Exploitative competition and food stoichiometry: experimental analyses wi th Daphnia

	いわぶち　つばさ
氏名（本籍地）	岩渕　翼
学位の種類	博士（生命科学）
学位記番号	生博第197号
学位授与年月日	平成23年3月25日
学位授与の要件	学位規則第4条第1項該当
研究科，専攻	東北大学大学院生命科学研究科 （博士課程）生態システム生命科学専攻
論文題目	Exploitative competition and food stoichiometry: experimental analyses with *Daphnia*（消費型競争と餌の化学量：ミジンコを用いた実験的解析）
博士論文審査委員	（主査）教授　占部城太郎 教授　中静　透 教授　河田　雅圭

論文内容の要旨

Exploitative competition for food among consumer species is considered to have a substantial impact on their spatial and seasonal dynamics. In the competition, threshold food concentration (TFC) is one of the important traits determining competitive superiority among consumer species. TFC represents a food level at which growth rate of consumers equals zero, and thus a minimum food level to sustain the population. A number of studies have shown that competition outcomes among heterotrophic organisms such as zooplankton can be predicted by TFC. However, it has been shown that TFC of consumers can vary according to relative contents of nutritionally important elements such as phosphorus (P) in the food. The fact suggests that competitive superiority of an organism for food resource is not fixed, but changes with elemental composition of the food. Because relative demands for nutritionally important elements is likely taxon-specific and depends on their life histories, quantitative response of growth rate and TFC to changes in elemental composition of food would differ among consumer species. Thus, dominant species may change if elemental composition of the food is changed. However, such stoichiometric effects of food resource on competitive interactions have not yet been studied well.

In this thesis, therefore, I examined the effect of algal C to P ratio on the competition among herbivorous zooplankton to test the hypothesis that food stoichiometry can change competition outcomes. Algae, the primary food for herbivorous zooplankton is known to greatly change the elemental composition depending on relative supplies of light and nutrient. Among zooplankton, *Daphnia* are one of key organisms in freshwater habitats. Because they are filter feeders and are poor in ability of food selection, *Daphnia* are one of zooplankton vulnerable to changes in elemental composition of algae. Thus, algae-*Daphnia* system is ideal for examining the effects of changes in elemental contents of food (algal C:P ratio) on competitive superiority among consumer animals.

In Chapter 2, I examined the mechanism behind the competition between large (*Daphnia pulex*) and small zooplankton (*Ceriodaphnia quadrangula*). According to the size efficiency hypothesis, larger species have lower TFC because they are more efficient in food collection with lower expenditures for metabolism. Contrary to an expectation from the size-efficiency hypothesis, *Ceriodaphnia* often competitively predominate against *Daphnia*. However, little is known about critical feeding conditions favoring *Ceriodaphnia* over *Daphnia*. To elucidate these conditions, a series of growth experiments was performed with various types of foods in terms of phosphorus (P) contents and composition (algae and bacteria). An experiment with P-rich algae showed that TFC was not significantly different between the two species. However, the food P:C ratio, at which the growth rate becomes zero, was lower for *Daphnia* than for *Ceriodaphnia*, suggesting that the latter species is rather disfavored by P-poor algae. *Ceriodaphnia* showed a higher growth rate than *Daphnia* only when a substantial amount of bacteria was supplied together with a low amount of P-poor algae as food. These results suggest that an abundance of bacteria relative to

algae plays a crucial role in favoring *Ceriodaphnia* over *Daphnia* because these are an important food resource for the former species but not for the latter.

In Chapter 3, I performed experiments to clarify (1) how TFC of *Daphnia* species varies according to changes in P content of food relative to C, and (2) how the rank order of TFC among the species would change according to food P content and mortality rate. Using the simple diagrams with the different assumptions, I first theoretically examined how growth rates of *Daphnia* responded to changes in relative P content of food. Then, we experimentally examined the growth response using seven *Daphnia* species with different body sizes. The results showed that when food P content was low, *Daphnia* decreased the slopes of growth regression against food abundances and subsequently increased the TFC. These results support the assumption theoretically considered that metabolic loss for P has a substantial impact on the response of *Daphnia* to change in P content of food. In addition, the experiments showed that *Daphnia* species having the lowest TFC under high P food exhibited the highest TFC under low P food. The result suggests that competitively superiority of the species can vary according to P content of food. I also examined if the effects of food elemental composition on competition would differ according to mortality rates, because TFC sustaining the population should change with a mortality rate. The experiments showed that when mortality rate was high, much less species were significantly different in TFC at high mortality rate especially when relative P content of food was low. The result suggests that the intensity of competition is somewhat relaxed when low P food is supplied and the mortality rate is high. Finally, I estimated the threshold food concentrations in terms of P (TFP) for *Daphnia* fed LOP algae as TFC for nutritionally rich food. TFP and TFC represent the threshold food levels and illustrate that species-specific "resource" space by TFP and TFC is useful to predict competitive superiority or inferiority among species under given food conditions in terms of abundance and relative P content.

In Chapter 4, I performed the competition experiments to verify the prediction from Chapter 3 using three *Daphnia* species (*D. tanakai*, *D. galeata*, and *D. pulicaria*). According to their TFCs, I predicted that when fed high P food, *D. tanakai* and *D. pulicaria* would be competitively equal to each other but superior to *D. galeata.* By contrast, based on their TFP, it was predicted that when fed low P food, *D. pulicaria* would outcompete *D. tanakai* and *D. galeata*, while neither of the latter two would be competitively superior to the other. The results showed that a competitively superior species reduced the food abundance as low level as its own TFC, which was lower than TFC of the other inferior species and that the biomass of the former was much less affected by the competition. Likewise, my experiment showed that when the two competing species were competitively equal, the competition effect decreased their biomass at the same magnitude. These results confirmed the prediction on changes in

competitive outcomes among *D. tanakai*, *D. galeata*, and *D. pulicaria* due to changes in relative content of C and P in food.

The resource ratio theory states that when there are two or more limiting resources, a supply ratio of these resources determines an outcome of resource competition. This theory has been successfully substantiated especially in the chemostat studies with phytoplankton. Although the theory had been tested even on higher plants and microorganisms, however, it has been not examined using animals except the study showing that the competitive outcomes between two rotifer species were predictably determined by supply rates and ratios of two algal food that were substitutable to each other. Chapter 2 suggested that under P-deficient conditions, competition outcomes between *Daphnia* and *Ceriodaphnia* change depending on supply rate and ratio of algae and bacteria, which were substitutable to each other in some degree. In Chapter 3 and 4, I focused on the two essential elements (C and P) that are not substitutable to each other. This study is the first test examining if the theory can be applied to competition among animals for food differing in element composition. We clearly demonstrated that competition outcome among *Daphnia* species could stoichiometrically change depending on relative element contents of algae, which is changed by relative supply rates of light and nutrients. The fact implies that competition outcomes con change depending on environmental conditions even if players in prey-consumer systems are the same.

My study points that considering food as a package of multiple nutrients or elements, even a single food resource can induce different outcomes in competition by the same two consumer species. Thus, one should not understate the effect of elemental composition in the food resource when examining prey-consumer interactions are examined as in algae-nutrient interactions. The resource ratio hypothesis indicates that in the competition among algae, they can stably coexist depending on rate and ratio of resource supplies. However in the case of my study in Chapter 4, *Daphnia* species would not exhibit stable coexistence because relative content of C and P in the food did not change, as long as TFC and/or TFP are not the same between the species. However, stable coexistence of the species may be possible if nutrient recycling driven by consumers greatly influence relative content of C and P in algae. Further studies are necessary to test this expectation.

論文審査結果の要旨

生物間相互作用、特に餌をめぐる競争は生物群集の構造決定や栄養動態の中心的な生物過程であり、古くから生態学の重要な問題として扱われてきた。近年では、植物を対象に競争理論が進展し、競争の優劣は固定されているものではなく、代替不可の栄養資源の供給比によって異なることが示されている。しかし、動物については代替不可能な複数の栄養資源という視点からの資源獲得競争に関する研究は全く行われていない。動物の資源である餌生物には、炭素やリンなどの必要元素が含まれており、それら元素は代替不可資源と見ることが出来る。もし必要とする元素比が動物によって、また餌生物によって異なるなら、同じ２種間での競争の優劣は餌の元素比によって異なる可能性がある。そこで、このような生態化学量の視点から動物プランクトンである *Daphnia*（ミジンコ）類を対象に藻類を餌資源とした個体及び個体群レベルの実験を行い、植物の代替不可栄養資源に対する競争理論が動物にも適用出来るかを解析した。

動物プランクトンでは一般に小型種よりも大型種のほうが資源獲得競争で優位であると考えられてきたが、同じ２種間でも藻類を餌資源とする競争の優劣は研究によって異なっている。そこで小型種の *Ceriodaphnia quadrangula* と大型種の *Daphnia pulex* を対象に様々な餌条件で実験したところ、競争の優位性は餌となる藻類だけではなく、リンを豊富に含んでいる細菌の存在比によっても異なることを発見し、細菌を考慮することで矛盾する競争の結果が解消出来ることを示した。ついで、*Daphnia* 属の８種を用い、個体維持に必要な炭素の閾値餌密度を測定したところ、その値は種によって、また餌のリン含量によって変化すること、それは個体維持に必要なリン量が種によって異なるためであることを明らかにした。この結果は、餌の炭素：リン比によって同じ２種間でも競争の優劣が異なることを示している。そこで、３種の *Daphnia* 種について個体維持に必要な炭素とリン量から競争理論にもとづく競争の結果を予測し、それを実証する個体群競争実験を行った。その結果、実験は予測と一致し、餌の炭素：リン比によって競争の優劣が変化することを明らかにした。

この一連の研究成果は、代替不可能な栄養資源に対する競争理論は植物だけでなく動物にも適用できることを具体的に示したものであり、生態化学量論の視点からも高く評価出来るものである。理論や基礎データから相互作用の帰結を予測するとともに、それを実験により検証する手法は説得力があり、明快である。これら一連の研究とその成果は、自立して研究活動を行うに必要な高度の研究能力と学識を有することを示している。したがって，岩渕翼提出の論文は博士（生命科学）の博士論文として合格と認めた。