



The ecology and genetic structure of *Palaemon paucidens* populations with alternative life histories in Lake Biwa, Japan

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(別紙様式 4)

論文内容の要旨

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論文題目 (外国語の場合は、その和訳を併記すること。)

The ecology and genetic structure of *Palaemon paucidens* populations with alternative life histories in Lake Biwa, Japan

(琵琶湖産スジエビの生活史多型に関する生態的特性及び遺伝的構造の解明)

論文要旨

During different developmental stages of life history, organisms exhibit different behaviors, many of which are closely related to survival and reproduction. However, as has been observed in various taxa of animals, not all individual members of a group exhibit the same life history or identical behaviors. The study of polymorphic behaviors not only contributes to a more profound understanding of the species' current ecology and characteristics but also helps discern the meaning of behavior in the evolutionary process. In addition, such studies help understand species across various aspects and contribute to the protection of the species.

Palaemon paucidens inhabiting Lake Biwa is an economically important species. This species exhibits an interesting phenomenon that most individuals move from the shallow shores to the bottom of the lake to spend the winter season. Previous studies have suggested that the presence of non-

migratory individuals overwinter in the shallow shores of Lake Biwa. However, knowledge regarding non-migratory individuals is limited. While the species exhibits such a distinctive way of life, little research has been conducted on its ecology in the lake. The aims of this study were as follows: first, to confirm the cause of the migration of *P. paucidens* to deep water, chemical experiments were conducted to analyze changes in lipid and nucleic acid content, as well as stable isotope ratios both before and after migration to deep water. Then, to demonstrate the presence of non-migratory individuals of *P. paucidens*, environmental DNA (eDNA) analysis was applied to examine the distribution of overwintering individuals in the shallow waters of Lake Biwa. Following this, the genetic structure and ecological characteristics of migratory and non-migratory individuals were analyzed, and their differences were discussed. Finally, the eDNA distribution of *P. paucidens* (migratory and non-migratory individuals) in Lake Biwa was tracked over a one-year period and the relationship of habitat preferences of *P. paucidens* to shoreline landscape types was investigated.

In Chapter 2, chemical experiments conducted to analyze changes in nutritional conditions before and after migration to deep water are presented. Previous studies hypothesized that the migration to deep waters was for hibernation. However, the findings of this study contradict this hypothesis. The experimental results in this chapter suggested *P. paucidens* was physiologically active in the deep waters during winter; lipid content was the highest in January and gene expression activity (as measured by the RNA/DNA ratio) remained constant throughout the year, the species foraged in

winter, and different food sources between summer and winter were identified through observation of the carbon stable isotope. Thus, *P. paucidens* individuals that migrate to the bottom in winter are very likely to forage instead of hibernating. Nutrients gained in winter were not reflected in individual growth but might be allocated to gonadal growth and the production of gametes. In addition, both small individuals with no reproductive experience and some post-spawning females overwintered at the bottom, which indicated most females had a life span of one year; however, there were a small number of females with a life span of more than one year.

Chapter 3 presents a species-specific eDNA marker developed to detect *P. paucidens* in water samples and used to examine the distribution and relative abundance of overwintering individuals in the shallow waters of Lake Biwa. The *P. paucidens* eDNA was detected from shallow shores and freshwater lagoons of Lake Biwa in November and February. During this period, migratory individuals have moved to the bottom of the lake, suggesting the detected eDNA is derived from non-migratory individuals. The relative abundance of eDNA copies was estimated by quantitative real-time polymerase chain reaction. Simultaneous sampling of *P. paucidens* and its eDNA, conducted at the inlet and outlet of freshwater lagoons in December, validated the eDNA method as a quantitative measure of the relative abundance of *P. paucidens* local populations. The eDNA approach used here confirmed that some *P. paucidens* individuals overwinter in the shallow waters, suggesting diversity in the life-history of *P. paucidens* in Lake Biwa.

In Chapter 4, analyses of the genetic structure and morphological characteristics including sex, body size, and conditional factor of migratory and non-migratory individuals are presented. In addition, carbon and nitrogen stable isotope ratios are used to estimate the food sources and trophic level underpinning *P. paucidens* polymorphic migratory behaviors. Although this species exhibits two different migratory behaviors, both groups are genetically indistinguishable; the non-migratory female individuals are larger than their migratory counterparts in terms of body size and conditional factor. The stable isotope ratios of the migratory individuals had no significant differences between sampling sites, thereby suggesting the presence of identical food sources in the deep water. In contrast, stable isotope ratios of the non-migratory individuals had significant differences between sampling sites, which suggested the food sources of non-migratory individuals would vary according to the location in the shallow shores.

In Chapter 5, the tracking of the eDNA distribution of *P. paucidens*, using a quantitative real-time polymerase chain reaction method, in Lake Biwa over a one-year period is presented. Water samples were collected from offshore (both from the surface and the benthic areas), shallow shores, and freshwater lagoons. Offshore sampling took place in summer and winter, and shallow shore and freshwater lagoon sampling in all four seasons. During summer, eDNA concentrations were significantly higher in the shallow and lagoon areas than in the offshore bottom sites. Contrastingly, during winter, eDNA concentration were higher in offshore bottom sites, with relatively high and low

eDNA concentrations detected in the lagoons and shallow shores, respectively. These results most likely reflect the spatial and temporal distribution of this species in Lake Biwa. At shallow shores, eDNA concentrations peaked in early August, followed by a significant decline in mid-October, whereas low eDNA concentrations were recorded at the offshore bottom sites in late August. These results suggested *P. paucidens* migrates from the shallow waters to the offshore bottom sites between early August and mid-October.

Thus, in this study, several methods were used to clarify the life history and the distribution of *P. paucidens* in Lake Biwa. These results provide vital evidence for the future management and conservation of this species. The methods of this study would be effective in studying the life history and distribution of other organisms.

論文審査の結果の要旨

氏 名	邬倩倩		
論文題目	The ecology and genetic structure of <i>Palaemon paucidens</i> populations with alternative life histories in Lake Biwa, Japan (琵琶湖産スジエビの生活史多型に関した生態的特性及び遺伝的構造の解明)		
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要 旨			
<p>本博士論文では生態学および遺伝学的な様々な手法を用いて、琵琶湖のスジエビの生活史を明らかにすることを目的として研究を行っている。特に、これまで一般的に知られていた冬季に湖底に移動する個体に加え、移動せずに沿岸域に残留する個体が存在することを明らかにするとともに、そのような異なる行動を示す個体間での生活史の違いおよび遺伝的な背景について検証した。</p> <p>本論文は6章構成であり、全体を通した序論である第1章、スジエビが冬季に湖底に移動する生理的な意義を明らかにした第2章、冬季の沿岸に残留する個体の存在を環境DNA分析によって明らかにした第3章、冬季に湖底に移動する個体と沿岸に残留する個体の遺伝的および形態的な特徴を明らかにした第4章、環境DNA分析によって琵琶湖における年間にわたるスジエビの分布を明らかにした第5章、以上の個別研究で得た結果の総括を行う第6章、謝辞、引用文献からなる。</p> <p>第1章では琵琶湖におけるスジエビの先行研究をまとめるとともに、動物の移動生態を研究することの意義がまとめられている。第2章では、冬季に湖底に移動する個体について、季節ごとの栄養状態の違いを明らかにすることで、その移動がこれまで考えられていたような冬眠や捕食者からの逃避のための消極的なものではなく、栄養を得るための積極的なものである可能性を示した。第3章では、環境DNA分析を用いて冬季に沿岸の浅場に残留する個体が存在する可能性を示</p>			

し、それに続けて実際に個体を採取することで冬季残留個体の実在を明らかにした。第4章では、移動個体と残留個体の遺伝的および形態的特徴を調べて、両者の間では遺伝的な交流があり、これらの個体の生態的な特徴の違いは遺伝的な差異では説明できないことを示した。第5章では、琵琶湖全体のスジエビの分布を環境DNA分析を用いて明らかにし、冬季に内湖に多数の残留個体が存在することや、移動個体の移動タイミングの推定、スジエビの景観選考性などを議論した。第6章ではこれら研究の成果を受けてスジエビが条件戦略をとるという新たな仮説を提唱した。また、本種の保全にむけたサイエンスコミュニケーションの重要性を指摘した。

本論文ではこれまで詳細が不明であったスジエビの生活史について、冬季の沿岸残留個体が存在すること、移動個体が湖底付近で摂餌していること、これらの個体群の間の遺伝的な交流があることなど、新たな知見を数多く得ることができた。これらの知見を得るにあたっては、環境DNA分析、脂質分析、RNA/DNA比分析、安定同位体分析、マイクロサテライト分析などの現時点で用いることのできる様々な分析手法を駆使しており、信頼性の高いデータを得ている。また、これらの結果を総合し、スジエビがそれぞれの栄養条件や成熟状態に応じて湖底に移動するか沿岸に残留するかを選択する条件戦略をとるという仮説を提唱した。このような淡水湖における甲殻類の深淺移動や条件戦略については他に報告例がなく、甲殻類の生態に関する新たな視点を与えた点において非常に高く評価できる。

なお、本論文を構成する各章(第2～5章)は個別の投稿論文としてまとめており、第2章はEcosphere誌(査読あり)、第3章はFreshwater Science誌(査読あり)、第5章はEnvironmental DNA誌(査読あり)にて出版済みである。また、第4章は投稿直前の段階である。下記に既に公表されている論文の詳細を示す。

Wu, Q., Takami, Y., Minamoto, T., Ishikawa, T. (2019) The life history with seasonal migration of the lacustrine shrimp *Palaemon paucidens* in an ancient lake in Japan. Ecosphere 10, 4, e02628.

Wu, Q., Kawano, K., Uehara, Y., Okuda, N., Hongo, M., Tsuji, S., Yamanaka, H., Minamoto, T. (2018) Environmental DNA reveals non-migratory individuals of *Palaemon paucidens* overwintering in Lake Biwa shallow waters. Freshwater Science 37 (2), 307-314.

Wu, Q., Kawano, K., Ishikawa, T., Sakata, M. K., Nakao, R., Hiraiwa, M. K., Tsuji, S., Yamanaka, H., Minamoto, T. (2019) Habitat selection and migration of the common shrimp, *Palaemon paucidens* in Lake Biwa, Japan - an eDNA-based study. Environmental DNA 1, 54-63.

本研究は琵琶湖に生息するスジエビについて、その生態的特性及び遺伝的構造を研究したものであり、甲殻類の深淺移動や条件戦略について重要な知見を得たものとして価値ある集積であると認める。

よって、学位申請者の邬倩倩は、博士(理学)の学位を得る資格があると認める。