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Seasonal population dynamics of *Neoechinorhynchus qinghaiensis* in the carp, *Gymnocypris przewalskii przewalskii*, from Qinghai Lake, China

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Abstract

Studies on the seasonal population dynamics of *Neoechinorhynchus qinghaiensis* (Acanthocephala: Neoechinorhynchidae) in its fish host *Gymnocypris przewalskii przewalskii* in the Qinghai Lake, China, were carried out with samples taken in May 1991, August 1992, November 1992 and February 1993. Prevalences were higher than 44% in all seasons. The mean intensity of infection was above 124 worms per fish. The maximum intensity of worms recovered from a single fish was 1402 in the autumn of 1992. Differences in the mean abundance, mean intensity and prevalence are not statistically significant relative to season and this is likely to be related to the stable temperatures recorded at the bottom of Qinghai Lake. Over-dispersed distributions of *N. qinghaiensis* in the host population, due to heterogeneity and feeding habits, were observed in all seasons. The size composition of both sexes of *N. qinghaiensis* showed males to be less than 3.5 mm and females between 0.5 and 4.25 mm, with the main recruitment phase in the worm populations occurring in the autumn, extending through winter and spring with the lowest recruitment occurring in the summer. The maturation and copulation of worms were mainly focused in the summer season. The sex ratio of female to male was both high in winter (1.51:1) and spring (1.48:1). The higher proportion of females and the change in the worm sex ratio in winter can be attributed to the reduced longevity of male worms. As immature male worms exhibit a higher proportion of the worm population than females in all seasons, further studies are needed to determine if such a situation compensates for the shorter life span of males.

Introduction

Qinghai lake, located in the northeast of the Qingzang plateau (Qinghai province and Tibet), is the largest inland brackish-water lake in China (salinity of 17‰ resulting from ancient geologic and lacustrine reasons), with an area of about 4500 square km and an altitude of 3200 m. There are only two species of fish living in the lake, the economically important carp species, *Gymnocypris przewalskii przewalskii*, and *Namachilus scleropterus* Herzenstein, which is a small fish only distributed close to the edge of the lake and of no considerable economic value (Biology Institute of Qinghai Province, 1974).

In Qinghai Lake, spring extends from April to June, during which time the ice cover completely melts and the surface water temperature rises to a mean of 8.1°C in May without any thermocline. Summer occurs from July to September when the water temperature reaches a peak of 14.2°C in July, whereas near the bottom, at 25 m, the temperature is only 8°C. Autumn is between October and December when the surface water temperature declines to 6.9°C in October, and finally the whole lake is covered

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Table 1. Seasonal parameters of *Neoechinorhynchus qinghaiensis* in *Gymnocypris przewalskii przewalskii*.

	Spring (May 1991)	Summer (Aug. 1992)	Autumn (Nov. 1992)	Winter (Feb. 1993)
No. of fish sampled	58	63	62	66
Length of fish (mm)*	332±2.1	320±2.5	306±2.7	301±1.7
Prevalence (%)	44.83	61.90	67.74	62.12
Mean intensity*	129.5±50.1	124.5±37.1	178.8±36.4	134.9±33.1
Intensity	1~1090	1~1002	1~1402	1~995
Abundance*	58.2±24.2	76.26±24.0	121.1±31.7	83.8±22.1
Variance/mean ratio	583.2	684.6	513.8	381.0
k value	0.09	0.14	0.15	0.15
Sex ratio (f/m)	1.48	1.33	0.89	1.51
Length of female*	1.55±0.06	2.30±0.07	1.60±0.09	1.71±0.06
Length of male*	1.29±0.05	1.93±0.07	1.23±0.06	1.25±0.05
Width of niche	0.67	0.67	0.69	0.68

* Mean ± standard error.

with ice by December. The thermocline is broken down by the strong northwest winds. During the winter from January to March the entire lake is covered with thick ice (0°C at 5 m in February) and the temperature at the bottom is 4.5°C.

Liu *et al.* (1982) described two species of acanthocephalans (*Neoechinorhynchus qinghaiensis* and *Echinorhynchus gymnocyprii*) infecting *G. przewalskii przewalskii* from the Qinghai Lake. The mean abundance and intensity of *N. qinghaiensis* in *G. przewalskii przewalskii* in the Qinghai Lake increased with an increase in fish body length, which was probably related to the larger food consumption by older fish (Yang, 1991). No seasonal studies have been undertaken on *N. qinghaiensis* in Qinghai Lake, although a number of studies on seasonal population dynamics of neoechinorhynchid acanthocephalans in fish from inland waters have been reported (Walkey, 1967; Eure, 1976; Muzzall & Bullock, 1978; Muzzall, 1980, 1984; Font, 1983; Hubschman, 1985; Amin, 1986; Lasee, 1989; Moravec & Scholz, 1994). The present study therefore focuses on the seasonality of *N. qinghaiensis* population dynamics in Qinghai Lake.

Materials and methods

The present study was conducted in the fishing grounds of Qinghai Lake from May 1991 to February 1993. Fish ranging between 300 mm and 350 mm in body length were selectively sampled in order to avoid any biased effect of host size on the results because the bigger fish have more *N. qinghaiensis* in fish less than 300 mm in body length (Yang, 1991). Fish were obtained from fishermen on the lake but climatic factors prevented sampling taking place on a monthly basis.

Fish were taken to the field laboratory alive, measured, sexed, and dissected within 36 h of capture. The entire alimentary canal was removed and divided into ten sections based on percentages of the total length from the anterior end. Each section was opened and examined for acanthocephalans which were placed into physiological saline solution for 4–12 h at 10°C to enhance eversion of the proboscis prior to being preserved in 70% ethanol solution. The number of *N. qinghaiensis* in each fish was recorded.

About 200 worms from each season sample were prepared for staining by standard methods. Female worms were divided into three developmental stages: (i) immature ovary not fragmented; (ii) ovarian balls present; and (iii) gravid-ovarian ball and eggs present and those with eggs only. Males were also divided into three groups, immature (testes and sperm duct smaller and indistinct in stained specimen), mature and mature with everted bursa (Muzzall, 1980). Worm length was measured in millimetres from the top of the proboscis to the posterior end of the body as worms become fully extended when placed in cold water prior to fixation.

Prevalence, mean intensity and mean abundance of parasites were used as defined by Bush *et al.* (1997).

The software SPSS (Statistic Package for Social Science) 6.0 for Windows was used to analyse the data. The significance test for seasonal changes in abundance, mean intensity, mean length of parasites and mean length of fish was carried out using one way ANOVA (Bryman & Duncan, 1997). The method of calculating the negative binomial distribution parameter k, which is inversely related to the degree of aggregation, was taken from Southwood (1978). Niche breadth was calculated using equation 29 of Hurlbert (1978) and the significance of seasonal changes of *N. qinghaiensis* distribution along the host intestine was tested by the dependence test of r × c crosstabs (Li & Wang, 1998).

Results

Seasonal changes in infection parameters of N. qinghaiensis

A total of 31242 individuals of *N. qinghaiensis* was collected from 249 individuals of *G. przewalskii przewalskii* between May 1991 and February 1993 for seasonality analyses. The prevalence, intensity and other parameters of *N. qinghaiensis* in the fish host throughout the seasons are shown in table 1. Prevalence values were above 44% in all seasons sampled but without a distinct seasonal trend. Mean intensity reached a peak in the autumn, and then decreased throughout the winter and spring to reach its lowest level in summer. However, no significant seasonal differences were found in mean intensities

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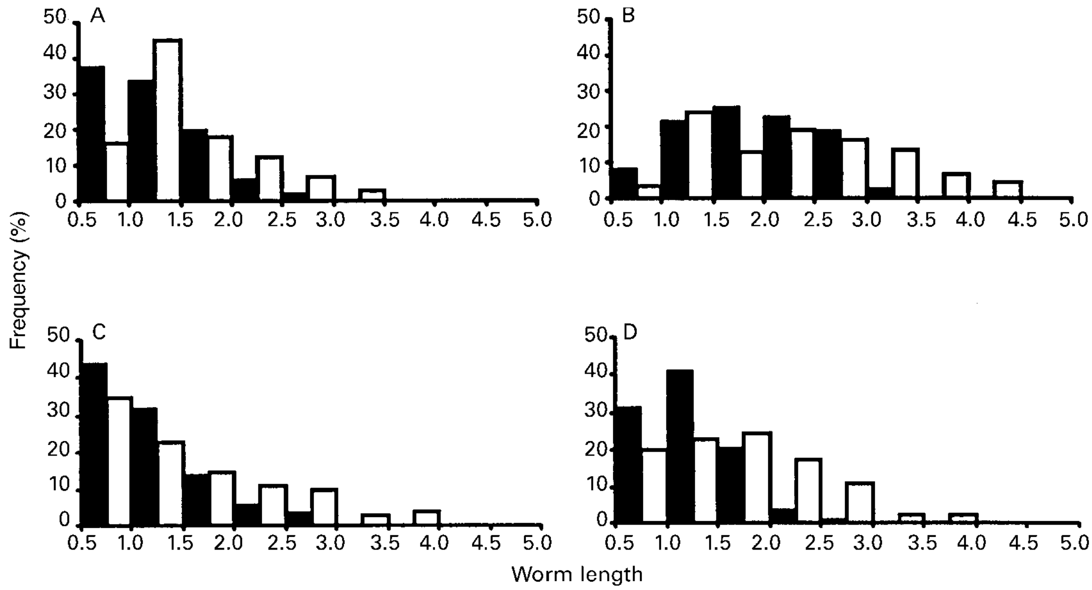

Fig. 1. The length of male (■) and female (□) *Neoechinorhynchus qinghaiensis* populations in the host *Gymnocypris przewalskii przewalskii* in spring (A), summer (B), autumn (C) and winter (D).

(F ratio = 0.3306, $P = 0.8023$) and abundance (F ratio = 0.7966, $P = 0.5118$).

The sex ratio of females to males was highest in the winter (1.51:1), then decreased through the spring (1.48:1) and summer (1.33:1) and reached its lowest level in the autumn (0.89:1).

The results of t-tests for mean worm lengths in different seasons demonstrated that both the males and females in the summer were significantly higher than those in other seasons. From the summer to autumn the mean lengths of both sexes significantly decreased (for males 2-tailed sig. <0.0001, df = 167; for female 2-tailed sig. <0.0001, df = 267). From the autumn to winter the change was not statistically significant (2-tailed sig. >0.33 and 0.77 for males and females respectively). From the winter to spring the increase in the mean male

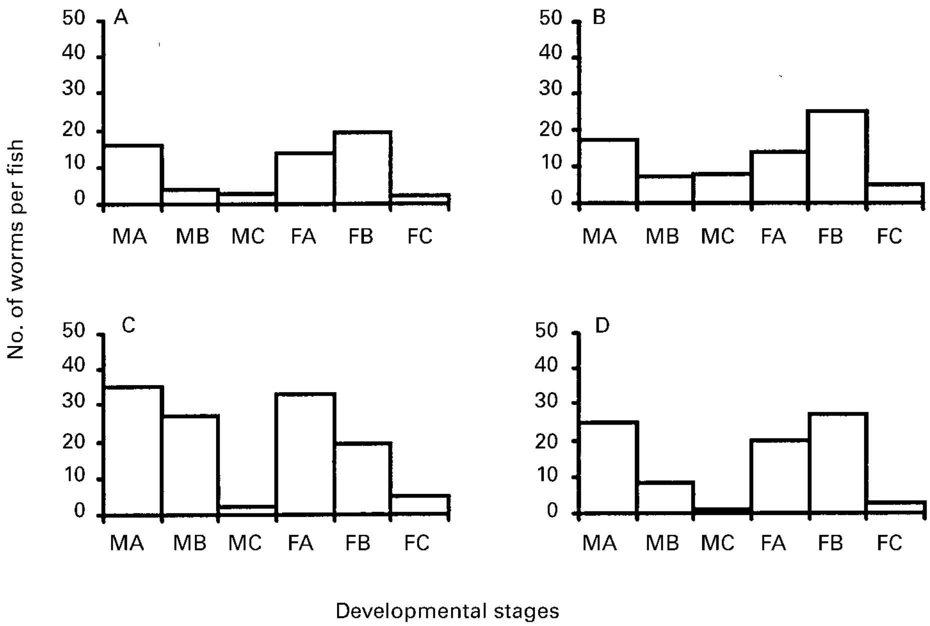

Fig. 2. The population structure of *Neoechinorhynchus qinghaiensis* in *Gymnocypris przewalskii przewalskii* in different seasons (MA, immature male; MB, mature without everted bursa; MC, mature male with everted bursa; FA, immature female; FB, ovarian ball female; FC, gravid female.)

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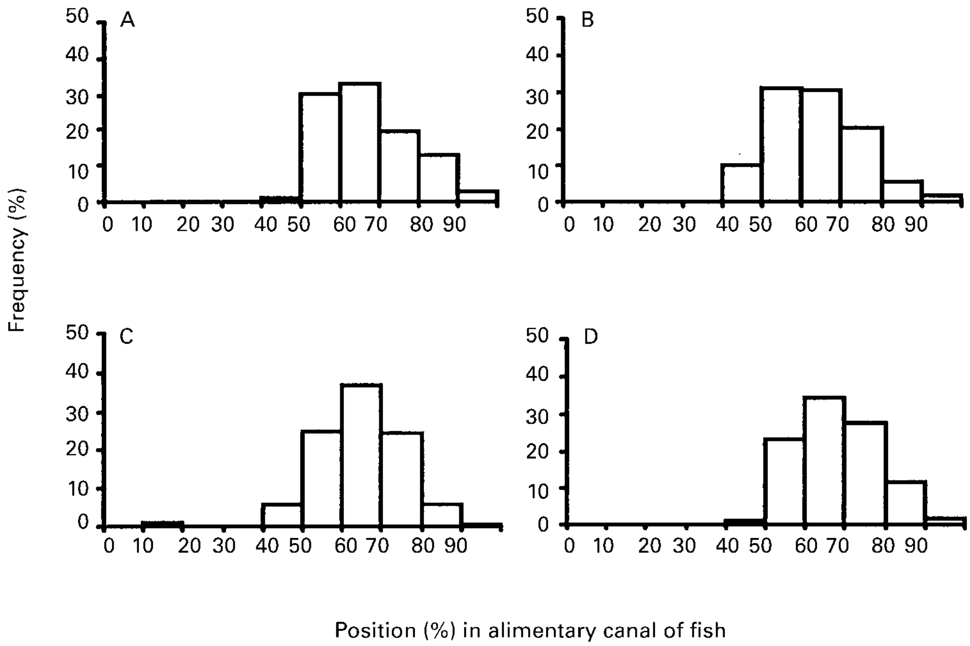

Fig. 3. Distribution of *Neoechinorhynchus qinghaiensis* in alimentary canal of *Gymnocypris przewalskii przewalskii* in spring (A), summer (B), autumn (C) and winter (D).

length was not significant (2-tailed sig. >0.58, df = 175) but the decrease in the mean female length was significant (2-tailed sig. <0.1, df = 233). The mean length of both sexes reached their peak from spring to summer during the entire sampling period (2-tailed sig. <0.0005, df = 167 and 267 for male and female respectively).

Frequency distribution of N. qinghaiensis

The distributions were highly over-dispersed (table 1) with the frequency distributions showing similar patterns in different seasons. Variations in the binomial distribution parameter k tended to parallel the change in prevalence values, with a higher prevalence generating a lower degree of over-dispersion.

Size composition of the N. qinghaiensis *population*

The lengths of female *N. qinghaiensis* ranged between 0.48 mm and 4.25 mm and those of males between 0.47 mm and 3.50 mm. The mean female length was significantly higher than that of males (2-tailed sig. P = 0.0000 df = 824). The proportion of individual females and males less than 1 mm was lowest during the summer (3.09% and 8.11%), peaked in the autumn (34.65% and 44.04%), and then declined slowly throughout the winter (20.3% and 31.7%) and spring (15.8% and 37.8%) (fig. 1). These changes indicate that worm recruitment was active throughout the seasons, especially in the autumn, winter and spring. Males less than 1 mm formed a higher proportion of the population than females. The proportion of males larger than 2.5 mm in length decreased considerably from the summer (21.62%) to the autumn (3.57%) and winter (1.22%), whereas females with lengths more than 3 mm which had begun to decrease at the same time as the males continued to decrease from 4.68% in winter to 2.8% in spring (fig. 1). This indicated a significant loss of larger males, which continued through to the spring.

Population structure of N. qinghaiensis

Males with an everted bursa and gravid females were present throughout the seasons, with maximum numbers in the summer (fig. 2). Immature worms were also recovered throughout the seasons, with a peak in the autumn. There was a clear loss of mature males from the summer to the autumn, with a loss of females occurring from autumn to winter. This demonstrated an earlier loss of post-copulatory males than gravid females.

Distribution of N. qinghaiensis *along the alimentary canal*

The distribution of *N. qinghaiensis* population along the alimentary canal was stable in all four seasons ($X^2 = 25.91, < X^2_{0.5} = 26.34, P > 0.5$, df = 27) (fig. 3). Only a small number of worms was recovered from the anterior 10–20% of the alimentary canal and no posterior migration was detected. The niche breadths of worms in different seasons were similar, although niche breadth did vary with the mean intensity of infection. Seasons with higher mean intensities had wider ecological niches.

Discussion

No pronounced seasonality of the prevalence and abundance of *N. qinghaiensis* in the host *G. przewalskii przewalskii* in Qinghai Lake was observed. This indicated

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that recruitment and mortality were counteracted or simply that there was no prolonged period when mortality exceeded recruitment, or vice versa. This 'stability' could be explained by the fact that increased establishment was accompanied by a significant loss of worms from autumn to spring and balanced by the decreased recruitment with the ebbed loss of worms during the summer. The size composition and population structure of *N. qinghaiensis* populations revealed that both recruitment and loss of worms took place mainly in the colder seasons of autumn, winter and spring. Aho *et al.* (1982) suggested that long-term consistency of seasonal patterns of parasites in aquatic systems might often be the result of ecosystem stability, rather than of factors such as density-dependent regulation or premunition. This is especially true of parasites that complete their entire life cycle within the aquatic system. This explanation is helpful in understanding the stability of *N. qinghaiensis* in Qinghai Lake, as the existence of a thermocline in winter and summer keeps the temperature at the bottom of the lake relatively stable.

When compared with some of those parasite species in the same genus in their hosts (Walkey, 1967; Muzzall & Bullock, 1978; Muzzall, 1980; Hubschman, 1985; Amin, 1986; Lasee, 1989; Valtonen & Crompton, 1990; Dorucu *et al.*, 1995), both the prevalence and mean intensity of *N. qinghaiensis* in *G. przewalskii przewalskii* were of a higher rank. This might result from more frequent interactions and adaptations between parasite and host due to the scarcity of host species in Qinghai Lake.

Over-dispersed distributions of *N. qinghaiensis* populations in *G. przewalskii przewalskii* in the four seasons are observed, which follow the common distribution pattern of parasites in their host population (Pennycuick, 1971; Anderson, 1974; Gordon & Rau, 1982; Scott, 1982). This pattern is generally described as the negative binomial distribution model of a different parameter k, an index used to judge the relative degree of aggregation (Crofton, 1971). The distribution pattern reported herein might be primarily determined by density independent factors such as heterogeneity in temporal and spatial distribution of infective stages together with changes in the feeding behaviour and food selectivity of *G. przewalskii przewalskii*. The ecological features of the fish host were notable, as three groups of fish (herbivores, carnivores and omnivores) were observed (Biology Institute of Qinghai Province, 1974). The degree of over-dispersion of *N. qinghaiensis* in *G. przewalskii przewalskii* in Qinghai lake was very high by comparison with variance to mean ratios of *N. rutili* in some definitive hosts (Valtonen & Crompton, 1990). This may be attributed to the high abundance of *N. qinghaiensis* in *G. przewalskii przewalskii* in Qinghai Lake, which resulted from the superimposition of random recruitment. Boxwell & Patil (1970) proposed that over-dispersion could simply result from the superimposition of one randomly varying factor upon another.

For dioecious parasites like nematodes, acanthocephalans, some species of trematodes, and some parasitic protozoa, the sex ratio and mating system (monogamous or polygamous) have a profound impact on the fecundity and relationship of host and parasite (Morand & Rivault, 1992). Eure (1976) observed a drastic loss in the male acanthocephalan, *Neoechinorhynchus cylindratus*, during the summer when copulation had already been completed. Similar results were reported for *Echinorhynchus clavula* (Chubb, 1964), *E. truttae* (Awachie, 1965), *Acanthocephalus parksidei* (Amin, 1975), *Moniliformis dubius*, *Macracanthorhynchus hirudinaceus*, *Polymorphus minutus* and *Neoechinorhynchus saginatus* (Parshad *et al.*, 1981) and this may result in the loss of presumably short-lived males. Variation in the population structure of *N. qinghaiensis* in *G. przewalskii przewalskii* was also observed in Qinghai Lake in different seasons. A higher sex ratio of females to males of *N. qinghaiensis* was recorded in winter and spring. Female *N. qinghaiensis* outnumbered males in winter and spring, which was probably due to the earlier expulsion of short-lived males in winter as a result of a large amount of new recruitment and relatively poor host nutrition in colder seasons. Crompton *et al.* (1984) suggested that mechanisms of over-dispersion may result from differences in worm survival due to availability of carbohydrate in the host intestine (Crompton *et al.*, 1984). A sharp decrease in the sex ratio in autumn was linked with maximum recruitment of new worms. Interestingly, numbers of immature males were larger than those of immature females in all seasons and this could explain the female to male ratio of less than one in the autumn when new recruitment was most active. Further studies are required to investigate whether the infra-population in the intermediate host is biased to males in order to compensate for its shorter life span. The increase in the sex ratio in winter might be the result of a decrease in recruitment and an earlier expulsion of males.

No significant changes in the distribution of *N. qinghaiensis* along the alimentary canal of the fish were observed throughout the seasons.

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