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Distribution of the Snail *Pirenella conica* in Sinai and Israel and its Infection by Heterophydae and Other Trematodes

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ABSTRACT: Occurrence of *Pirenella conica* (Prosobranchia) along the coasts of Sinai and Israel is confined to marine lagoons and bays (Red Sea) and to hypersaline landlocked lagoons (Mediterranean Sea, Red Sea). The upper salinity tolerance limit lies between 80 and 90 ‰ S. Trematode infection of snails > 5 mm in length varies between 83 % and 0 in different biotopes, without showing seasonal fluctuation. Trematode infection is affected by physical conditions, size, location and faunal diversity of the habitat. The recorded types of larval trematodes belong to the families: Heterophyidae, Echinostomatidae, Microphallidae, Notocotylidae, Haploporidae, Haplosplanchnidae, and, apparently, Cyathocotylidae and Strigeidae. Through experimental infestation of grey mullets and mice, 3 types of heterophyids were identified: *Heterophyes heterophyes*, *H. aequalis* and *Stictodora sawakinensis*. Transmission of these heterophyids takes place in sea-linked lagoons of the Red Sea and the Mediterranean Sea, where all the hosts co-occur Unlike in the Nile Delta region, along the scarcely populated arid coasts of Sinai, they should have sylvatic cycles where wild piscivorous birds and mammals serve as definitive hosts.

INTRODUCTION

Pirenella conica (Blainville, 1829) (Potamididae, Prosobranchia) is a euryhaline lagoon-living gastropod (Fig 2). Khalil (1937) demonstrated this species to be the vector of heterophyasis, a common intestinal parasitic disease of humans in the Nile Delta, caused by the trematode *Heterophyes heterophyes* (Khalil, 1937; Wells and Blagg, 1956; Sheir and El-Shabrawy Aboul Enein, 1970). *P. conica* has been reported from coastal habitats along the eastern and southern Mediterranean Sea, the Red Sea and the Persian Gulf (Potiez and Michaud, 1838; Pallary, 1909; Biggs, 1973; Jones et al., 1978); it has also been collected in Libya, Sardinia and Malta (Hebrew University, Zoological Museum).

In Egypt, *Pirenella conica* is common in the hypohaline Nile Delta lakes (Khalil, 1937; Martin, 1959) and in inland saline lakes such as Birket Gessebaya (Crawford, 1948) and Birket Maragi (Ibrahim, 1975) of the Siwa Depression and Lake Qarun (Demian et al., 1963). In Sinai, *P. conica* has been reported from the Bardawil lagoon, the Bitter Lakes (Fig. 1, Site B) and Lake Timsah in the Suez region (Tillier and Bavay, 1905; Martin, 1959; Demian et al., 1963; Barash and Danin, 1971, 1972/73; Por, 1971), and from the mangrove lagoons and the pool of Dahab on the coast of the Gulf of Aqaba (Por and Dor, 1975; Por et al., 1977).

Until recently, Red Sea *Pirenella conica* populations were regarded as *P. caillaudi* (Potiez and Michaud, 1838; Por, 1971; Barash and Danin, 1971, 1972/73), but Taraschewski (1978) has shown that *P. caillaudi* is a synonym for *P. conica*.

Apart from humans, the most important definitive hosts of *Heterophyes heterophyes* are dogs and cats, but it also occurs in a variety of wild mammalian and avian piscivorous ı osts (Witenberg, 1929; Abdel Azim, 1938; Balozet and Callot, 1939; Kuntz and Chandler, 1956; Wells and Randall, 1956; Mimioglu and Sayin, 1957; Fahmy and Selim, 1959; Deiana, 1961; Himonas, 1964). Among euryhaline lagoon fishes, mullets (Mugilidae) are the predominant second intermediate hosts of *H. heterophyes* (Khalil, 1923, 1937; Witenberg, 1929; Wells and Randall, 1956; Paperna, 1964, 1975). Transmission occurs when infested fish is consumed raw or insufficiently cooked (Hamed and Elias, 1969). In addition to *H. heterophyes*, *Pirenella conica* also

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serves as intermediate host for several other trematode species – *Heterophyes aequalis*, heterophyids of the genus *Stictodora* (Martin and Kuntz, 1955; Kuntz and Chandler, 1956; Kuntz, 1957; Martin, 1959) and several nonheterophyid trematodes of unidentified genera and species (Demian et al., 1963; El Gindy and Hanna, 1963; Yousif, 1970).

MATERIALS AND METHODS

A survey of *Pirenella conica* habitats was carried out from July 1978 to March 1980. Sites supporting *P. conica* populations were visited once during winter and once during summer. Data from previous surveys (1973–1977) are also included in the results. The mangrove lagoon Shura el Manqata (Site 4a) was visited more frequently. The resulting data are being published in a parasitological journal (Taraschewski and Paperna, in press). Site locations are shown in Fig 1. In addition to sampling snails, salinity and temperature were measured at most sites. In Wadi Kid Sabkha (Site 5) and Ras Muhammad Pool (Site 8) salinities in the seawater spring zone were taken monthly from February to August 78. Snails were collected by sieving the upper 5 cm substrate layer of a 1–3 m^2 area with a 1.5 mm^2 mesh sieve. Snails were counted and measured (shell height) in the laboratory and checked for larval trematode infection by examining the digestive glands.

Attempts to identify larval trematodes were made by exposing infection-free juvenile mullets (reared from fry in the laboratory) to cercariae shed by the snails. Metacercariae were examined microscopically by crushing cysts under a coverslip or by digesting cysts in Pepsin (in pH-2) and subsequently in Trypsin-Taurocholin (in pH-8). Infected mullets were fed to mice. The mice were sacrificed after 2–6 d and examined for trematodes in the small intestines.

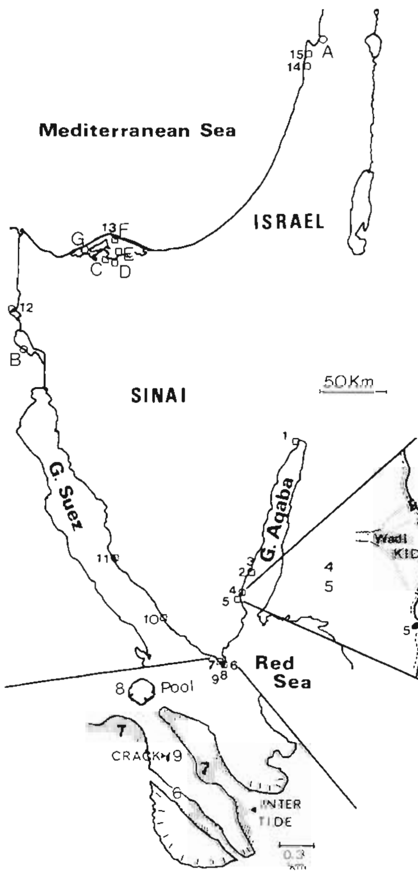

Fig. 1 Map of Sinai and Israel showing study sites. Site A: Naáman stream near Haifa; B: Bitter Lakes; 1: Eilat, fishponds; 2. El Kura bay; 3: Dahab Pool; 4: Mangrove lagoons; a: Shura el Manqata; b: Shura el Arwashi; c: Shura el Garqana; 5: Wadi Kid Sabkha; 6: Ras Muhammad Mangrove Canal; 7: Ras Muhammad beaches; 8: Ras Muhammad Pool; 9: Ras Muhammad Crack; 10: A-Tur harbor; 11: El Bilayim; 12: Lake Timsah; 13: Bardawil lagoon; C: Mitzfaq; D: Tlul, inner bay; E: Tlul; F: Kalas; G: Rumia; 14: Dor, fishponds; 15: Atlit, saltpans

RESULTS

Distribution

Survey findings are summarized in Table 1. Along the Mediterranean coast the hypersaline Bardawil lagoon (Table 1, Site 13; Fig. 3a) is the only large water

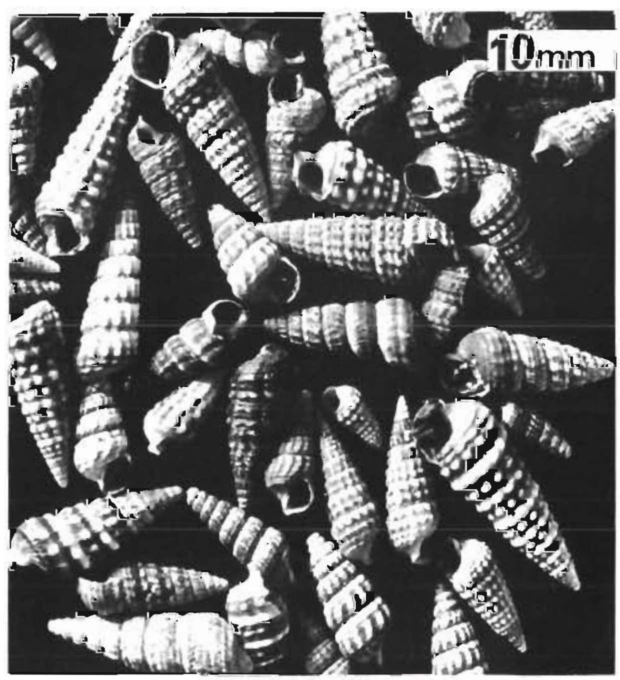

Fig. 2. *Pirenella conica*: Shells

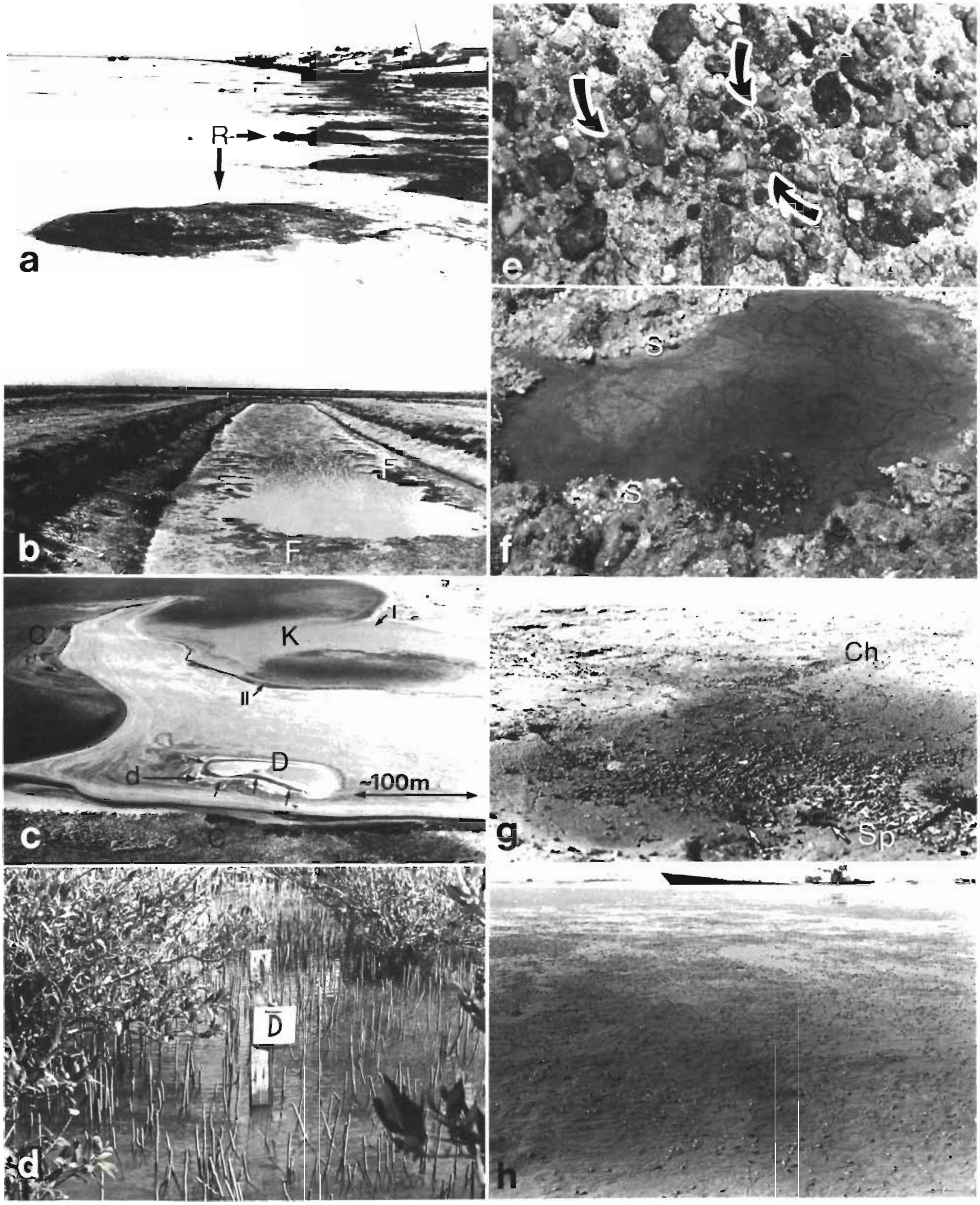

Fig. 3. Study sites. (a) Bardawil lagoon; Tlul (Site 13 E), *Ruppia maritima* (R) washed ashore. (b) Dor (Site 14); seawater fish pond with floating mats of filamentous algae (F). (c) Dahab area (aerial photograph); K: El Kura Bay; I, II: sampling stations in the bay; D: Dahab Pool; d: adjacent flood depression; C: coral reef. Areas in Dahab Pool inhabited by *Pirenella conica* indicated by arrows. (d) Mangrove lagoon (Shura el Manqata) at high tide. (e) Pebble substrate in Dahab Pool. (f) *P. conica* at a small seawater 'spring' in Wadi Kid Sabkha; S: salt crusts. (g) *P. conica* in seawater 'spring' (Sp) and flow channel (Ch) at Ras Muhammad Pool at low tide. (h) Mudflats at A-Tur harbor, populated by *P. conica*

Table 1 Physical and hydrographical conditions in *Pirenella conica* habitats*. Site numbers refer to map in Fig. 1

Site No.	Location	Habitat type	Substrate	Water temp. (°C) (+ annual range)	Air temp. (°C)	Salinity (‰ S)
	Gulf of Aqaba					
1	Eilat Station	Fish ponds and drainage	Sand and clay, bottom eutrophic	17–21 (Jan) 23–33 (Aug.)	10–21 (Jan.) 26–40 (Aug.)	40–42
2	El Kura (Dahab)	Semiclosed bay	Outer zone: sandy, scattered beachrock & oysterbed areas. Inner zone: muddy	+ 21–27	13–21 (Jan.) 27–33 (Aug.)	41–43 seaside 41–45 inland side
3	Dahab Pool	Seepage pool & adjacent sometimes flooded small depression	Varying between fine sand, gravel and beachrock [1]	15–24 (min. 8) (winds prevent heating) [1]	see Site 2	45–65 [1]
4 4a 4b 4c	Mangrove lagoons Shura el Manqata Shura el Arwashi Shura el Garqana	Mangrove (*Avicennia marina*) fringed lagoons	Diverse: sand, beachrock, eroded reef, mud and detritus beds, exposed or shadowed by trees	Low tide: 7–35 High tide: 21–27	Approx. as in Site 2	40–42 (4a) 41–47 (4b) [2] innermost sectors up to 58 (4b) [2]
5	Wadi Kid Sabkha	Coastal saltpan, fed by seepage through seawater springs	Soft sediment covered by blue-green algae. Filamentous green algae present in the seawater spring zone	Approx. air temp.	Approx. as in Site 2	Seawater spring belt: 46–97 Pan: 100–300 [5]
	Red Sea					
6	Ras Muhammad Mangrove Canal	Narrow channel cut between coral rocks, sparsely fringed by *Avicennia marina*	Mixed beds, corallinous sand and mud	Not measured	13–21 (Jan) 27–33 (Aug.)	Similar to open sea (Open sea: 41–43) [3]
7	Ras Muhammad beaches	Bays of flat beaches	Sand	Not measured	see Site 6	Not measured (Open sea: 41–43) [3]
8	Ras Muhammad Pool	Hypersaline pool fed by seawater seepage springs	Mudflate overgrown by blue-green algae. Filamentous green algae present in seawater flow channels	Not measured	see Site 6	Seawater springs: 45–90 Pond: 102–200 [4]
9	Ras Muhammad Crack	Narrow fault, fed by seawater seepage	Steep rocky margin, one end with sandy slope	Not measured, approx. sea temp. (22–24) [3]	see Site 6	As in open sea [6]
	Gulf of Suez					
10	A-Tur harbor	Semi-closed bay	Flats of sand and mud (patchy cover of blue-green algae)	Not measured (Open sea: 16–27) [3]	19–21 (Jan.) 23–35 (Aug.)	Not measured (Open sea: 41–42) [3]
11	El Bilayim	Lagoon connected with the sea by a narrow canal	Sand to mud, heavily polluted with crude oil	Not measured	Approx. Site 10	41–48 [7]

Suez Canal						
12	Lake Timsah	Saline Lake, part of the Suez Canal system	Sand, mud, gravel. In areas with fresh water inflow fringed by reeds	Not measured	Not measured	In recent years 36–42, stratified [7]
Mediterranean Sea						
13	Bardawil lagoon	650 km^2 lagoon, supplied by seawater through three narrow openings	Variable: mud, sand, seashell. *Ruppia maritima* abundant in sublittoral	10-16 (Jan.) 28–34 (Aug.)	8–19 (Jan) 21–31 (Aug.)	Seaside: 38–42 Landside: 50–80 Landside fringes: 80–100 [8]
14	Dor	Seawater fishponds (since 1976 dried out)	Muddy, some ponds densely covered by filamentous algae	Not measured	9–17 (Jan.) 22–31 (Aug.)	39–45
15	Atlit	Commercial saltpans with frequently changing water level, some dry with residual pools	Mud and clay, often anaerobic below surface	Not measured	see Site 14	Variable, depending on use (see Table 2) 44–82 (summer) 25–49 (winter) (see Table 2)

* Air temperatures obtained from the Meteorological Services of Israel as multiannual means of maxima and minima for January and August.
[1] Por and Dor (1975); [2] Por et al. (1977); [3] Morcos (1970); [4] Por (1975); [5] Krumbein (pers. com.); [6] Por and Tsurnamal (1973); [7] Por (1978); [8] Ben Tuvia and Gilboa (1975)

body which supports *Pirenella conica*. North of Bardawil lagoon the only known sites inhabited by *P. conica* are the Atlit salt pans (Site 15) and the seawater fish ponds at Dor (Site 14 and Fig. 3b), which have been drained since 1976. Prior to 1960, *P. conica* was abundant in the estuarine and hypersaline pools and marshes associated with the lower reaches of the Naáman Stream south of Akko (Fig. 1, Site A), but have since been eliminated by industrial pollution.

Habitats of *Pirenella conica* are more numerous along the Red Sea coasts of Sinai in the Gulfs of Suez and Aqaba. Habitats in the area include large and small land-locked hypersaline water bodies (Fig. 3f, g), tide-exposed lagoons, including mangrove-fringed lagoons (Fig. 3d) as well as sheltered bays (Fig. 3c) and harbors (Fig. 3h). In these habitats *P. conica* commonly occurs on fine sandy or muddy substrates but usually avoids mobile sand. Snails showed an overall preference for mudflats (Fig. 3h) covered by blue-green algae, which represent their major diet. Only at one site, Dahab Pool, did snails occur on a substrate consisting of coarse sand and pebbles (Fig. 3e).

Distribution Pattern in Marine and Hypersaline Habitats Below 50 ‰ S

In the bays and open lagoons, salinity is not a limiting factor for the distribution of *Pirenella conica*. On exposed sandy and muddy beaches at the upper tidal limit, *P. conica* aggregated in small depressions which retain water when the tide recedes. In lower reaches of the intertidal zone, the snails show a preference for shallow enclaves. Below the low-tide mark, they are usually rare or absent, except in Bardawil lagoon (Site 13) where they extend their range below the intertidal belt. In habitats such as El Kura bay (Site 2), Ras Muhammad Mangrove Canal (Site 6) and the surrounding beaches (Site 7) and A-Tur harbor (Site 10), snail populations are sparse, usually less than 50 ind. m^{-2}. Snails are significantly more abundant (200 ind. m^{-2}) in parts of Bardawil lagoon, El Bilayim lagoon (Suez Gulf, Site 11) and the mangrove lagoons (Gulf of Aqaba, Site 4). In the mangrove lagoons no particular preference as to the presence or absence of trees is shown by the snails, but they were absent from the most dense thickets, where heavy organically enriched sediment produced anaerobic strata. In the seawater ponds, at Dor (Site 14) and Eilat (Site 1), snails aggregated only along the banks and in shallow corners and were absent from the deeper organically enriched substrate. However, filamentous algal mats in the Dor ponds (Fig. 3b) supported a prolific snail population exceeding 500 m^{-2}. In the shallow waters of the Bardawil lagoon (less than 1 m deep) with a muddy substrate dotted with the phanerogam plant *Ruppia maritima* snails occurred in very small numbers, often less than 1 m^{-2} and usually only in the vicinity of the *Ruppia thickets*.

Bardawil lagoon (Fig. 3a) represents an extremely heterogeneous biotope, with salinities ranging from 38 to 100 ‰ S. In the moderately hypersaline (38–50 ‰ S) seaside sector of the lagoon (Site 13F) which is under tidal influence and has a coarse sandy substrate, snails are sparse. Snail densities increase towards the inner, more sheltered zone, where mud substrates and more hypersaline conditions prevail. Such conditions exist at Tlul (Site 13E and Fig. 3a) and Mitzfaq (Site 13C), where salinity, particularly during early fall, reaches 65–75 ‰ S. Snails under these conditions still maintain very dense populations (up to 300 m^{-2}).

Distribution Pattern in Extreme Hypersaline Habitats

In extreme hypersaline habitats such as landlocked pools and salt-pans, *Pirenella conica* distribution is limited to waters with salinities lower than 80 ‰ S. Depleted snail populations were also found at habitats with salinities as high as 90 ‰ (Table 1). In the sites in Sinai, snails are also exposed to extreme water temperatures which approximate air temperature ranging from a minimum of 8°–10 °C in winter to a maximum of 30°–45 °C in summer. In Wadi Kid Sabkha (Site 5) and Ras Muhammad Pool (Site 8) salinity gradients are created by seawater seepage into the pan. Here *P. conica* demonstrates distinct zonation with respect to the salinity gradient. Snails are limited to areas adjacent to the seepage zone. The highest densities of snails (up to 300 m^{-2}) were observed in the belt closest to the seawater 'springs' with salinities of 46–68 ‰ S in Wadi Kid Sabkha (Fig 3f), 45–90 ‰ S in Ras Muhammad Pool (Fig 3g). Snails were absent from the more saline (> 100 ‰ S) sectors and the main pool with salinities of 100–300 ‰ S in Wadi Kid Sabkha, and 100–200 ‰ S in Ras Muhammad Pool. Seasonal interruption in seawater seepage results in catastrophic snail mortalities.

Salinity was also the limiting factor in the salt-pans of Atlit on the Mediterranean coast (Site 15; Table 2): here salinity increased with the pan's distance from the seawater pumping point. Abundance of *Pirenella conica* varied accordingly Ponds 1 and 2 of the Atlit salt-pans, however, unlike the hypersaline habitats of Sinai, became hyposaline during winter rains. This dilution was not found to be detrimental to the snails. Absence of *P. conica* in Ponds 4–5 (Table 2) during winter suggest that extreme hypersaline summer conditions eliminated the snails. Snails were already rare in these ponds during August 1978. Salinities may also reach extreme values of over 100 ‰ S in the most remote bays of Bardawil lagoon. Population densities were found to decrease respectively.

In Dahab Pool (Site 3), salinities ranged from 45 ‰ to 65 ‰ S; there is neither distinct horizontal zonation nor vertical stratification in salinity. The *Pirenella conica* population, however, is restricted to the southeastern shore and, unlike elsewhere, lives on a coarse substrate (Fig. 3e), while being absent on the fine sand belt at the north end. The southeastern sector is at the closest proximity to the seaward side of the lagoon bar (Fig. 3c). Snails also intermittently invade a small

Table 2. *Pirenella conica*. Distribution and prevalence of infection in Atlit salt-pans (Site 15)*

Pond No.	Month	Salinity (‰ S)	Estimated snail density ind. m^{-2}	Sample size	% infection	% immature infection	% heterophyidae	% non-heterophyidae
1	August 78	44	200 +	69	62	6	4.5	52
	February 79	25	< 200	138	58	17	1.5	40
2	August 78	60	300 +	57	33	10.5	0	23
	February 79	27	< 200	141	65	11	4	49
3	August 78	51	300 +	49	41	2	0	39
	February 79	35	< 200	155	83	12	0.5	70
4	August 78	70	0–10	110	78	0.5	11	67
	February 79	41	0	–	–	–	–	–
5	August 78	72	< 1	15	73	7	20	46
	February 79	49	0	–	–	–	–	–
6	August 78	81	0	–	–	–	–	–
	February 79	42	0	–	–	–	–	–

* Snails < 6 mm excluded from calculated infection levels, because no specimens in this size range were ever infected

depression located between the pool and the seashore (Fig. 3c:d), which is occasionally flooded by seepage from the sea. At these times it may adjoin the main pool.

Associates and Predators

Wherever *Pirenella conica* occurs, it is not only the most conspicuous molluscan, but often the most conspicuous faunal element of its biotope; this is especially so in extreme hypersaline waters. In Bardawil lagoon, other molluscan species – such as *Cerithium scabridum*, *Mactra corallina*, *Cardium edule* etc. – occur but rarely in biotopes predominated by *P. conica*.

Thus far, data on predation are available only for piscine predators. Sparid fishes were found to be important predators. Shells of *Pirenella conica* were identified from stomach contents of *Sparus auratus* in Bardawil, confirming previous reports of Barash and Danin (1971). In the Shura el Manqata mangrove lagoon, 7 out of 22 examined *Acanthopagrus bifasciatus* and 1 out of 10 *Rhabdosargus haffara*, all 90–150 mm in length, were found to contain *P. conica* in their guts. Studies of stomach contents of young *Sparus auratus*, nursed in a pond at Eilat heavily populated by *P. conica* have shown that nurslings 30–50 mm in length predominantly fed on *P. conica* spat. Spat and juvenile snails, unlike large specimens consumed by larger fish, were swallowed whole without crushing.

Larval Trematode Infections in *Pirenella conica*: Occurrence and Prevalence

Most investigated populations of *Pirenella conica* exhibited at least some infection by larval trematodes (Tables 2, 3; Fig. 4). Low infection levels (< 10 %) were found in snails of the Red Sea salt-pans, Wadi Kid Sabkha and Ras Muhammad Pool (Fig. 4: 2 and 3). Infection levels were very low (< 3 %) in Dor and Eilat seawater ponds. Variations in prevalence of infection were evident between snail populations sampled at different sites in Bardawil lagoon. Infection was extremely low (< 1 %) among the sparse snail populations of the seaside coast of the lagoon and was higher in those of the muddy landside shore (13 %, 29 %, 38 %; Fig. 4: 4).

Elsewhere along the coastline of the Gulfs of Suez and Aqaba, El Bilayim lagoon, A-Tur harbor, Ras Muhammad Mangrove Canal, in the mangrove lagoons and in El Kura bay with adjacent Dahab Pool, as well as in the salt-pans of Atlit on the Mediterranean coast, infection levels ranged from 27 % to 83 % No appreciable differences in infection were noted between snail samples examined during winter and

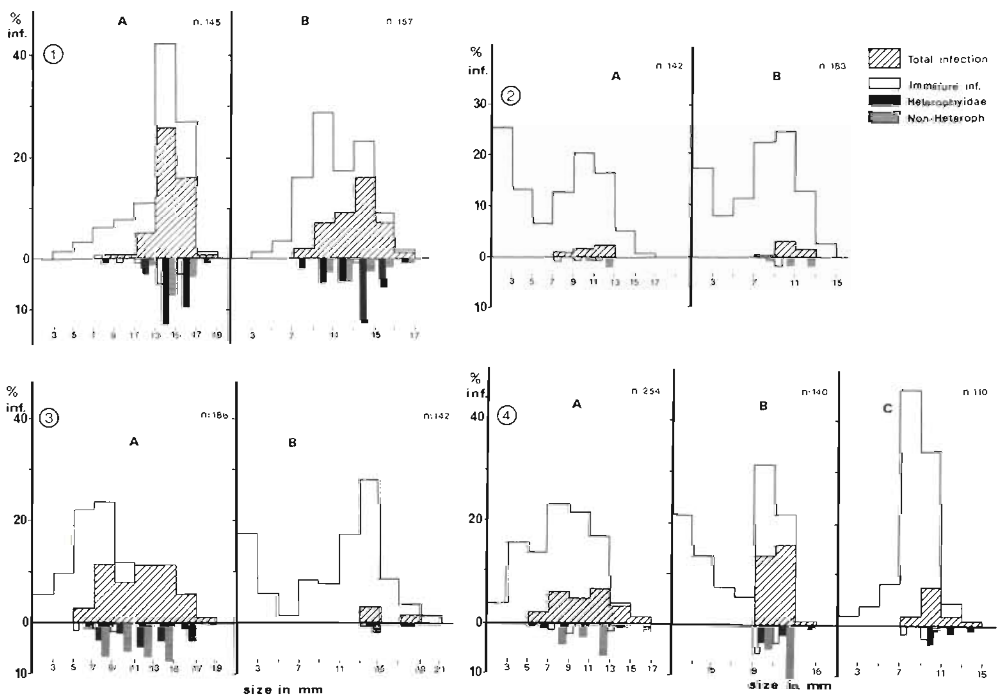

Fig. 4. Percentage of infection by trematodes (ordinate) versus length of snails in mm (abscissa). Above zero line: Open field = non-infected snails; for other explanation see inset (upper right). (1) El Kura bay; February (A) versus August (B) sample (Station I). (2) Wadi Kid Sabkha; February (A) versus August (B) sample (Station III). (3) Hypersaline pools. Dahab Pool (A) versus Ras Muhammad Pool (B); February/March samples. (4) Bardawil lagoon; comparison of 3 sites: A: Tlul (Site 13 E), B: Mitzfaq (Site 13 C), C: Tlul inner bay (Site 13 D); Febr

summer. This also applies to the sparsely infected snail populations mentioned above (Fig. 4: 2 and 3B; Table 3).

Distribution Pattern of Infection Within the Snail Populations

Infection was absent in all snails shorter in length than 6 mm, and occasional in snails between 6 and 10 mm. Likelihood of infection increases in larger specimens; it is most prevalent, often approximating 100 %, in the largest snails of the sample (i.e. above 14 mm) (Fig. 4: 3A and 4; Fig. 5: 1 and 2). Thus, although snails below 6 mm were omitted from the calculation, prevalence of the trematodes is still grossly influenced by differences in size distribution of snails in the different samples. Overall infection levels, calculated from samples dominated by juveniles, could therefore be lower than samples consisting predominantly of larger (older?) snails. This was particularly evident in samples from extreme habitats, where reproduction activity shows a more pronounced intermittent pattern and samples were often dominated by juvenile cohorts (Fig. 4: 2 and 3; Fig. 5, 2B). Snails of Ras Muhammad Crack, which were free of infection, were smaller than 7 mm. The distributional pattern of infections in size classes of snails as described above, is similar in all sites where infection levels are above 10 %. In sparsely infected snail populations, infection levels are also higher in larger snails, although the largest snails of the samples are often free of infection (Fig. 4: 2 and 3B).

Type and Diversity of Infection

Up to 8 different types of cercaria (which undoubtedly represent a much higher number of species) could be recognized from a particular snail population. Double infection occurs, and in some heavily infected sites prevalence of double infection may reach 10 % (Dahab Pool and Atlit). Snails were found to harbor larval trematodes of the following families: Heterophyidae, Echinostomatidae, Microphallidae, Notocotylidae, Haploporidae, and Haplosplanchnidae, as well as furcocercariae apparently belonging to the families Cyathocotylidae and Strigeidae. Diversity of trematode infection in snails is directly related to intensity of infection in the population under study. Where infection levels and diversity of infection was high (e.g. at least 5 types of cercariae could be recognized) heterophyids were usually abundant (Fig. 4: 1,

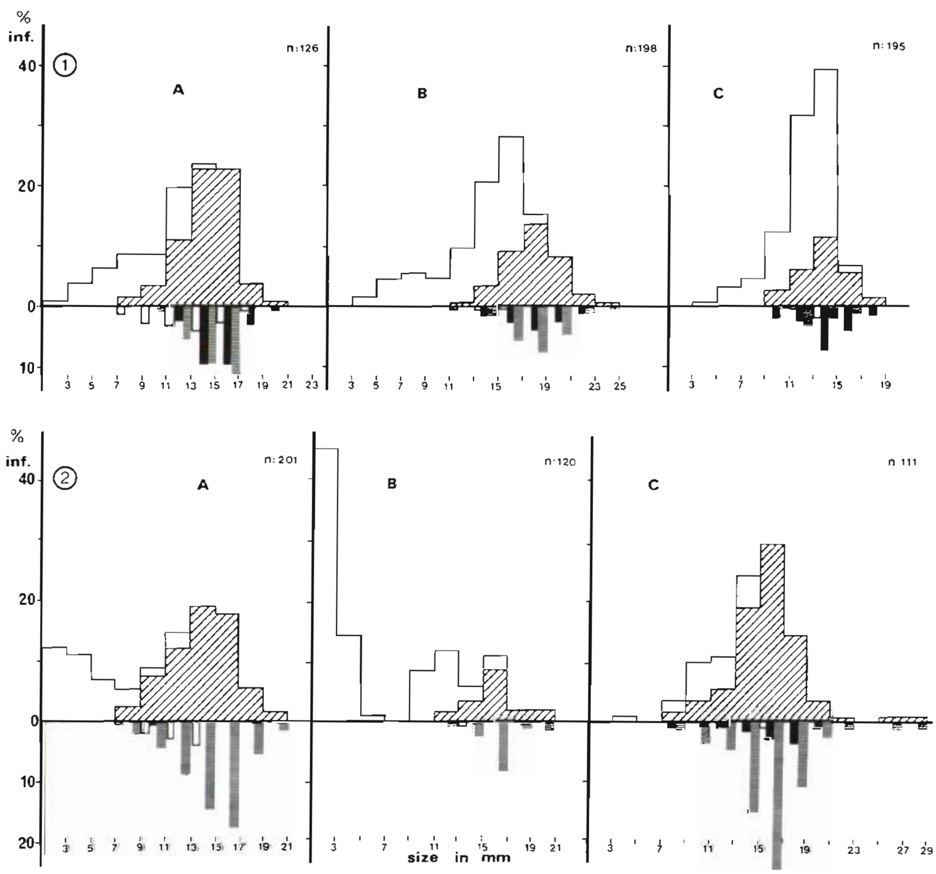

Fig. 5. (1) Biotopes with heterophyid abundance; A: Shura el Manqata (Station I); B: Ras Muhammad Mangrove Canal (Station I); C: A-Tur harbor; February March samples. (2) Salt-pans of Atlit; A: Pond III, Febr.; B: Pond III, Aug.; C: Pond IV, Aug. For further explanation consult legend to Fig. 4

Table 3. *Pirenella conica*. Abundance and infection rates* in sites surveyed

Site No.	Location	Sampling stations	Abundance (ind. m^{-2})	Month	Sample size	% Infection	% immature infection	% Heterophyidae	% Non-heterophyidae
1	Eilat (a) fish ponds		up to 500	Febr 80	110	0	0	0	0
	(b) drainage canals		up to 500	Febr. 80	116	1.5	0	0	1.5
2	El Kura bay	I	0–30	Febr 79	145	49	9	28	12
		II	up to 100	Febr 79	115	55	15	28	12
		I	0–30	Aug. 78	157	42	0.5	30	11.5
3	(a) Dahab Pool		0–50	Febr. 79	116	60	6	18	36
				Aug. 78	114	46	1	20	25
	(b) Adjacent flood depression		few (many empty shells)	Aug. 78	28	57	39	14	3.5
4 a	Shura el Manqata	I	up to 200	Febr. 78	120	70	15	27	28
		II		Febr 78	136	42	10	9.5	22
		I		Aug. 78	92	61	7.5	34	19.5
		II		Aug. 78	211	45.5	6	21	19
5	Wadi Kid Sabkha	I	up to 300	Febr 79	127	0.8	0	0	0.8
		II		Febr 79	101	2	0	0	2
		III		Febr 79	87	7	3.5	0	3.5
		I		Aug. 78	107	9	0.5	0	8.5
		II		Aug. 78	113	6	1	0	5
		III		Aug. 78	136	7	2	0	5
6	Ras Muhammad Mangrove Canal	I	up to 50	Mar 79	195	38	4	12	21.5
		II		Mar. 79	144	30	5	6	19
		I		Aug. 78	136	57	1.5	20	35
7	Ras Muhammad bay beaches		up to 50	not sampled	–	–	–	–	–
8	Ras Muhammad Pool	I	up to 300	Mar 79	74	3	0	0	3
		II		Mar. 79	109	5.5	1	2	2.5
		I		Aug. 78	114	5.5	0	0	5.5
		II		Aug. 78	49	0	0	0	0

Table 3. Continued

Site No.	Location	Sampling stations	Abundance (ind. m^{-2})	Month	Sample size	% Infection	% immature infection	% Heterophyidae	% Non-heterophyidae
9	Ras Muhammad Crack		50	Mar 79	40	0	all snails < 7 mm		
10	A-Tur harbor		0–100	Febr. 79	194	27	3	17.5	7
11	El-Bilayim		(patchy) 50	Aug. 75	31	–	+	+	+ +
12	Lake Timsah		(patchy) 0–100	Aug. 79	present (few snails checked)				
13	Bardawil lagoon								
C	Mitzfaq		up to 300	Febr. 79	111	38	12	7	19
D	Tlul, inner bay		up to 20	Febr. 79	104	13	4.5	7	1
E	Tlul		up to 100	Febr 79	205	29	7	1	21
F	Kalas		0–10	Aug. 73	174	0.6	0	0	0.6
G	Rumia		0–10	Aug. 73	100	0	0	0	0
14	Dor, seawater fish ponds		500 and more	Nov. 76	105	3	0	0	3
15	Atlit salt-pans		data presented in Table 2						

• Snails < 6 mm length excluded from calculated infection levels, because no specimens in this size range were ever infected

3A and 4; Fig. 5: 1). Where infection as well as diversity was low, heterophyids were rare or absent (Fig. 4: 2 and 3B). Atlit salt-pans located in the arable Mediterranean zone are an exception. There inspite of the relatively high infection levels non-heterophyids predominate (Fig. 5: 2). Thus, heterophyids were prevalent in most investigated sites along the Red Sea coasts of Sinai and the Mediterranean coast of Sinai and Israel. Although overall infection levels did not vary between summer and winter, infections by heterophyids were more abundant (and consequently non-heterophyids were less abundant) in summer samples than in winter samples in the mangrove habitats Shura el Manqata and Ras Muhammad Mangrove Canal (Table 3).

The following species of heterophyid cercariae were identified through infestations of mullets *(Liza subviridis, L. ramada, Mugil cephalus)* and mice. (a) Snails from Bardawil lagoon: *Heterophyes heterophyes* (v. Siebold, 1852) (recovered from infested mice). *Stictodora sawakinensis* (Loos, 1899) (identified from metacercariae in mullet muscles). (b) Snails of three of the mangrove lagoons in the Gulf of Aqaba (Shura el Manqata, Site 4a, Shura el Arwashi, Site 4b, Shura el Garqana, Site 4c)· *Heterophyes aequalis* (Loos, 1902) (dominant) *H. heterophyes* (at a ratio of 1 : 100 or less to *H. aequalis*) and *Stictodora sawakinensis* (obtained from infested mice).

DISCUSSION

The distribution pattern of *Pirenella conica* suggests that this snail is a regressive species to sheltered habitats rather than an active 'colonizer' as can be implied from discussions on the faunal exchanges between the Red Sea and the Mediterranean (Por, 1971, 1978; Barash and Danin, 1972). Within its geographic range, from the Persian Gulf to the southwestern Mediterranean, *P. conica* has an extremely patchy distribution. The pattern is reminiscent of species considered Tethys relicts, e.g. the cyprinodont fish *Aphanius dispar* (Kosswig, 1967; Por, 1978). As inhabitant of lagoon habitats, with extreme physical conditions. *P. conica* demonstrates tolerance to extreme temperatures (5 °–45 °C) and salinities (15–90 ‰ S). This wide tolerance was confirmed in laboratory tests (Taraschewski, 1978). Hedgpeth (1956) suggested 80 ‰ S as the upper tolerance limit for euryhaline gastropods. *P. conica* cannot survive in marine intertidal or littoral habitats exposed to waves. This is confirmed by observations in the Persian Gulf (Evans et al., 1973).

Although a few predators of *Pirenella conica* were identified (sparid fishes), the effect of predation on snail distribution and habitat selection remains unsolved. Restriction of snails to the intertidal belt of sea-linked lagoons may be a result of predation pressure. Alternatively, physical factors may be dominant – since, in the smaller extreme habitats, where fish are absent, the snails still show preference for the shallowest habitat zone.

Transmission of a trematode is confined to areas where all its hosts co-occur. Therefore, the diversity of trematode infection in snails of a given habitat depends largely on its faunal and floral diversity, as well as on the availability of definitive terrestrial hosts in the surrounding area (e.g. hypersaline habitats of Atlit near cultivated surroundings vs desert habitats of Wadi Kid Sabkha and Ras Muhammad Pool) (Honer, 1961; Bartoli and Prevot, 1976; Lauckner, 1980). The size of the habitat (for example small fish ponds vs lagoons and large salt-pans) is an important factor in its attraction to definitive hosts. Tolerance limits of the free-living stages of the trematodes (cercariae and miracidia) to extreme physical conditions prevailing in habitats dominated by *Pirenella conica* is another highly restrictive factor. Heterophyid cercariae (*Heterophyes heterophyes*, *H. aequalis* and *'Stictodora'* types), as well as xiphidiocercariae demonstrated relatively wide salinity tolerances (20–65 ‰ S) in laboratory trials (Paperna and Taraschewski, unpubl.) but narrower than the tolerance limits demonstrated for *P. conica*. In the more extreme habitats which are usually smaller in size, physical factors may aid in lowering the probability of trematode transmission. In such environments (Wadi Kid Sabkha, Ras Muhammad Pool, certain inner bays of Bardawil lagoon), overall snail infection rates were low. The probability of infections should further decline when snails aggregate to restricted sectors of the habitat (Wadi Kid Sabkha, Ras Muhammad Pool) and their breeding activity assumes a discontinuous pattern. In the absence of piscine fauna (Wadi Kid Sabkha, Ras Muhammad Pool, and most Atlit salt-pans), the heterophyids, dependent on fish as the second intermediate host, loose their dominance in favour of species utilizing aquatic larval insects and insectivorous hosts (xiphidiocercariae in particular).

Transmission of heterophyids, including *Heterophyes heterophyes*, the causative agent of human heterophyasis of the Levant, serves to illustrate the advantage of an impoverished fauna for efficient heterophyid transmission. In these lagoon environments the fauna is dominated by a few euryhaline species, viz. the hosts of heterophyids: *Pirenella conica* and Mugilidae. This becomes evident from the high infection levels by heterophyids observed both in snails and mullets of such habitats. In the Nile Delta and Bardawil lagoon, the prevalence of infection by heterophyids in the two mullets *Liza ramada* and *Mugil cephalus* approaches 100 % with infections per fish of 200–6000 metacercariae g^{-1} muscle (Wells and Randall, 1956; Paperna, 1975; Paperna and Overstrett, in press). Transmission in the habitats along the Red Sea coast (El Bilayim lagoon, mangrove lagoons and El Kura bay) appears to be less efficient, although infection levels in *P. conica* are as high or even higher than those recorded from Bardawil lagoon and the Nile Delta lakes. Infection levels in mullets were considerably lower than in Mediterranean sites (usually 30 %, rarely above 50 %, 10–600 metacercariae g^{-1} muscle $fish^{-1}$; Paperna and Overstreet, in press), however other species of mullets (*Liza subviridis*, *Valimugil seheli*) are involved and a different heterophyid species dominates. Heterophyid species identified from cercariae shed by *P. conica* correspond with those identified from naturally infested mullets (Paperna, 1975; Paperna and Overstreet, in press). *H. heterophyes*, *H. aequalis* and *Stictodora sawakinensis* are transmitted in Mediterranean and Red Sea sites; in Bardawil lagoon *H. heterophyes* is dominant, in the mangrove lagoons *H. aequalis*. Unlike in the Nile Delta region, along the arid coasts of Sinai (including Bardawil lagoon) the human population density is low, and consequently dogs and cats are scarce; therefore, wild piscivorous birds or mammals are apparently involved in transmission.

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