行政院國家科學委員會專題研究計畫研究成果報告

福山魚怪的生活史及性轉變

Life history and sex change of *Ichthyoxenus fushanensis* (1/2)

計畫編號:NSC89-2611-B-002-001

執行期間:88 **年** 8 **月** 1 **日至** 89 **年** 7 **月** 31 **日**

計畫主持人: **戴昌鳳　台灣大學海洋究所**

一、　中英文摘要

福山魚怪屬於等足類係一新發現之台灣特有種類，以一囊狀薄膜，成對地寄生在台灣鏟頷魚腹腔。魚怪具有先雄後雌的性轉變現象。本研究提出「為何天擇有利於福山魚怪性轉變的演化？」的可能解釋。

福山魚怪必需在短暫的幼生階段尋獲並附著宿主，因此，其幼生階段有很高的死亡率，僅很少數的幼生能成功地與宿主形成寄生關係。高死亡率使得天擇作用有利於能產生更多子代的雌性。而雌性孕卵數則直接與其體型大小呈正相關。雖然，福山魚怪的雌雄個體體型大小均與宿主的體型成正相關，但在排除宿主體型的影響因子後，雌雄體型間則成負相關。因此，在同一宿主之雌雄性別間，可能存在著空間或食物上的競爭。這種空間或食物上上的限制因素，導致雌雄性體型上的互易作用(trade-off)**；亦即，在一定體型的宿主內，越小的雄性越有助於形成較大而且多產的配偶雌性。此時，天擇將有利於先雄後雌性轉換性的演化。**

A flesh burrowing parasitic isopod, *Ichthyoxenus fushanensis*, was found infecting the body cavity of a freshwater fish, *Varicorhinus bacbatulus*, in pairs. The pattern of sequential hermaphroditism of *I. fushanensis* is protandrous. Here we investigate the question why selection favors protandrous sex change for *I. fushanensis,* through analyzing the interactions among clutch size, female size, male size and the host size.

The number of young per brood was positively correlated with the body size of female. When the effect of host size is removed, there is a significant negative correlation between the sizes of paired males and females. This suggests that the resources available from host fish are limited, and that both larger female body size and smaller male body size are important determinants of *Ichthyoxenus fushanensis* offspring number. Due to the constraint of very low success rate in hunting for a host of mancas, the selection pressure favor larger female which produce more mancas. The pattern of interactions among host, male, female in size and the number of mancas, may be considered as a selection pressure for *I. fushanensis*, where the resource or available space is constrained by the size of host.

Keywords: *Ichthyoxenus fushanensis*, parasitism, sex change, selection

二、　計畫緣由與目的

Both protandry and protogyny have

possibly developed independently several times in the crustaceans, and the Isopoda is the only crustacean order in which both protandrous and protogynous species occur (Brook, et al., 1994).

Ichthyonxenus fushanensis is a newly described parasitic isopod of Cymothoidae collected from the freshwater fish, *Varicorhinus bacbatulus*. The isopod is found in a thin-walled membranous sac in the body cavity of the host (Tsai and Dai, 1999). The opening of the sac is an orifice near the posterior, ventral margin of the pectoral fin of the host fish. Usually a male and an upside-down female lie in the sac, with their posterior ends oriented toward the orifice. The orifice opens directly to the outer environment, and provides a channel for gas exchange, excretion for the occupants and release of mancas. They establish the parasitic relationship only with *V. bacbatulus*. Brooding females were found from April to July. The free-living mancas occurred from June to October. The mancas have a short free-living stage with good swimming ability. Once they enter the host, they lose the swimming ability completely. When the mancas are released, they hunt for the host immediately, and die within a week if they do not infect the host fish successfully (Tsai and Dai, 1999). *Ichthyonxenus fushanensis* was usually found in pairs (male and female). Some were found as single males, but never as single females. When present in pair, female is larger than male. The present of vestiges of penes in all females provide a evidence of protandrous sex change in *I. Fushanensis* (Tsai and Dai, 1999).

The size-advantage model proposes that sequential hermaphroditism occurs when an individual reproduces most efficiently as a member of one sex when small or young, but as a member of the other sex when it gets older and larger (Brook, et al., 1994). It predicts protogyny where there is sexual selection for larger males, and protandry where the young stages must hunt for a suitable environment. This model was originally proposed by Ghiselin (1969), and has been extensively modeled. Protandry may be advantageous when female's fecundity increase is dependent of age or size but male mating success remains independent of size (Warner, 1988; Brook, et al., 1994). Conversely, protogyny may arise when small males are prevented from mating with females by larger males, making it advantageous to become male only when a competitive larger size is reached (Warner, 1988; Brook, et al., 1994).

Poulin (1995a) examined the evolutionary influences on body size and fecundity in free-living and parasitic isopods using comparative methods, and concluded that the body size of some parasitic isopod groups may have been inherited from free-living ancestors, and that parasitic isopods appear to have evolved toward higher fecundity despite not having evolved toward larger body size after diverging from free-living ancestors. Here, we provide an explanation for selective pressure favoring protandrous sex change for *Ichthyoxenus fushanensis.* We focus on the interactions among the size of host, male and female that may affect the number of offspring, and the association with the pattern of sex change.

三、 結果及討論

Parasitism and the patterns of sex change

The widely accepted myth about parasites is that they are evolved toward smaller body size (Hanken and Wake, 1993) and extremely high fecundity (Price, 1974; Poulin, 1995b). Poulin (1995a) found some evidences, from proper phylogenetic studies, that switching to parasitism resulted in decreases in body size in isopods which is independent of the type of hosts colonized. The size of parasitic crustaceans might be limited by the space available at their site of attachment; for instance, parasitic copepods attaching to the fins or skin of fish could grow to larger sizes than endoparasites (Poulin, 1995b). The space available for parasite occupation in the host may constraint the evolution of parasite body size (Poulin, 1995b). Poulin (1995a,b) concluded that parasitic isopods appeared to have evolved toward higher fecundity despite not having evolved toward larger body sizes after diverging from free-living ancestors.

Generally, body size is positively correlated with fecundity, both within and across species in invertebrates (Poulin, 1995b). If the trend of evolution toward high fecundity is important for transmission success from free-living to parasitic life-style in isopod (Poulin, 1995a, b), we may then expect natural selection to favor protandrous sex change which result in a larger female and consequently higher fecundity. All the parasitic forms are protandry, but free-living species are either protandrous or protogynous. It implies that protandrous sex change may be a meaningful determinant of transmission success. The side-advantage model predicts protandry where the young stages must hunt for a suitable environment (Ghiselin, 1969; Brook, et al., 1994). In laboratory, 99.6 ± 0.4 % of the manca of *Ichthyoxenus fushanensis* died within a week after releasing from host (personal observation). Due to this constraint of very low success rate of hunting for a host (lower than 0.5 %), the selection pressure would favor protandrous sex change resulting in larger females which could produce more mancas.

The effect of male size on clutch size

In *Ichthyoxenus fushanensis*, the number of manca produced per brood increases with the size of female. The effect of male size increases on the clutch size is negative, when the effect of host and female size are removed. It seems unlikely that there is a benefit for the increase of male size by affecting an individual's mating and fertilization success. Besides, there is a significant negative relationship between male size and female size, when the effects of host size are removed. This implies that the resource (either available space or food) supplied by host fish is limited, and that there appears a competition between male and female sizes. In *I. fushanensis*, the effect of increasing male size on the number of manca is negative, either directly by reducing the available space for development of manca or indirectly through the decrease of female's capacity via the competition with the paired male. This competition between paired individuals also suggests that the male will be smaller, in order to obtain a larger female and consequently more offspring per brood. Therefore, smaller male in a pair is beneficial for increasing fecundity. This negative relationship between female and male size is not the evolutionary result of protandrous sex change, because it may vary theoretically from positive to negative. The female size and the consequent clutch size may increase or reduce, or even vary independently with the male size. The negative correlation between male size and female size would favor the organisms evolving to extreme condition in either protandry (smaller male and larger female) or protogyny (larger male and smaller female). In *I. fushanensis*, the trade-off between paired individuals infecting same host may, thus, be considered as a selection pressure rather than an evolutionary result of protandrous sex change, where the resource or available space is, however, constrained by the host size.

Effect of host size

Within some species of cymothoid isopod parasitic on fish, there is a positive relationship between isopod size and host size (Brusca, 1981; Poulin, 1995a). The same phenomenon has been observed in several species of bopyrid isopods parasitic on crustaceans (e.g. Allen, 1966; Warren, 1974). Within species, parasitic isopods provides some evidence of development plasticity in size, with individual parasite attaining a size proportional to the size of their host (Wenner and Windsor, 1979). In this study, the clutch size was represented by the number of released mancas. This measurement comprises two components: the reproductive potential (fecundity) of the female, and the brooding mortality (mortality during the development from egg to manca). Host size affects not only on the body size of female and male, but also the number of manca released. This positive effect on clutch size is probably due to the result of increasing available space by the continuous growth of host during brooding.

五、計畫成果自評

本計畫已順利完成，並已將成果發表於 Evolutionary Ecology 13: 327-338.

六、參考文獻

Allen, J. A. (1966). Notes on the relationship of the bopyrid parasite *Hemiathrus abdominalis* (Krφyer) with its host. Crustaceana 10: 1- 6.

Brook, H. J., Rawlings, T. A. and Davies, R W. (1994). Protogynous sex change in the intertidal isopod *Gnorimosphaeroma oregonense* (Crustacea: Isopoda). Biol. Bull. 187: 99- 111.

Brusca, R. C. (1981). A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zool. J. Linn. Soci. 73: 117- 199.

Carefoot, T. H. (1973). Studies on growth, reproduction, and life cycle of supralittoral isopod *Ligia pallasii*. Mar Biol. 18: 302- 311.

Charnov, E. L. (1986). Size advantage may not always favor sex change. J. Theor. Biol. 119: 283- 285.

Ghiselin, M. T. (1969). The evolution of hermaphroditism among animals. Q. Rev. Biol. 44: 189- 208.

Hanken, J. and Wake, D. B. (1993). Miniaturization of body size: organismal consequences and evolutionary significance. Annu. Rev. Ecol. Syst. 24: 501- 519.

Kittlein, M. J. (1991). Population biology of *Sphaeroma serratum* Fabricius (Isopoda; Flabellifera) at the port of Mar del Plata, Argentina. J. Nat. Hist. 25: 1449-1459.

Poulin, R. (1995a). Evolutionary influences on body size in free-living and parasitic isopods. Biol. J. Linn. Soc. 54: 231- 244.

Poulin, R. (1995b). Evolution of parasite life-history traits: myths and reality. Parasitol. Today 11: 342-345

Price, P. W. (1974). Strategies for egg production. Evolution 28: 76- 84.

Tsai, M. L. and Dai, C. F. (1999). *Ichthyoxenus fushanensis,* new species (Isopoda: Cymothoidae) parasite of the freshwater fish, *Varicorhinus bacbatulus,* from northern Taiwan. J. Crust. Biol. (in press).

Warner, R. R. (1988). Sex change and the size-advantage model. Trends Ecol. Evol. 3: 133- 136.