Temporal variations in the infection of a population of *Cerithidea cingulata* by larval trematodes in Kuwait Bay

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Abstract

The prosobranch gastropod *Cerithidea cingulata* (Gastropoda : Potamididae) in Kuwait Bay was examined for larval trematode infections over a 17-month period. A total of 2537 snails were examined and 1265 (49.9%) found to be infected with one or more species of trematodes. The component community in the snail comprised 12 species representing the families Cyathocotylidae (2), Echinostomatidae (2), Haplosplanchnidae (1), Heterophyidae (2), Microphallidae (1), Philophthalmidae (2), Plagiorchiidae (1) and Schistosomatidae (1). Cyathocotylid II (41.6%) was by far the most prevalent species followed by the microphallid (3.9%), the two species comprised 90% of the total trematode fauna. The prevalence of infection increased with shell size and was significantly higher in male (47%) than female (33%) snails. Multiple infections were observed in only 15 (1.2%) of the infected snails; cyathocotylid I and cyathocotylid II combination occurred 14 times and heterophyid I and the microphallid occurred once. Trematode species were more diverse and prevalent in winter, and cercarial shedding peaked in summer. Behaviour of the definitive host and snail population dynamics were probably the major contributors to the detected temporal pattern in the infections.

Introduction

Studies on trematode infections in snail intermediate hosts have often revealed rich and taxonomically diverse species, occurring in highly structured and dynamic communities (Kuris, 1990; Sousa, 1990, 1993, 1994; Bush *et al*., 1993; Esch & Fernandez, 1993; Kuris & Lafferty, 1994; Curtis, 1997). Esch *et al*. (1993) reviewed various internal and external structuring forces that are collectively responsible for shaping trematode communities in snails. Species antagonisms, spatial and temporal heterogeneity of infective stages, and host behaviour and population dynamics are thought to play a dominant role in determining trematode community structure.

Members of the genus *Cerithidea* (Gastropoda: Potamididae) are common intertidal snails in tropical and subtropical regions, and typically inhabit *Salicornia* marshes, intertidal creeks and mudflats of bays and estuaries (Houbrick, 1984). *Cerithidea* along the coasts of California and Florida (Martin, 1972; Yoshino, 1975; Bush *et al*., 1993), Gulf of Mexico (Cable, 1956; Holliman, 1961), Tokyo Bay (Ito, 1956, 1957), and Bengal Bay (Mani & Rao, 1993) serve as intermediate host for at least 50 species of trematodes. In Kuwait Bay, six species were recorded in *C. cingulata* (Gmelin, 1791) (Abdul-Salam & Sreelatha, 1991).

The present study is an attempt to determine the occurrence of larval trematodes in a population of *C. cingulata* in Kuwait Bay, and to assess temporal changes in the prevalence, diversity, and cercarial shedding, and occurrence of multiple infections during a 17-month period.

Materials and methods

Kuwait Bay is characterized by extensive tidal mudflats formed by the settling of silt drifted by the rivers Tigris and Euphrates through the Shatt Al-Arab waterway. The study site is located in Sulaibikhat Bay, a small embayment south of the larger Kuwait Bay, about 10 km

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west of Kuwait City. The Sulaibikhat shoreline is a typical of the muddy tidal flats of the Bay and it is relatively undisturbed. Tides are diurnal, varying from 3.5 to 4.0 m. At high tide, the tidal flats serve as an important nursery ground for larvae and juveniles of many species of invertebrates and fishes. At low tide, the vast intertidal zone is a major resting and feeding ground for large populations of endogenous and migratory birds. *Cerithidea cingulata* is the most predominant mollusc in the Bay occurring in dense aggregates at the lower shore. Monthly surface water temperatures in Kuwait Bay for the study period were obtained from the Mariculture and Fisheries Department, Kuwait Institute for Scientific Research. The water temperatures showed a mean annual range of 10–20°C in winter and 20–45°C in summer.

A sample of up to 150 *C. cingulata*, representing a range in shell length, was collected monthly from March 1995 to July 1996. The shell length (apex to aperture) of each snail was measured to the nearest millimetre using a dial micrometer caliper (Rabone Chesterman Ltd, Switzerland). Each snail was isolated at room temperature (23–25°C) in a 10-ml glass vial containing 5 ml filtered seawater. Snails were placed under diffuse overhead fluorescent light (1400 lux) for 72 h, and vials were then examined daily under a dissecting microscope for the presence of cercariae. Cercariae released after 24 h exposure to light were stained in Lugol's solution and counted under a dissecting microscope. Snails not shedding cercariae were crushed and the digestive gland–gonad complex was checked for the presence of prepatent infections. The sex of snails was determined by gonad colour, bright yellow in males and blue-green in females. Snails shedding cercariae were not crushed, but were marked by nail polish and maintained in 2-l beakers containing about 1-cm layer of mud from the field and 100 ml sea water. Twice a month the snails were shed to check if there were species switches or patent multiple infections. The snails were fed dried algae (*Halocnemon* sp. and *Salicornia* sp.). The life cycles of the recovered trematode species are not known and they could only be identified to familial level after Schell (1985).

Analysis of data was conducted using methods similar to those employed by Fernandez & Esch (1991a,b) and Snyder & Esch (1993). The Statistical Package for Social Science (SPSS) software was used for data processing. A chi-square analysis was use to test the monthly prevalence of the overall infection, the monthly prevalence of snails shedding cercariae and differences in the proportion of infection between male and female snails. A one-way analysis of variance (ANOVA) was used to compare the monthly mean length of the examined snails, and the monthly differences in the number of emerged cercariae per snail per 24 h. The G-test (Monte Carlo Simulation) (Sokal & Rohlf, 1981) was used to compare observed and expected frequencies of double infections.

Results

Size characteristics of Cerithidea cingulata

From March 1995 to July 1996, 2537 snails were examined for larval trematode infections. The monthly mean length of the examined snails is shown in fig. 1. The mean length peaked at 22.5 mm in April 1995 and declined to a low of 18.6 mm in June 1995. When monthly mean lengths were compared statistically, snail length was not significantly different between April 1995 and January 1996 but snails in these two months were significantly larger than snails in all other months. On the other hand, snails in May 1995 and June 1995 were significantly smaller than snails in all other months ($F = 27.96$, $P < 0.001$).

Trematode infections

Of the examined snails, 1265 (49.9%) were infected. The component community comprised 12 species of trematodes. Table 1 shows the prevalence and probable life-cycle pattern for the recovered species. The haplosplanchnid is the only species that utilizes fish as its definitive host, the others are found in piscivorous birds. Cyathocotylid II (41.6%) was by far the most prevalent species followed by the microphallid (3.9%), cyathocotylid I (1.3%), and echinostomatid I (1.0%). The remaining eight species were found infrequently, each in less than 1% of the snails. Figure 2 shows the prevalence of trematode infections in relation to shell length. Trematode prevalence increased significantly with shell length ($P < 0.001$). Only 8.0% of the snails with shell length < 15 mm were infected, in contrast to 98.0% of the snails with shell length > 26 mm. Prevalence of trematode infections was significantly higher in male (47.0%) than female (33.0%) ($P < 0.001$) snails.

Multiple trematode infections were observed in only 15 (1.2%) of the infected snails. The cyathocotylid I and cyathocotylid II combination occurred 14 times and the heterophyid I and the microphallid occurred once. Table 2 shows observed and expected multiple trematode infections. The G-test showed no significant difference for the species combinations. Shedding patterns of 579 snails with patent infections were followed in the laboratory including 11 snails with double infections (cyathocotylid I and cyathocotylid II). All the snails continued to shed cercariae of the same species until the death of the host. There was no apparent loss of infections or species switches.

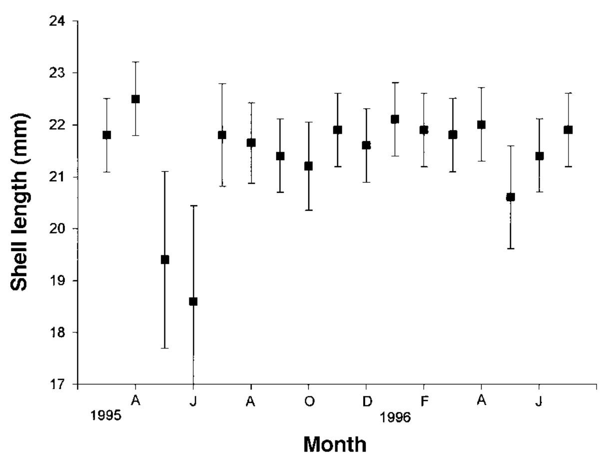

Fig. 1. Monthly mean shell length of *Cerithidea cingulata* in Kuwait Bay, from March 1995 to July 1996.

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Table 1. Prevalence and probable life-cycle patterns for trematodes infecting *Cerithidea cingulata* in Kuwait Bay (n = 2537).

Trematode species	Snail infected* (%)	Life-cycle pattern
Cyathocotylid I	32 (01.25)	Snail–fish–birds
Cyathocotylid II	1054 (41.55)	Snail–fish–birds
Echinostome I	26 (01.03)	Snail–molluscs–birds
Echinostome II	5 (00.20)	Snail–mollusc–birds
Haplosplanchnid	13 (00.51)	Snail–fish
Heterophyid I	10 (00.39)	Snail–fish–birds
Heterophyid II	19 (00.75)	Snail–fish–birds
Microphallid	98 (03.86)	Snail–crustaceans–birds
Philophthalmid I	8 (00.32)	Snail–birds
Philophthalmid II	13 (00.51)	Snail–birds
Plagiorchiid	1 (00.04)	Snail–mollusc–birds
Schistosome	1 (00.04)	Snail–birds
Total	1280 (50.45)	

*15 of the snails harboured double infections.

Temporal pattern

Monthly prevalences of larval trematodes in *C. cingulata* in relation to temperatures are shown in table 3. The temporal pattern of infections in the snails showed peak prevalence during autumn and winter, from November to April, and significantly lower prevalence during spring and summer, from May to October, ($P < 0.001$). Species diversity indicated a seasonal pattern in the occurrence of the trematodes, 10–11 species were detected in autumn and winter and 6–7 species in spring and summer. Cyathocotylid II was the dominant species throughout the study period. Snails were infected with the two cyathocotylids, echinostomatid I and the microphallid species throughout the year, the remaining eight species occurred mostly during winter. Table 4 shows monthly prevalences of *C. cingulata* shedding cercariae (mature infections) and the mean number of emerged cercariae per snail per 24 h relative to surface water temperatures. The prevalence of mature infections

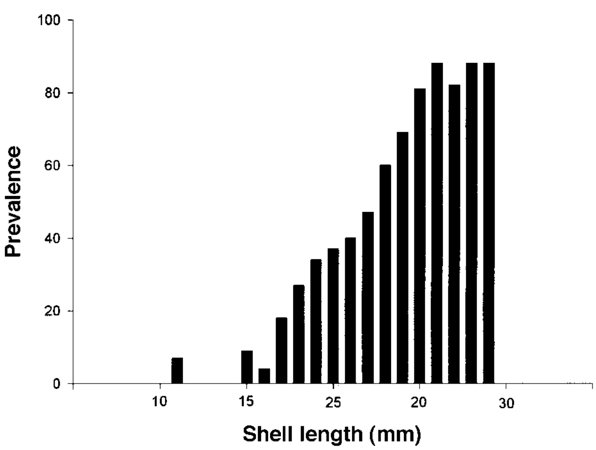

Fig. 2. Prevalence (%) of trematode infections in *Cerithidea cingulata* in Kuwait Bay relative to shell length. Size was established for 1 mm intervals of shell length.

Table 2. Observed (fo) and expected (fe) numbers of multiple trematode infections in *Cerithidea cingulata* in Kuwait Bay.

	Trematode combinations*			
	CI & CII		M & H	
Month	fo	fe	fo	fe
March ’95	1	0.48	0	0.10
April	2	1.23	1	0.07
May	0	0.23	0	0
June	0	0.09	0	0
July	1	0.88	0	0
August	0	0.94	0	0
September	0	0.68	0	0.01
October	2	1.01	0	0.04
November	1	1.53	0	0
December	2	1.01	0	0.05
January ’96	0	1.19	0	0.15
February	0	0.7	0	0.05
March	1	0.75	0	0
April	2	2.2	0	0.05
May	2	0.94	0	0
June	0	0	0	0
July	0	0	0	0
Total	14	13.29	1	0.39

*CI, cyathocotylid I; CII, cyathocotylid II; H, heterophyid I; M, microphallid.

peaked in summer, from July to September, and a significantly lower prevalence was detected in winter, from January to February, ($P < 0.001$). There was a significant difference in the monthly mean numbers of emerged cercariae per snail ($F = 17.59$, $P < 0.001$). Cercarial emergence was correlated with a rise in temperature, reaching a peak in the summer ($P < 0.001$).

Discussion

Cerithidea cingulata in Kuwait Bay plays an important role in the dynamics of transmission of at least 12 species of trematodes. Over 50% of 2537 snails examined were infected with one or more species, all but the haplosplanchnid species utilizing piscivorous birds as definitive hosts. The overall prevalence of infection concurs with that previously reported by Abdul-Salam & Sreelatha (1991) for *C. cingulata* in Kuwait Bay, although their sample was smaller and contained only six species. The scope of species and prevalence of infections in *C. cingulata* in Kuwait Bay are largely in accordance with those recorded for other members of the genus from other localities in the world. The dominance of cyathocotylid II species in the Bay clearly indicates continuous exposure of *C. cingulata* to the infective stage. A reliable supply of infective stages depends on a complex of physical and biological factors that collectively create conditions for promoting transmission. Among the biological factors are an abundant occurrence of several species of fish and piscivorous birds that serve as hosts, and susceptible populations of the snail host. The stability of the transmission system in the Bay is further augmented by the involvement of a relatively long lived snail host, with life spans exceeding 10 years (Houbrick, 1984). In a study

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Table 3. Monthly prevalence of larval trematodes in *Cerithidea cingulata* in relation to temperature, March 1995 to July 1996.

Month	Temp. (°C)	Snail examined	Prevalence*												
			CI	CII	EI	EII	Hp	HI	HII	Mc	PI	PII	Pg	Sc	Total
March '95	20	146	0.7	48.0	1.4	0	0.7	1.4	0	4.8	0	2.1	0	0	58.2
April	22	149	1.3	61.8	2.7	0	0.7	0.7	0.7	7.4	0	0.7	0	0	73.8
May	26	150	6.7	22.7	0	0	0	0	0	2.0	1.3	0	0	0	26.7
June	27	150	6.7	8.7	0.7	0	0	0	0	2.7	0	0	0	0	12.7
July	28	150	1.3	44.0	0	0	0	0.7	0.7	4.7	0	0	0	0.7	50.7
August	29	150	2.0	31.3	0.7	0.7	0	2.7	2.7	2.7	0	0	0	0	40.0
September	31	150	1.3	34.0	2.0	0	0	0	0	0.7	0	0	0	0	38.7
October	29	147	2.7	25.1	0.7	0	0	0.7	0.7	4.1	0	0.7	0	0	33.3
November	24	149	2.0	51.0	1.3	0	1.3	2.7	2.7	0.7	0	0.7	0	0	59.1
December	17	146	2.1	33.6	0.7	0.7	4.8	1.4	1.4	4.8	0.7	1.4	0	0	49.3
January '96	12	150	1.3	59.3	2.0	0	0	0.7	0.7	7.3	0.7	0	0	0	72.7
February	13	150	0.7	70.0	1.3	1.3	0	0.7	0.7	5.3	2.7	0.7	0.7	0	83.3
March	17	150	0.7	75.3	1.3	0.7	1.3	2.0	2.0	7.3	0	0.7	0	0	88.7
April	21	150	2.0	73.3	0	0	0	0	0	5.3	0	0	0	0	80.0
May	24	150	2.0	31.3	0.7	0	0	0	0	2.0	0	0	0	0	37.7
June	26	150	0	11.3	0.7	0	0	0	0	1.3	0	0.7	0	0	14.0
July	27	150	0	26.0	1.3	0	0	1.3	1.3	2.7	0	1.3	0	0	32.0
Total		2537	1.3	41.6	1.0	0.2	0.5	0.8	0.8	3.9	0.3	0.5	0.04	0.04	49.9

* CI, cyathocotylid I; CII, cyathocotylid II; EI, echinostome I; EII, echinostome II; Hp, haplosplanchnid; HI, heterophyid I; HII, heterophyid II; Mc, microphallid; PI, philophthalmid I; PII, philophthalmid II; Pg, plagiorchid; Sc, schistosome.

employing sentinel snails, Curtis (1996) found that trematode colonization of the marine snail *Ilyanassa obsoleta* is a very slow process.

The results from the present study are consistent with other studies on larval trematode assemblages in marine snails where infracommunities seldom exceed one species (Kuris, 1990; Sousa, 1990; Lafferty *et al*., 1994). Only 1.2% of the infected *C. cingulata* harboured double infections, which does not reflect a random process based on the availability of the infective stage, egg or miracidia of the different trematode species. Similarly, in infected *C. californica* only 3% of 12,995 snails (Kuris, 1990), 2% of 4462 snails (Sousa, 1990), and 2.5% of 5025 snails (Sousa, 1993) harboured multiple trematode infections. Sousa (1993) and Lafferty *et al*. (1994) assumed that interspecific antagonism (competition) is the best explanation for the scarcity of double infections in *C. californica*, and the latter workers proposed a systematic process determining the species composition of a guild of larval trematodes based on diversity and abundance of species, spatial and temporal heterogeneity in recruitment and structuring competition. The small number of multiple infections reported in *C. cingulata* in Kuwait Bay can be explained on the basis of hierarchical interspecific antagonism; with time the most dominant species, cyathocotylid II, replaces the other species. The coexistence of cyathocotylid I and cyathocotylid II, observed 14 times, perhaps represents positive interspecific association resulting from niche partitioning within the snail. Cyathocotylid I infects the pallial gonoduct region of the snail while cyathocotylid II develops in the hepatopancreas and gonad.

Sousa (1990) emphasized the role of spatial and temporal patterns of trematode recruitment and duration of host exposure in determining the component community of trematodes in *C. californica*, while interspecific interactions were significantly involved in structuring infracommunities. Most of the available data on the influence of temporal factors on the community dynamics of trematodes in snails have been derived from studies conducted in temperate climates (Esch & Fernandez, 1993). The influence of temperature changes on trematode communities is well-documented and it is often expressed as regular cyclic fluctuations in the prevalence and intensity of infections. Fluctuations in temperature influence the population biology of trematodes by inducing seasonal changes in behaviour and abundance of the host, longevity and infectivity of the larval stages (eggs,

Table 4. Monthly prevalences of *Cerithidea cingulata* shedding cercariae and the mean number of emerged cercariae per snail per 24 h relative to the surface water temperature.

Month	Snail examined	Snail shedding cercariae	Mean no. of emerged cercariae/snail/24 h	Temp °C
March '95	146	22	33	20
April	149	57	133	22
May	150	32	167	26
June	150	13	120	27
July	150	66	233	28
August	150	49	267	29
September	150	51	340	31
October	147	33	267	29
November	149	62	1333	24
December	146	47	67	17
January '96	150	41	33	12
February	150	45	33	13
March	150	67	33	17
April	150	97	400	21
May	150	46	2933	24
June	150	15	1000	26
July	150	41	1000	27

miracidia, cercariae and metacercariae), and development of the larval and adult stages. The results of temporal patterns of the infections in snails in Kuwait Bay provide evidence that transmission cycles are in part influenced by the behaviour of the definitive hosts and population dynamics of the snail host. The observed winter peak in prevalence and species richness coincided both with the autumn arrival of migratory birds at the mudflats and the introduction of a new snail cohort. On the other hand, the summer decline in the prevalence coincided with a high mortality rate among infected older snails and probably a decrease in the availability of infective stages due to heat stress.

The observed increase in cercarial emergence during the summer months is probably induced by acceleration in the physiological activity of the snail host. Schmidt & Fried (1996) showed that a change in temperature was the most important factor in inducing release of cercariae of *Echinostoma trivolvis* from *Helisoma trivolvis*. The summer peak in cercarial emergence is probably synchronized with the life-history patterns of the second intermediate hosts, mainly intertidal fish and crustaceans. A study on ichthyoplankton abundance and diversity in the western Arabian Gulf (Houde *et al*., 1986) showed that most species of fish spawn in Kuwaiti waters during the period from late spring to early autumn. In addition to the effect of temporal heterogeneity on the infective stages, variations in the prevalence of infections may also reflect temperature-related effects on the populations dynamics of the snail, second intermediate hosts and definitive hosts (Esch *et al*., 1993).

Although numerous workers have shown proportional increases in the prevalence of infection with trematodes in relation to snail size (age), the contributing factor(s) is not known (Sousa, 1983; Minchella *et al*., 1985; Rosen, 1994). Among the speculative explanations are age-specific susceptibility, high mortality among young infected snails, increased survival of infected snails or chronic exposure of larger snails to infective stages (Rothschild, 1941). Factors responsible for the observed higher prevalence of infection in male (47%) than female (33%) snails are obscure. Whether this phenomenon reflects physiological differences between the sexes, preferential selection by the infective stage or differences in mortality rates between the sexes is yet to be investigated.

The present study has shown that temporal changes in the population dynamics of the snail host and behaviour of the definitive avian host are primary contributing factors to fluctuations in the prevalence and diversity of trematodes in *C. cingulata*. However, interpretations of the results are hindered by the lack of knowledge of the life cycles of the recovered trematode species. Understanding trematode community structure and processes in Kuwait Bay requires further studies on the behaviour and ecology of the relevant hosts.

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