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Determinants of predator-prey interaction on
salmonid fish species and their survival rate

（サケ科魚類の捕食・被食関係と生残率決定要因の解明）

Predator-prey interaction is one of the key factors in animal ecology. Understanding predator-prey interaction is essential for the study of ecosystems and evolution because predation has a critical effect on ecosystem structure and function (Berger et al., 2001; Hawlena and Schmitz 2010). Predators often control the dynamics of prey populations through their influence on survival (Skelly 1994), growth (Peckarsky et al. 1993), behavior (Werner et al. 1983), size structure (Hall et al. 1976) and distribution (Beauchamp et al. 2007). Meanwhile, prey animals adjust their traits and behaviors as a response to predation risk (Kishida and Nishimura 2004; Bongi et al. 2008; Sönnichsen et al. 2013). Therefore, understanding the mechanisms of predator-prey interaction is necessary for the broader study of animal ecology.

Juvenile fish are vulnerable to predation everywhere and in many different manners (e.g. wading birds at the beach, piscivorous fish at reefs; Gibson and Robb 1996; Connell 1998). Predation by riparian wildlife is also widely recognized as a key factor affecting the survival of fish in stream ecosystems (Draulans 1987; Kruuk 1995; Roby et al. 2003; Steinmetz et al. 2003; Sahashi and Yoshiyama 2015). Predation pressure on

juvenile salmon in particular is of broad interest because of their economic and social values. Declines in salmonid populations as a result of predation by riparian wildlife have been reported not only for stocked salmon populations but also for wild salmon populations (e.g., Osterback et al. 2013; Frechette et al. 2015). It is also noteworthy that stocked salmonids are often intensively preyed upon by fish predators (McCrimmon 1954; Symons 1974; Pepper et al. 1985), birds (Wood 1987; Martel and Dill 1995; Harvey and Nakamoto 2013), and mammals (Roberts and Garcia de Leaniz 2011). Hatchery-reared salmonid fish are routinely stocked in natural waterways as part of propagation and stock enhancement programs (Brown and Laland 2003; Salvanes and Braithwaite 2006; Naish et al. 2007; Fraser 2008). Therefore, if one can implement a management strategy that decreases local predation pressures on salmon juveniles through a profound understanding of the predator-prey interaction between predators and stocked fishes, it will contribute to an improvement of these programs.

Studies examining the predator-prey interaction on fish species have been generally based on either investigation into the predation pressure of wild animals without observing fish responses (Draulans 1987; Post et al. 1998; Harvey and Nakamoto 2013) or these into the mortality rate of fish without observing the behavior of predators (Penaluna et al. 2016). On the other hand, predation risk is influenced by many factors, including conditions of fish (Hostetter et al. 2012), fish migrations (Roberts et al. 2009), the type of local predators and their abundance, the duration of the predators' sojourn (Gawlik 2002; Steinmetz et al. 2003), their habitat [e.g., water depth (Kushlan 1976) and structure complexity (Penaluna et al. 2016)]. However, it is still not clear how these factors fit together to form the predator-prey interaction between predator animals and stocked salmonids. In order to understand the mechanisms of predator-prey interactions,

it is necessary to first develop a profound understanding of the interactions between the traits of predators and prey relative to their environment. For example, size of prey fish needs to be taken into consideration in the context of the type of predator and their relative sizes because food size preference depends on predator species (Carss and Marquiss 1991; Sogard 1997) and because the ability of prey to avoid predation depends on size (Dill and Fraser 1984). However, the number of studies on these relationships is limited partly owing to the difficulties in identifying local species of riparian predators and directly observing their predation activities. These surveys are further complicated because of varieties of cause of migration exhibited by predator species, such as migration for feeding and nesting needs (Collis et al. 2002), migration due to changes in prey densities (Kushlan 1976; Gawlik 2002), and migration resulting from human disturbance (Klein 1993).

Recently, many ecological tools have been developed for better understanding predator-prey interactions. Camera trapping is one of them. Camera trapping that uses fixed cameras, triggered by infrared sensors, to ‘trap’ images of passing animals has recently provided the opportunity for researchers to collect more detailed information about predators, including species identity, daily presence, appearance frequency and duration of sojourns (Silveira et al. 2003; Wegge et al. 2004). Because camera trapping is a non-invasive technique, it causes minimal environmental disturbance (Henschel and Ray 2003; Silveira et al. 2003). In this dissertation, I conducted a predation test using camera traps on outdoor experimental tanks and a semi-natural stream to investigate the relationships between the predator species, their behavior and traits of stocked salmon.

This dissertation has four Chapters. In Chapter-1, 24-h predation experiments were conducted on masu salmon *Oncorhynchus masou* in tanks in order to understand the

predator and prey body size effects on predator-prey interaction. Four ranges of fork length (FL) were examined for masu salmon as a prey, in combination with three ranges of FL for white-spotted charr *Salvelinus leucomaenis* as a predator. The results show that not only predator and prey sizes, but also interaction between prey size and predator size, strongly affected the survival rate of masu salmon. Specifically, the survival rates of stocked salmon were extremely low ($\leq 10\%$) when their body size was less than 30% that of predator fish. A logistic regression suggests that 37% relative FL of masu salmon to white-spotted charr results in the 50% survival of masu salmon. My results suggest that adjusting relative size of fish to the size of local fish predators will have a significant impact on the survival of fish in the wild.

In Chapter-2, to evaluate the effects of predation by riparian animals inclusively, I conducted predation experiments in outdoor tanks and a seminatural stream with exposure to local predators. Masu salmon of two different size classes were used as experimental prey fish in the present study. Camera trap data showed that grey herons (*Ardea cinerea*) were the primary predator in the experimental system, and that most herons used shallow areas in the morning or evening while feeding. Increasing the density of stocked salmon led to increases in the number of occurrences of grey heron. More importantly, when the density of small and large salmon was relatively high, predation by grey herons resulted in a significantly lower survival rate of larger salmon compared with smaller salmon. The results suggest that size-selective predation by grey herons depends on the density of the preferred prey size.

In Chapter-3, I evaluated the effects of fish traits including behaviors (normal and post-stimulus behaviors) on the predation risk of masu salmon juveniles. I first conducted experiments on fish behaviors in an aquarium, followed by an evaluation of

their survival after release in a semi-natural stream. Within the 56 days of the test, by my observation, 48.3% of fish were lost in the stream. On-site camera trapping identified an ambush predator - the grey heron, as the most frequently visiting species. By individually matching the fish behaviors in the aquarium test with their survival in the semi-natural stream, I found that the most critical determinant for the survival of juvenile fish was their behavior under normal circumstances (i.e., how long fish used shelter or gravel when they were not exposed to a stimulus), rather than their post-stimulus behavior. My results suggest that the most critical determinant for the survival of juvenile fish was their behavior under normal conditions, rather than their post-stimulus behavior. One of the possible reasons for this could be the fact that the primary predator in the experimental area was an ambush predator (grey heron).

In Chapter-4, I focus on the effect of water depth on the predator-prey interaction between riparian predatory animals and white-spotted charr by using outdoor tanks together with camera trapping. Additionally, I also evaluate the effects of structural complexity on the predator-prey interaction in shallow water. Survival of the charr was lower in the shallow tanks (15 cm water depth) than in the deeper ones. Similarly, more fish survived in the tanks with artificial structures (cobbles with Ringlong tape) compared to those without them. The grey heron was the most frequently observed predator during the tank experiment. My results show that declining water levels and loss of structural complexity can increase the predation risk of stocked fish by making the process of hunting easier for the grey heron. These results suggest that the predator-prey interaction in my experimental settings is mainly determined by a combination of predator and prey traits, whereas the intensity of predator-prey interaction is mainly determined by physical habitat.

In conclusion, the predator-prey interaction, in my experimental settings at least, was mainly determined by a combination of predator and prey traits (behavior, density and body size), while the intensity of predator-prey interaction was mainly determined by physical habitat. The grey heron is native throughout temperate Europe, Asia and parts of Africa. According to the latest available records (1987-2007), the population size of grey heron has been increasing in Northern/Western Europe and Western/South-western Asia (Heron Conservation 2012 <https://www.heronconservation.org/>). In Japan, according to the latest available records, grey heron habitats have expanded considerably (Biodiversity center of japan 2004) and might continue to expand in the future. This phenomenon results in difficulties for fishermen and fish farmers because of increased consumption of fish by the grey heron, leading to actions being taken (usually hunting) in trying to manage grey heron populations. Therefore, in order to avoid conflicts between grey heron and humans, the results of this study should prove useful in developing non-invasive methods of mitigating predation on fish by the grey heron.