serious conflict between the great cormorant (*Phalacrocorax carbo hanedae*) and fisheries. The basis of this conflict is that the cormorants feed on ayu (*Plecoglossus altivelis*), a commercially important fish that is stocked primarily for recreational fishing. To understand how cormorants alter their foraging habitats in relation to the stocked fish and fishing activities, we examined the relationship between cormorant abundance and ayu biomass during the cormorant breeding season (from April to July) using two approaches that differ in spatial scale. First, we compared cormorant numbers in different river sections that were defined based on ayu stocking. The cormorant numbers in the sections stocked with ayu increased during the ayu release period, whereas the cormorant numbers in other sections showed no clear seasonal patterns. Second, we tested whether cormorant numbers were correlated with the biomass of ayu caught with cast nets. Positive correlations were observed between the biomass of ayu and the number of cormorants that were within 900 m, 1 km, or 2 km of fish sampling points; however, such correlations were not observed within 100m to 800 m of the sampling points. The biomass of ayu caught with cast nets increased steadily from April to June despite predation by cormorants; however, this biomass decreased sharply in July when the fishing season opened. This study indicates that although cormorants altered their feeding areas in accordance with the mass stocking of ayu in a Japanese river, sufficient numbers of ayu were still maintained for anglers.

Keywords: ayu, fish stocking, foraging, great cormorant, spatial scale

1. Introduction

Cormorants are piscivorous birds and are distributed worldwide. Two cormorant species, the great cormorant (*Phalacrocorax carbo*) in Eurasia and the double-crested cormorant (*Phalacrocorax auritus*) in North America, declined in population during the early 20th century and rapidly increased thereafter (De Nie 1995; Grémillet et al. 1995; Lindell et al. 1995; Hatch 1995; Weseloh et al. 1995). This rapid increase has led to growing conflicts between these birds and fisheries (Suter 1995; Bearhop et al. 1999; Boström et al. 2009; Glahn and Stickley 1995; Glahn et al. 1995). In Europe, great cormorants cause numerous problems in terms of the utilization of fish in fishponds (Kloskowski 2010), rivers (Cech and Vejrik 2011) and seas (Leopold et al. 1998). In North America, double-crested cormorants feed on channel catfish (*Ictalurus punctatus*) (Glahn et al. 1995), alewife (*Alosa pseudoharengus*) (Dalton et al. 2009) and other fish. Such conflicts are also serious in Japan. The Japanese great cormorant population (*P. c. hanedae*) declined to 3,000 individuals in the 1970s; however, it has recovered rapidly since the 1980s (Fukuda et al. 2002). During the first decade of the current century, approximately 50,000-60,000 cormorants were present in Japan, and their numbers continue to increase. Cormorants damage freshwater fish, such as ayu (also termed sweetfish, *Plecoglossus altivelis*). According to an unofficial report from the National Federation of Inland Water Fisheries Cooperatives, cormorant-related damage to commercial fish populations and cormorant management costs totaled 140 million yen (approximately $1,840,000) in 2009.

Ayu is an amphidromous fish with a one-year lifespan, and it is the most economically important fish in Japanese rivers because of its popularity with anglers. Under natural conditions, ayu spawn during the autumn months in downstream basins. The hatched fry spend the winter near coastal areas, and young fish migrate upstream in the spring and grow rapidly in rivers, where they must alter their diet from zooplankton to algae on rock surfaces. Local fisheries cooperative associations stock many rivers with a large number of juvenile ayu in the spring, in part because weirs and dams prevent the young ayu from migrating upstream. Previous studies have shown that the proportion of ayu in the diet of cormorants varies depending on the location, season, and year, ranging from 7 to 67 % (Toita 2002; Torii and Takano 2005; Takahashi et al. 2006; Tezuka 2008; Ashizawa and Tsuboi 2011). In our study area (see below), ayu represented 17 % of the mass of 35 stomach samples collected from April to June between 2002 and 2010 (Ashizawa and Tsuboi 2011). However, only a few studies have investigated the spatial distribution patterns of foraging cormorants in relation to the release of ayu (Fujioka and Matsuka 2006; Matsuka and Fujioka 2006; Iguchi et al. 2008). To protect ayu against cormorant predation, it is important to understand how cormorants respond to the biomass of ayu, which fluctuates greatly in space and time due to mass stocking and recreational fishing.

Predator-prey interaction patterns typically vary depending on the spatial scale (Mehlum et al. 1999; Fauchald et al. 2000; Tellería and Pérez-Tris 2003). For example, Fauchald et al. (2000) observed a spatial overlap between murres and their prey (capelin) on a large scale but did not observe the same overlap on a smaller scale. Amano and Katayama (2009) showed that foraging intermediate egrets (*Egretta intermedia*) make different decisions (i.e., to remain in one area and search for prey or to fly to another patch) depending on the spatial scale involved. Quantifying the spatial associations between the abundance of predators and their prey on multiple spatial scales can be a useful approach for understanding hierarchical predator-prey interactions (Fauchald et al. 2000). Fish stocking and fishing create rapid changes in the distribution and abundance of cormorant prey. Cormorants depart from a night roost in the morning and fly to a foraging area, where they repeatedly dive and perform short-distance flights. Cormorants might also make hierarchical decisions depending on the spatial scale. Because these decisions could produce different distribution patterns, we chose to examine the interactions between cormorants and ayu based on two approaches at different spatial scales.

The objective of this study was to reveal the pattern of cormorant-ayu interactions on two spatial scales in relation to changes in the fish population in rivers caused by the release of ayu and the opening of the recreational fishing season. On a larger scale, we compared the abundance of cormorants among river sections that vary in the amount of stocked ayu; on a smaller scale, we tested whether the abundance of cormorants is correlated with the biomass of ayu caught with cast nets.

2. Methods

2.1. Study area

This study was conducted in the Kofu Basin of the Yamanashi Prefecture in central Japan (Fig. 1). This basin is surrounded by mountain ranges and is approximately 50 km from the Pacific Ocean. In view of these topographic features, we assumed that cormorants rarely fly into our study area from outside of the basin and vice versa. Due to the presence of weirs and dams, there is little natural ayu migration from the sea, and ayu is primarily supplied to the basin by fish stocking. We searched for cormorants in rivers and streams ranging in width from approximately 10 to 200 m. The studied rivers and streams, 230 km in total length, were divided into three sections based on the release of ayu. Most of the ayu disperse within a range of approximately 1 km around the point of release (Tsuboi, unpublished data). Therefore, sections within 1 km from the point of ayu release were defined as "Release Sections" (59.5 km in total). Ayu have been released in these sections every spring for more than 30 years. The other sections of the river where ayu were stocked were defined as "Non-release Sections" (61.6 km in total). Note that relatively large rivers have been referred to as either Release Sections or Non-release Sections. Several smaller streams were not stocked with ayu, and these were referred to as "Streams" (109.2 km in total) (Fig. 1).

Cormorants were observed nesting and roosting in a riparian wood (the Shimosone colony, Fig. 1) along the Fuefuki River, a tributary of the Fuji River (35°35'46"N, 138°33′56"E). Approximately 150 cormorant pairs were breeding in the colony from April to July of 2009. Within this colony, the Yamanashi Prefectural Fisheries Technology Center restricts the cormorants' breeding by replacing cormorant eggs with gypsum eggs every year to protect ayu; this practice results in the production of only 8-17 nestlings per year (Tsuboi and Ashizawa 2011). No additional colonies were confirmed in the basin. We restricted our survey to an area within 20-25 km of the colony because the foraging ranges of the great cormorant are usually no more than 20-25 km from their wintering roosts or breeding colonies (Platteeuw and Van Eerden 1995; Paillisson et al. 2004).

Local fishery cooperatives repeatedly disturb foraging cormorants after ayu have been stocked; however, we were unable to collect quantitative data on such activities.

2.2. Cormorant and angler surveys

We divided our study period into four phases based on major events related to ayu stocking and the commencement of the fishing season. The "Pre-release Phase" was from 4 April to 9 April (prior to ayu stocking), the "Release Phase" was from 21 April to 10 May (when the ayu were repeatedly released) and the "Post-release Phase" was the period following the completion of ayu stocking (from 11 May to 20 June). The last phase, termed the "Fishing Phase", was from 21 June to 10 July, although the fishing season continued until November. During the period between the Pre-release and the Release Phase (from 10 April to 20 April), the state of ayu stocking varied depending on the river because the timing of release initiation varied among the fisheries cooperative associations. Therefore, we did not use the data from the second survey conducted during this period in our analysis of ayu-cormorant interactions.

We conducted ten cormorant surveys (one to four times per phase) approximately once every ten days from early April to early July. Each survey was two or three days in duration (Table 1). Using a car or bicycle, we counted cormorants along the Fuji River and its 17 tributaries during the day from 30 minutes after sunrise to 30 minutes before sunset. Usually, one observer would drive the car slowly while the other observer looked for cormorants; we also stopped at most bridges to search for cormorants. We used a bicycle to travel along small streams in urban areas where car access was limited. We varied the order of river and stream visitations in each survey depending on weather or other conditions. When cormorants were observed, their number, behavior (foraging, resting or flying) and GPS location were recorded. We regarded repeated swimming and diving behavior as foraging; cormorants repeating only swimming behaviors were recorded as resting.

We also recorded the locations of ayu anglers during the fishing season (20 June to 31 November).

2.3. Fish survey

We performed fish sampling (with 10 replicates) concurrently with the cormorant survey (Table 1). Fish were sampled with 9-mm square mesh nets at twelve sites: five in the Fuefuki River, five in the Kamanashi River and two in the Shio River (Fig. 1). These sites were selected primarily because they had widths and depths that were appropriate for casting nets into their tributaries, which were stocked with ayu. In the first survey, the mean river width (± SD) was 42.6 m (± 19.3), the water depth was 0.55 m (± 0.18), and the velocity was 0.84 m/s (± 0.24). One person cast the net five times at each site, and we recorded the species, total length, and body mass of all the captured fish.

We obtained data regarding the amounts, dates and locations of ayu releases from three local fisheries cooperatives. The fisheries typically released ayu with a total length of approximately 10 cm or a weight of 8 g.

2.4. Statistical analyses

We analyzed the correlation between cormorant abundance and fish biomass on two scales. On the larger scale, we examined cormorant numbers with respect to the river sections defined based on ayu releasing/fishing. We applied generalized linear models (GLMs) using R software with the MASS package (R Development Core Team 2009). The response variable was the number of cormorants, and the explanatory variables were the ayu-related phases, the river sections and their interaction terms. We constructed models with a negative binomial error structure with a log link function. The length of each river section was used as an offset term. The most parsimonious model was selected based on Akaike's Information Criterion (AIC).

On the smaller scale, we tested the correlation between ayu biomass at the fish sampling points and the cormorant numbers around these points. Although there were temporal discrepancies (up to eight days) between fish sampling and cormorant counts (Table 1), which were primarily due to the limits of our field survey capabilities, we do not consider these discrepancies to be critical because ayu is a territorial fish and migrates slowly from its release sites. We analyzed cormorant numbers at several distances from each fish sampling point (i.e., from 100 m to 1 km in 100 m intervals and once at 2 km). Because no cormorants were counted within circles around many fish sampling points, we used zero-inflated Poisson models, which included ayu biomass as a fixed effect and the fish sampling point as a random effect. Zero-inflated Poisson models are two-component mixture models that include a count sub-model analyzing the relationship between cormorant numbers and explanatory variables and a binomial sub-model analyzing the relationship between non-occurrence and the explanatory variables. These models are appropriate for count data with an excess of zeroes in comparison with what is assumed by the Poisson distribution (Martin et al. 2005). The models were fitted using the Bayesian statistical modeling freeware package WinBUGs (Spiegelhalter et al. 2003). We considered the prior distributions of these models' parameters to be non-informative. Therefore, we used normal distributions with a mean of zero and precision parameters equal to 0.001 for fish biomass. We ran these models 11,000 times, sampled every 10 times (after ignoring the first 1,000 repetitions) and used three chains. The sample plots and R hat values were used for convergence diagnostics, and values below 1.1 indicated model convergence (Gelman et al. 2003).

3. Results

3.1. Seasonal changes in cormorant numbers and fish biomass

A total of 825 individual cormorants were observed in ten surveys (82.5 ± 21.8, mean ± SD per survey): 219 (26.5 %) were foraging, 417 (50.5 %) were resting, and 186 (22.5 %) were flying. The total number of cormorants observed was relatively stable throughout the study period with no clear seasonal trends (F test: $F = 1.04$, $df = 659$, $P = 0.608$; KS test: $D = 0.0616$, $P = 0.1636$) (Fig. 2). Assuming that one member of a breeding pair remained at the nest in the colony, our surveys indicated that 33 to 80 % of the 150 breeding cormorants were potentially at foraging sites. Flying cormorants were excluded from the analyses.

A total of 197 ayu anglers were observed in six surveys (32.8 ± 17.6, mean ± SD per survey): 135 (68.5 %) were in the Release Sections, 48 (24.3 %) were in the Non-release Sections, and 14 (7.1 %) were in the Streams.

A total of 1,687 fishes (23.3 kg in fresh weight) were caught with cast nets in the ten surveys (2.33 kg ± 1.30, mean ± SD). We identified 11 species of fish: by weight, 68.5 % were ayu, 9.6 % were Japanese dace

(*Tribolodon hakonensis*), 8.8 % were oikawa (*Zacco platypus*), 6.9 % were red-spotted masu salmon (*Oncorhynchus masou ishikawae*), 2.8 % were Amur minnow (*Phoxinus lagowskii steindachneri*), 1.6 % were whitespotted char (*Salvelinus leucomaenis japonicus*), 1.3 % were pike gudgeon (*Pseudogobio esocinus esocinus*), 0.2 % were Japanese fluvial sculpin (*Cottus pollux*), 0.2 % were rainbow trout (*Oncorhynchus mykiss*), 0.1 % were *Rhinogobius* sp. and 0.004 % were field gudgeon (*Gnathopogon elongates elongatus*). The mean total length of the fish was 108 mm ± 31 (SD). Most of these fish were within the size range of the cormorant diet (7 to 60 cm; Cramps and Simmons 1977). The biomass of ayu caught with cast nets increased rapidly from the beginning of the study until the middle of June, after which it suddenly decreased soon after the fishing season began (i.e., late June) (Fig. 3). We compared two alternative linear regression models. In the first model, the biomass of ayu was predicted by the study phase (first to 10th). In the second model, the biomass of ayu was predicted by the study phase and its square term. These two models test whether the response variables are linearly or unimodally related to the study phase (Forsman et al., 2008). The observed seasonal change in ayu biomass was not linear ([study phase]: effect size = 182.6, SE = 108.1, $P = 0.13$) but rather unimodal, and it could be expressed by including the study phase and its square term in the regression formula ($[\text{study phase}]^2$: effect size = -83.6, SE = 32.7, $P < 0.05$; [study phase]: effect size = 1102.3, SE = 372.1, $P < 0.05$). The mean fresh weight (± SD) of a single ayu increased from 8.7 g (± 2.3) in the second survey to 28.5 g (± 14.1) in the last survey. In contrast, the total biomass of the other fish species increased linearly throughout the study period (study phase: effect size = 148.5, SE = 23.7, $P < 0.05$) and doubled during the last two surveys as the ayu declined.

Three fisheries cooperative associations released 6,210 kg of ayu into the Release Sections of our study area at 49 release points from 10 April to 14 May. In the Fuefuki River, 2,000 kg of ayu were released at 12 release points over five non-consecutive days within this period; in the Kamanashi River, 2,810 kg of ayu were released at 21 release points over five non-consecutive days; and in the Shio River, 1,400 kg of ayu were released at 16 release points over four non-consecutive dates. The largest and smallest amounts of ayu released at a time were 80 kg and 10 kg, respectively.

3.2. Cormorant numbers in relation to river sections

Figure 4 illustrates the seasonal changes in cormorant numbers with respect to the river sections, which vary in ayu release. The cormorant numbers in the Release Sections increased from the Pre-release Phase to the Release Phase and decreased thereafter; however, in the Non-release Sections, cormorants were more abundant during the Fishing Phase. Cormorants were consistently less abundant in the Streams than they were in the other two section types (Steel-Dwass multiple test, $P < 0.05$).

Among the GLMs (Table 2), the full model was the most parsimonious in explaining the observed seasonal pattern (Fig. 4). Models that did not count the interaction term between phases and sections had much larger AIC values than the full model, indicating that the interaction term was important (Table 2). This result indicated that the changes in cormorant numbers in each section exhibited various seasonal patterns. Specifically, the cormorant numbers in the Release Sections generally increased from the Pre-release Phase (14 cormorants) to the Release Phase (57 and 43 cormorants) and decreased thereafter (16, 28 and 30 at the Post-release Phase and 16, 16 and 9 at the Fishing Phase); however, in the Non-release Sections, the cormorants were more abundant during the Fishing Phase (Fig. 4). The model that counted only the ayu-related phases had a higher AIC value (238.77) than the null model (233.38), indicating no clear seasonal trend (Table 2). In contrast, the model using only the section type had a lower AIC value (207.29) than the null model, indicating that cormorant abundance varied spatially in accordance with the section types (Table 2).

3.3. Cormorant numbers in relation to ayu biomass

The relationship between cormorant number and ayu biomass varied depending on the spatial scale on which the cormorants were counted. At 100-800 m from the fish sampling points, 95% credible intervals of the fixed effect ranged from positive to negative values, indicating the absence of meaningful correlations. At 900 m, 1 km and 2 km scales, the 95% credible intervals included only positive values, indicating a positive correlation between ayu biomass and cormorant numbers (Table 3).

4. Discussion

Cormorant population density varied depending on the river section and phase. The increase in cormorant numbers in the Release Sections during the Release Phase was particularly clear (Fig. 4). These results suggest that the mass release of ayu affected foraging habitat use by cormorants breeding at the single colony in the basin. The biomass of ayu released in our study area (6,210 kg) is equivalent to the amount of food required for the 300 cormorants at the colony over at least 40 days (assuming 500 g of daily consumption) (Sato et al. 1988). The actual biomass of ayu could be higher because the released ayu grow rapidly in rivers, as shown by our fish survey data (Fig. 3). Previous studies also indicated that a rapid increase in fish abundance, caused either by a fish run or by stocking, promotes the aggregation of great cormorants (Kennedy and Greer 1988) and double-crested cormorants (Dalton et al. 2009). During the Release Phase, we occasionally observed foraging by groups of ten or more cormorants in the Release Sections where released ayu tended to form a school around the release point. However, during the Fishing Phase, some cormorants presumably altered their foraging habitat from the Release Sections to the Non-release Sections. This phenomenon may be due to two related factors. First, the biomass of ayu may have declined due to intensive fishing by anglers in the Release Sections, as suggested by the sharp decline in ayu caught with cast nets (Fig. 3). Second, the presence of anglers, who are generally antagonistic toward cormorants, may have decreased the attractiveness of the Release Sections as cormorant foraging habitat even if fish were abundant. We were unable to separate the two factors in this study; however, we hypothesize that both fish biomass and human activities (particularly fishing) affect the foraging habitat choice of cormorants on a relatively large scale.

Earlier studies on cormorant-ayu interactions performed in the Tochigi Prefecture (approximately 140 km northeast of our study area) produced different results (Fujioka and Matsuka 2006; Matsuka and Fujioka 2006). In Tochigi, approximately 50 to 250 cormorants were counted from late March to mid-April within the studied river section of 46 km; however, these cormorants nearly disappeared from the section when most of the ayu releases ceased in late April. The potential causes for this discrepancy may be differences in topography, human disturbance and the amount of ayu released. It is important to note that our study area was surrounded by mountain ranges, so the breeding cormorants were somewhat separated from other local populations. In Tochigi, however, it may have been relatively simple for cormorants to join larger colonies outside Tochigi in the spring. Moreover, it is probable that human disturbance of roosts was more serious in Tochigi than in our study area, Yamanashi. The largest roost in Tochigi, which was used by more than 300 cormorants, disappeared in April immediately following a nighttime disturbance by local fisheries cooperatives. In Yamanashi, the breeding colony was carefully maintained, and breeding was kept to a minimum because disturbances could cause cormorants to form new colonies in unmanageable places. Thirdly, the Release Sections of our study area were stocked with approximately twice as many ayu as comparable sections in Tochigi, i.e., approximately 103 kg/km in Yamanashi vs. approximately 60 kg/km in Tochigi. These three factors, along with potential unknown factors, may have contributed to the differences between the two areas; however, it appears logical that both fish abundance and human disturbance critically affect the habitat choice of cormorants inhabiting inland Japan.

Positive correlations were only observed between the numbers of cormorants and ayu caught with cast nets at larger distances (900 m, 1 km and 2 km) from the fish sampling point. Generally, the smaller spatial scale we take, the lower predictability of prey abundance would be expected due to the more rapid time scales of ecological processes (Fauchald et al. 2000; Watanuki 2004). In fact, Iguchi et al. (2008) compared ayu biomass in an area where cormorants were foraging with ayu biomass in another nearby area where cormorants were absent in the same study area used in the current study. Interestingly, Iguchi et al. found positive (but weak) relationships between the presence of cormorants and the abundance of ayu on smaller spatial and faster time scales than ours. Alternatively, our method of fish sampling (with cast nets) was not necessarily comparable with the relative evaluation of fish resources by cormorants, which can access much wider ranges of river environments than we can. Another possible problem is that our fish sampling methodology primarily targeted ayu, whereas other fish species may have been more important for cormorants than ayu.

We used two approaches that differ in spatial scale to analyze the interactions between cormorants and ayu. Cormorants in our study area fly directly from the colony to a certain foraging site every morning. We intended to use one of our two approaches, i.e., the analysis of shifts in foraging sites on a larger scale, to address how the mass release of ayu and the opening of recreational fishing might affect the cormorants' choice of foraging sites. Cormorants used the Release Sections more frequently during the Release Phase than during the Pre-release or the Fishing Phase. This observation strongly suggests that both ayu release and fishing affected habitat choice of cormorants on the larger scale. Using our other approach, i.e., the analysis of the correlation between the biomass of ayu at net casting points and the numbers of nearby cormorants, we observed positive correlations between ayu biomass and cormorant numbers at 900 m or farther from the fish sampling points; however, we did not observe any correlation at closer distances. This pattern suggests that on a smaller scale (which corresponds to the choice of foraging spots using short-distance daytime flights), cormorants might have chosen sites with abundant ayu; however, this correlation was limited due to issues related to our study design, as stated above. In future research, direct behavioral studies should be performed at both scales.

Our results indicate that cormorants use foraging habitats containing large biomass of ayu, especially on the larger scale. However, this cormorant behavior may not have a serious impact on the released ayu populations. First, the biomass of ayu caught with cast nets increased until the opening of the fishing season despite the cormorants' preference for the Release Sections during the Release Phase. Second, the proportion of ayu in the diets of cormorants in our study area was only 17 % (see Introduction), much less than the 68 % in our sample caught with cast nets. Although cormorants are hypothesized to be generalists and their diets reflect the composition of the fish community in a given body of water (Kameda et al. 2002; Lorentsen et al. 2004; Casaux et al. 2009), ayu may be relatively difficult to catch. In a series of water tank experiments, ayu were shown to be faster and more maneuverable than some Cyprinidae, resulting in less predation by cormorants (H. Tanaka, personal communication). Furthermore, the total amount of food required by breeding cormorants could be greatly reduced by breeding management strategies such as egg replacement, which was utilized in our study area (Tsuboi and Kiryuu 2007). Additionally, the members of the fisheries cooperative associations repeatedly harassed cormorants in the Release Sections during the Release and Post-release Phase. This practice may have forced cormorants out of the Release Sections.

5. Conclusions

Cormorants tended to change their foraging behavior based on fish availability, which is closely related to ayu stocking and angling schedules in our study area. We observed positive correlations between the amount of ayu caught with cast nets and the number of nearby cormorants at specific distance ranges. However, despite suspected predation by cormorants, the biomass of ayu increased until the fishing season opened. In conclusion, ayu may be an important food resource for cormorants during a certain period of their breeding season; however, the impact of cormorants on the ayu population was not as substantial as the impact of anglers.

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Table 1.

The phases of the study period based on the release and fishing of ayu (with survey dates).

	Ayu releasing/fishing phases									
	Pre-release	(blank[1])	Release		Post-release				Fishing	
Cormorant	3-5 Apr	12-14 Apr	24-26 Apr	4-5 May	16-17,19 May	27-29 May	6,9 Jun	16-18 Jun	22,24-25 Jun	2-3 Jul
Fish	6 Apr	18 Apr	28 Apr	12 May	19 May	26 May	4 Jun	11 Jun	29 Jun	8 Jul

[1]We discarded data during this period for analyzing ayu-cormorant interactions because ayu-release dates varied with river sections.

Table 2.

AIC values of GLMs explaining the number of cormorants by the ayu-related phases, sections, and their interactions. ΔAIC is the difference in AIC values between the given model and the null model.

Model variables	AIC	ΔAIC
phases + sections + phases * sections	202.63	-30.75
sections	207.30	-26.09
phases + sections	210.63	-22.75
null model	233.38	0.00
phases	238.77	5.38

Table 3.

Sample means and 95% credible interval, showing the effect of ayu biomass on cormorant numbers at each distance range from the fish-sampling points using Bayesian statistical modeling.

Distance[1]	Sample mean	95% credible interval
100 m	-2.50	-10.9 - 3.04
200 m	0.64	-1.45 - 2.4
300 m	0.02	-1.06 - 0.96
400 m	0.50	-0.37 - 1.3
500 m	-0.13	-0.84 - 0.53
600 m	0.18	-0.47 - 0.77
700 m	0.27	-0.38 - 0.86
800 m	0.52	-0.07 - 1.07
900 m	0.59	0.01 - 1.13
1 km	0.41	0.01 - 0.78
2 km	0.57	0.22 - 0.91

[1]Distance is the radius of a circle around the fish-sampling point within which cormorant numbers were counted.

Figure 1. Study area for great cormorant-ayu interactions in the Fuji River Basin, central Japan. Rivers were categorized into three section types based on the release sites and fishing of ayu (see text). Shaded areas show mountain ranges, which cormorants rarely use as a foraging site. A broken-line circle shows a radius of 20 km from the colony.

Figure 2. Seasonal changes in the number of cormorants found in the river system and their behavior.

Figure 3. Seasonal changes in the mass of fish caught with cast nets.

Figure 4. Cormorant numbers with respect to the ayu-related river types and phases. Means with SDs are shown.

fig.1

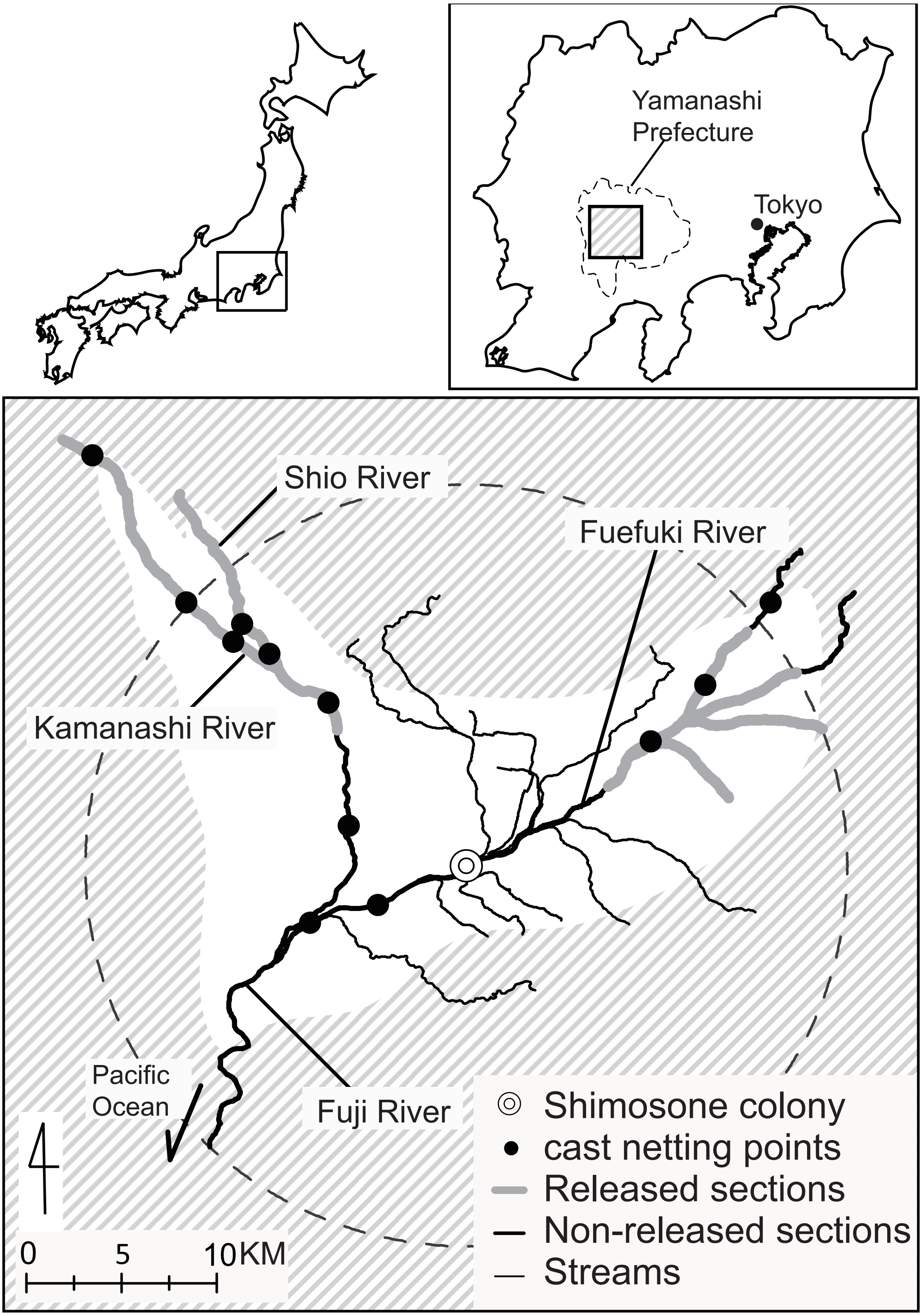
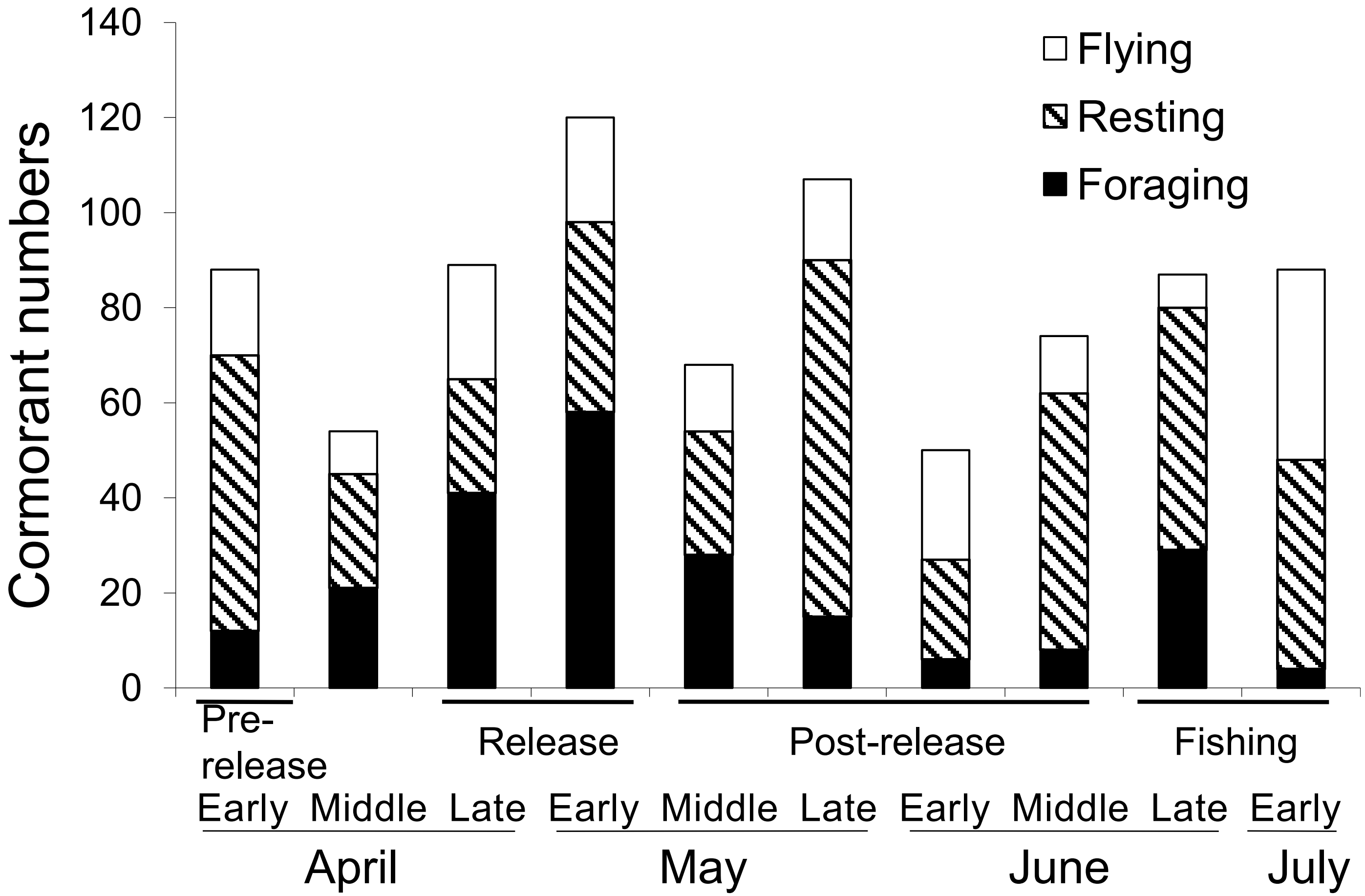
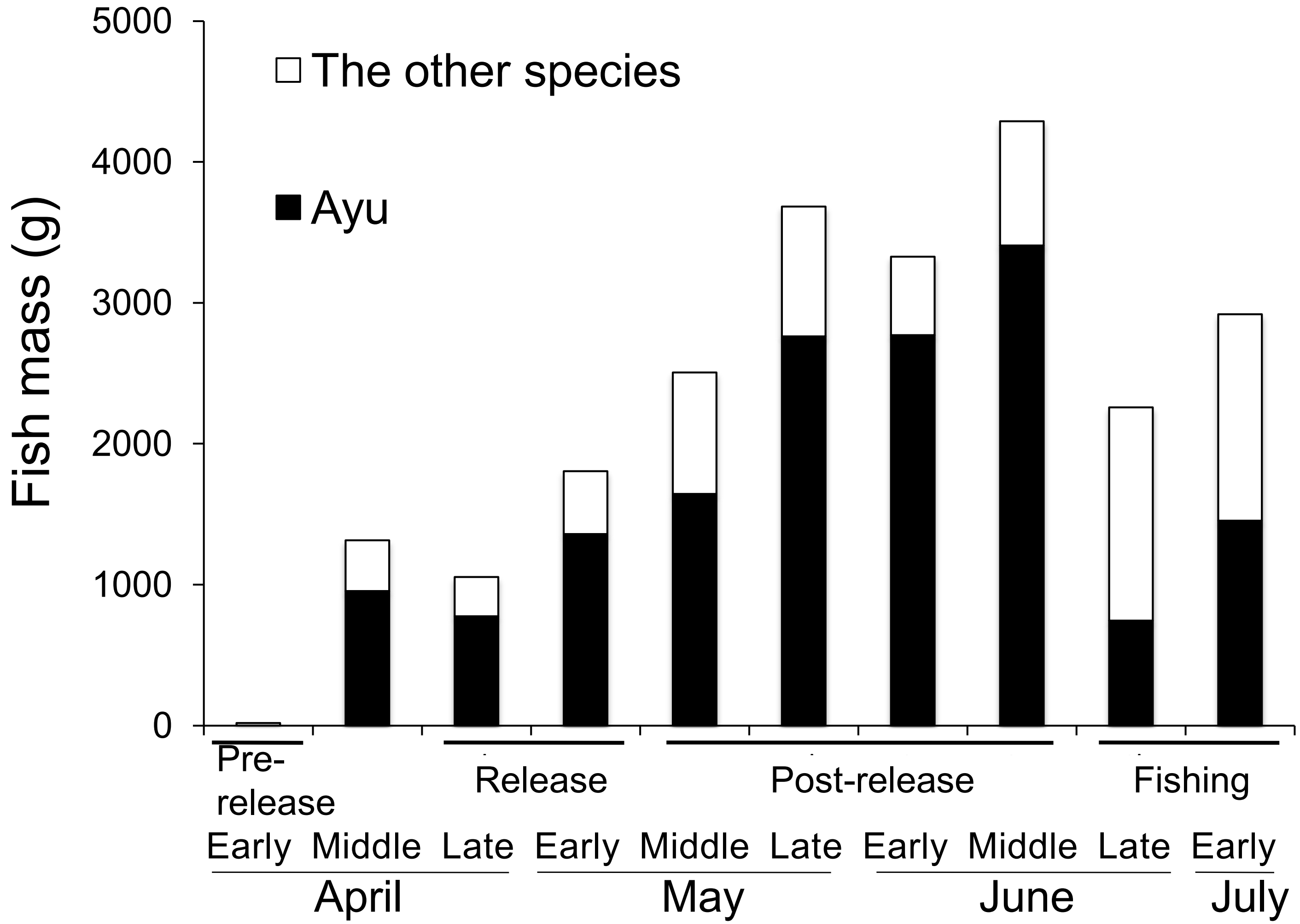

Yamanashi
Prefecture
Tokyo
Shio River
Fuefuki River
Kamanashi River
Pacific
Ocean
Fuji River
Shimosone colony
cast netting points
Released sections
Non-released sections
Streams
0
5
10KM

fig.2



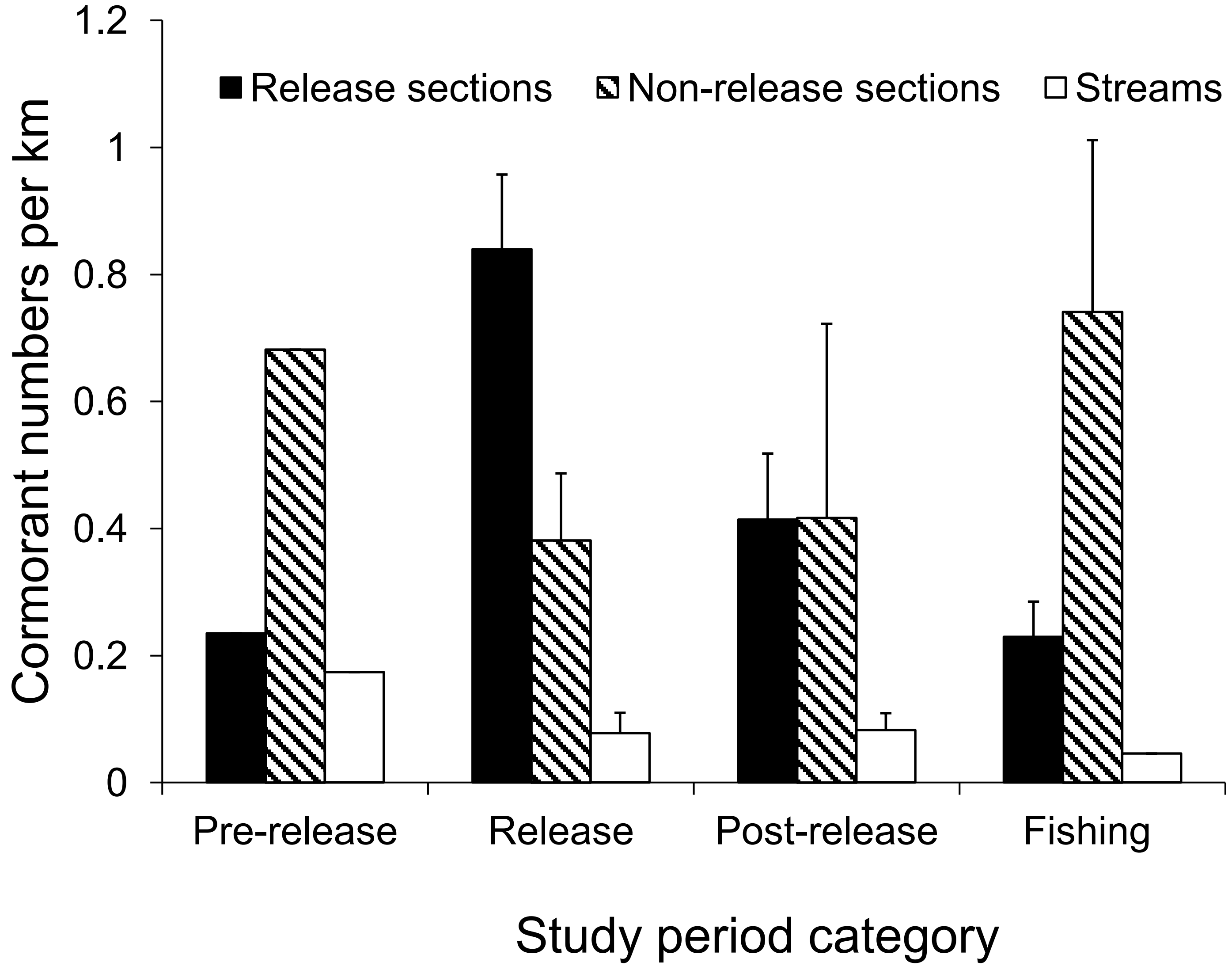
Cormorant numbers
140
120
100
80
60
40
20
0
Flying
Resting
Foraging
Pre-release
Release
Post-release
Fishing
Early Middle Late
Early Middle Late
Early Middle Late
Early
April
May
June
July

fig.3



Fish mass (g)
5000
4000
3000
2000
1000
0
The other species
Ayu
Pre-release
Release
Post-release
Fishing
Early Middle Late Early Middle Late Early Middle Late Early
April
May
June
July

fig.4


1.2
1
0.8
0.6
0.4
0.2
0
Release sections
Non-release sections
Streams
Cormorant numbers per km
Pre-release
Release
Post-release
Fishing
Study period category