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ORIGINAL PAPER

Reproductive strategy of a small endemic cyprinid, the Yarqon bleak (*Acanthobrama telavivensis*), in a mediterranean-type stream

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Abstract A mediterranean-type climate exists in five widely separated regions; the Mediterranean basin, parts of western North America, parts of western and southern Australia, southwestern South Africa and parts of central Chile. Streams in these regions feature seasonal disturbances of contrasting hydrology with high predictability of the timing of flooding and drying but low constancy. We would expect fish living in these streams to avoid scouring flow and breed after cessation of the flood period. The aim of the present study was to examine the adaptation of the Yarqon bleak, *Acanthobrama telavivensis*, an endemic cyprinid in the coastal streams of Israel, to mediterranean-type stream[1] conditions. For that we studied its reproductive strategy (age at maturity and life span, gonad activity, oocyte maturation, spawning activity and habitats, appearance of juveniles), in a major costal stream (Yarqon). Our findings show that the Yarqon bleak exhibits life history traits attuned with a mediterranean-climate hydrologic regime. It breeds in late winter and early spring, a window of opportunity between flash floods and habitat desiccation. Being a multiple spawner allows the fish to compensate for the potential loss of part of its reproductive output due to scouring flows of late floods. The ability of the Yarqon bleak to spawn on different substrate-types enables it to take advantage of different stream conditions that pertain in different years. The fish attains pre-adult size (ca. 33–42 mm) within the first year, prior to drying out of most stream reaches, and matures by the beginning of the second year (males >41; females >42 mm). The cost of these tactics is a short life span (4–5 age groups). The reproductive strategy of the Yarqon bleak falls into the category of in-channel breeding but, unlike the case suggested by a low flow recruitment model, the fish breed during the period of flood cessation, a transitional time between high and low flows, rather than at the time of low flow. Breeding at this time of the year in mediterranean-type streams puts early stages somewhat at risk of being washed away by late floods, but gains them a longer period of growth under favorable conditions. We suggest an additional positive tradeoff that should be investigated: the reduced competition with age 0 of other fish that breed later in the season. This suggested model of recruitment during the period of flood cessation seems appropriate for fish in streams with

[1] mediterranean—written with a small m, is used in connection with climate or ecological region and is distinguished from Mediterranean that is used in a geographical context, referring to the Mediterranean basin.

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seasonal contrasting flows of high predictability but low constancy.

Keywords *Acanthobrama telavivensis* · Reproduction · Flooding and drying · Mediterranean-type streams · Yarqon

Introduction

Recurrent disturbances relative to an organism's life span may be evolutionarily important (Lytle 2001), and are thus expected to play a role in shaping the life histories of aquatic organisms (Cambray and Bruton 1984; Fisher and Grimm 1988; Resh et al. 1988; Magalhães et al. 2003). Mediterranean-type streams (sensu Gasith and Resh 1999) are ecosystems featuring seasonal disturbances of contrasting hydrology (flooding and drying) that emanate from a distinctive rainfall pattern. Often 80% or more of the rainfall falls within 3–5 month period of winter (e.g., Gasith and Resh 1999; Magalhães et al. 2003), with most of the precipitation occurring during a few major storm events that produce flooding (Lulla 1987; LeHouórou 1990). Subsequent drying and a declining flow take place gradually over a period of several months in summer, ending abruptly in fall or early winter when the next year's rains commence. The strong seasonality in rainfall and the associated seasonal flooding and drying clearly distinguish the Mediterranean climate from most mesic or xeric temperate climates; in the latter climate regions, storms can occur during the colder wet season but also at other times of the year. Although occurrence of flood during fall, winter or spring in mediterranean-type streams is predictable, the intensity and frequency of the floods vary greatly from year to year depending on the frequency and intensity of rainfall. Such a hydrological pattern can be defined as having high predictability but low constancy (sensu Colwell 1974). Streams that are subject to this hydrological regime can be found in five widely separated regions; the Mediterranean basin, parts of western North America, parts of western and southern Australia, southwestern South Africa and parts of central Chile (Gasith and Resh 1999). Two main models associate flow regime with fish breeding and recruitment. The flood pulse concept (Junk et al. 1989; Harris and Gehrke 1994) suggests that fish take advantage of over-bank flow for breeding in inundated habitats in the flood plain. In temperate regions the rise in water level coincides with increasing temperature. This strategy can be effective provided that the inundation lasts long enough for the fish to spawn and for the larva to hatch and grow (King et al. 2003). A low flow recruitment model was suggested for situations when flood dynamic is unpredictable and flood plain inundation is potentially short (Humphries et al. 1999). The fish breed in the main channel of a river in summer, at a time of low flow and high temperature, when this condition is more predictable from year to year and generally of longer duration than the floods at this time of the year. In mediterranean-climate regions flooding occur following intense but brief rainstorms and inundation of the floodplain is short (often days). Fish breeding in such floodplains risk becoming stranded and losing reproductive output (King et al. 2003). Considering the fact that in streams in this climate region the timing of flooding and of drying are equally predictable from year to year, fish are expected to avoid scouring flow and breed after cessation of the floods. However, delaying breeding to the period of low flow may expose the fish to risk of early desiccation in drought years.

The Yarqon bleak, *Acanthobrama telavivensis*, is relatively small cyprinid (up to 120 mm TL), endemic to the coastal streams of Israel. The distribution of cyprinid fish in the coastal region in Israel occurred in at least three waves of migration from the Jordan Valley (Goren and Ortal 1999), the first, that brought the ancestors of the Yarqon bleak about 200,000 years ago (Levy 2004). The Yarqon bleak established large populations and became the most common fish in the coastal streams. The flourishing of this species suggests a life-history adaptation to seasonal, sequential, contrasting hydrologic regimes, typical of mediterranean-type streams. Since the 1950s, pollution of the streams has decimated its population to the extent that it is presently "critically endangered" (Goren 2004).

Based on observation of juveniles, Goren (1983) suggested that the Yarqon bleak breeds in winter and early spring (January–April). If indeed so, this would expose the early life stages to floods and contradict our expectation of its breeding in the intermediate period between flooding and drying. The aim of the present study was to examine the adaptation of the Yarqon bleak to mediterranean-type stream conditions by studying its reproductive strategy in a major coastal stream (Yarqon).

Materials and methods

Study site

The Yarqon is the southernmost perennial stream in the coastal plain of Israel (32°06′ N; 34°50′ E). This lowland stream (gradient 0.06%) meanders along 28 km through the largest metropolitan region (Tel-Aviv and vicinity) of Israel and drains into the Mediterranean. The Yarqon's drainage basin is ca. 1800 km^2, receiving an average annual rainfall of about 500–600 mm, 70% between December and February (Goldreich 1998). Prior to 1950, the Yarqon's annual base flow was over 200 million cubic meters (MCM). The discharge resulting from run-off varied between less than one MCM in drought years and up to 300 MCM in rainy years (Ben-Zvi et al. 1995). Diversion of the Yarqon's main springs for human use in the mid-1950s reduced base flow to ca. 1% of the average annual discharge, resulting in desiccation of the upper stream sections in drought years. At present, an annual discharge of about 1–2 MCM of spring flow and 10 MCM of effluent maintains a wet channel downstream. It turned out that the study was conducted during two consecutive drought years. However, the general mediterranean-type pattern of winter floods and summer desiccation still exist. It is base flow and intensity of flooding and drying that might be affected.

Based on the degree of perturbation and water quality the Yarqon stream can presently be divided into three sections (Fig. 1): upper unpolluted section, from Rosh HaAyin springs to the confluence with the Qane tributary (7.5 km); a central section (17.5 km) severely impacted by pollution of municipal effluents at its upper reaches with gradual recovery downstream; lowermost 4 km section (downstream "7 Mills dam"), partially polluted estuary. Of the six major tributaries of the Yarqon stream one discharges into the upper section, four into the central section and one into the lower section (Fig. 1). Correspondingly, the upper section usually experiences low to moderate floods relative to the downstream sites. Examples of the flood hydrographs of the Yarqon stream prior to water diversion (1953–1954, average rainfall) and after water diversion (1991–1992, extremely rainy year

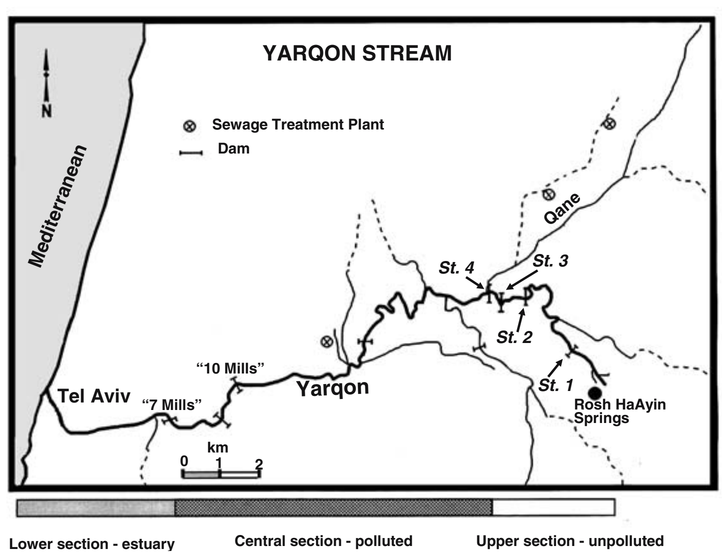

Fig. 1 Schematic map of the Yarqon stream, major tributaries, sources of pollution (wastewater treatment plants), and sampling stations (St.1–St.4)

and the first year of the present investigation, 1998–1999, drought year) are given in Fig. 2.

In the past the Yarqon bleak was distributed along the upper and central sections of the Yarqon (1951, museum records of fish collection, Hebrew University, Jerusalem; Avitzur 1958). Since 1967 there is scientific evidence (Goren 1974) that this fish is now restricted to the upper 7.5 km section of the river. This is the only section of the stream that remains unpolluted (Gasith et al. 1998; Gafny et al. 2000) with an ammonia level low enough to allow survival of this species (Elron et al. 2004).

Four stations were selected along the upper unpolluted section of the Yarqon stream (Fig. 1). In each station we sampled both lentic and lotic sites, above and below small dams. Site characteristics are shown in Table 1. Selected water quality variables and discharge of the upper Yarqon section in different seasons are shown in Table 2.

Fish collection

We collected fish on a monthly basis from April 1998 to March 1999 at the four selected stations using a non-selective shore-operated electroshocker (EFKO model FEG 6000; 350 V, 17 amp) with a hand-held electrode and a hand net (2 mm mesh size). The fish were brought to the laboratory on ice within 4 h of collection. They were measured (total length) to the nearest

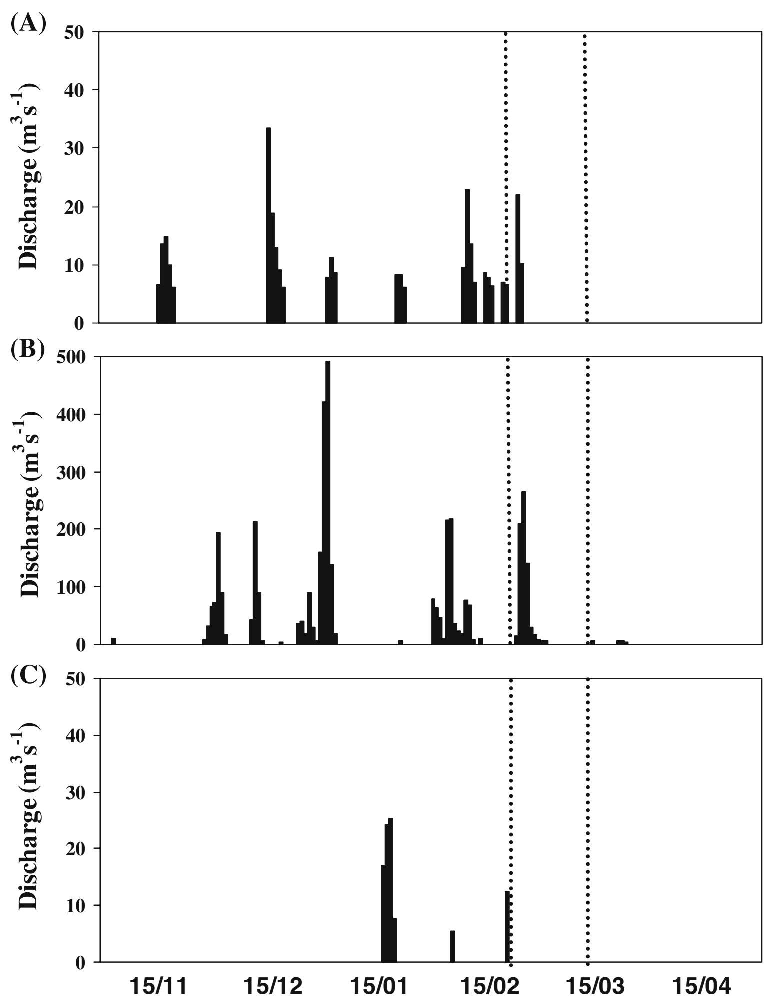

Fig. 2 Comparison of peak daily discharge (>5 m^3 s^{-1}) following rain events in the Yarqon stream. (**A**) 1953–1954 (a year of average rainfall, prior to water diversion), (**B**) 1991–1992 (an extremely rainy year), (**C**) 1998–1999 (drought year, first year of study). Dotted lines indicate first date of spawning and peak spawning of the Yarqon bleak, respectively. Discharge records—Hydrological Service of Israel, "10 Mills" site (Herzliyya road hydrological station no. 17135)

Table 1 Selected features of the Yarqon stream at the study sites

Variable	St. 1	St. 2	St. 3	St. 4
Channel width (m)	15	9	6	9
Channel depth (m)	0.4–2	0.5–2	0.4–1	0.5–2
Flow regime	Lentic	Lentic and lotic[a]	Lentic and lotic[a]	Lentic and lotic[a]
Substratum	Soft sediment	Soft sediment and rocks[a]	Soft sediment and rocks[a]	Soft sediment and rocks[a]
Instream vegetation	Present[b]	Rare[c]	Absent	Absent
Riparian vegetation	Present[d]	Present[e]	Present[f]	Present[g]

[a]Lentic conditions and soft sediment above a dam, lotic conditions and rocky substrate below the dam

[b]Patches mostly of pond lily (*Nuphar lutea*)

[c]Patches of pondweed (*Potamogeton nodosus*)

[d]Dense growth of common reed (*Phragmites australis*) and holy bramble (*Rubus sanctus*) with encroaching branches and roots on one bank. Large eucalyptus trees on the other bank

[e]Dense growth of common reed (*Phragmites australis*) and holy bramble (*Rubus sanctus*) with encroaching branches and roots on both banks

[f]Willow (*Salix acmophylla*) with encroaching roots, eucalyptus trees and holy bramble (*Rubus sanctus*) on both banks

[g]Willow (*Salix acmophylla*) with encroaching roots on both banks

Table 2 Ranges of selected water quality variables and discharge in the upper section of the Yarqon stream during the study period: winter (December–February), spring (March–May), summer (June–August), fall (September–November)

Variable	Winter	Spring	Summer	Fall
Temperature (°C)[a]	10.8–14.4	15.2–26.5	25.9–31.1	18.0–25.7
Dissolved Oxygen (mg/l)[a]	4.8–10.2	3.3–11.8	2.0–8.2	2.8–7.0
Conductivity (μS, @25°C)[a]	390–1205	810–1130	900–1200	1110–1190
Turbidity (NTU)[b]	13–52	12–75	10–35	17–21
pH[c]	7.8–7.9	7.8–7.9	7.8–7.9	7.8–7.9
BOD_5[d]	1.5–3.8	2.3–6.6	1.5–4.3	1.8–2.4
Total ammonia (mg/l)[c]	0.01–0.5	0–0.36	0–1.3	0.02–1.2
Discharge (m^3/s)[e]	0.002–3.0	0.002–0.007	0.002–0.47[f]	0.01–0.06

[a]YSI 85 meter

[b]HACH 2100 turbidimeter

[c]Orion 710A Ionalyzer

[d]APHA (1995)

[e]Hydrological Service of Israel

[f]Summer discharge supplemented by additional water (Mekorot—Israel National Water Company)

1.0 mm, and weighed (blot dry) to the nearest 0.1 g. Gonads were removed and weighed (blot dry) to the nearest 0.001 g.

Age determination and population structure

Fish age was interpreted through scale analysis (Jearld 1983). For that we selected the July sample that was relatively large and had representation of all size groups. A sub-sample of 49 fish (males and females) representing all size groups was examined. From each size group we removed and examined six scales taken from the left side of the body, between the dorsal fin and the lateral line. The scales were cleaned using 8% NaOH, mounted dry between two microscope slides and the annuli were examined using a projection microscope (×50). The three best-prepared scales from each fish were examined independently by two persons. Where no agreement could be reached on age interpretation the fish was rejected (3 out of 49 fish). Age was also interpreted from fish size frequency using Petersen's method. For this analysis we integrated samples of all fish collected at all stations for each month. Only samples containing >50 fish were used to construct multi-modal length frequency histograms (1 mm size intervals). Age was then estimated from successive modal length (Bagenal and Tesch 1978).

Reproduction

Gonad development of mature individuals was assessed using the gonado-somatic index, GSI: $\mathrm{GSI} = \frac{G_w}{W} \times 100$, where G_w and W are the gonad and total fish weight (in g), respectively. We assessed oocyte maturation stage during the breeding period (February–April) by measuring oocyte diameter in 20 females ranging in size from 47 to 107 mm. The oocytes were measured with a calibrated eyepiece micrometer under a binocular microscope at 40× magnification (resolution 10 μm). Fecundity (F) was estimated using the gravimetric method (Snyder 1983). We weighed gonads of 26 gravid females and counted the number of opaque and yolky eggs in three pre-weighed sub-samples. The total number of eggs per gonad was calculated by multiplying the gonad weight by the mean egg number per unit weight.

The spawning period was interpreted from the changes in the gonado-somatic index, presence of eggs and juveniles. We examined for presence of eggs on in-stream and submerged bank vegetation, roots and rocks (supporting the dams), in lentic and lotic situations at each of the four stations (Table 1). We also examined spawning on artificial substrates that we introduced into the study sites. These consisted of bricks (17 × 11 × 5.5 cm), to which we attached a plastic net (0.5 cm opening) folded in the form of a cylinder (5 cm diameter, 25 cm long). The bricks were placed on the bottom to hold the folded net in the water column. Five sets of artificial substrate were introduced at each station.

To confirm the fish species identity we sampled 30 eggs from different sites, reared them in the laboratory and examined the larvae (Goren et al. 1973). All eggs belonged to the Yarqon bleak. To determine incubation period we used eggs spawned on bricks under laboratory conditions (690 l tanks, aerated tap water) on two dates (mid March and early April, 1998). On their first day, the eggs (n = 39 and 118, respectively) were transferred to small aquaria (30 × 16 × 18 cm) and were kept at room temperature (13–17 and 18–23°C, respectively).

Statistical procedure

Statistical tests were performed using STATISTICA 7.1 for Windows™ (StatSoft 1995). We performed a χ^2 test to determine whether male and female (M:F) sex ratio differed from 1:1 during the study period. Regression analysis was used to establish the relationship between female total length (TL) and total fecundity (F) and to determine the relationship between fish size and the percentage of mature males and females (after arcsin transformation).

Results

The study was conducted during consecutive drought years. Water discharge in the upper unpolluted section of Yarqon stream (St. 1, Fig. 1) ranged from 0.002 to 3.0 $m^3 s^{-1}$ (median 0.04 $m^3 s^{-1}$). Water temperatures varied between 12 and 29°C in January and August, respectively. During the spawning period (February–April) water temperatures ranged between 14 and 20°C (Table 2).

Sex-ratio, length and age at maturity

A total of 739 individuals (mature and juveniles) were collected during the study period. The sex-ratio was 2.26:1, significantly skewed towards males (chi-square, χ^2 = 38.7, $P < 0.001$; n = 258). Scale annuli analysis of specimens caught in July suggested five age groups (Table 3). Only two fish larger than 101 mm (4+) were recorded during the study period (one was collected in July). The size of fish at a certain age as determined by scale analysis was within the size range of fish of the same age determined by size frequency distribution (Table 4). Size frequency distribution data suggest growth of the 0+ and 1+ age groups in spring and early summer (May–July). Fish size at age 1+ recorded in February 1999 were within the

Table 3 Annuli analysis, total and average (±SD) fish length and interpreted age of the Yarqon bleak, Yarqon stream, July 1998 (*n* = number of fish)

Number of annuli	*n*	Length range (mm)	Average (±SD) (mm)	Estimated age
0	6	34–44	40.0 ± 3.0	0+
1	15	49–58	53.9 ± 3.2	1+
2	16	59–79	66.4 ± 5.7	2+
3	8	77–101	87.0 ± 8.6	3+
4	1	107		4+

Table 4 Mean modal length (±SD) of the Yarqon bleak collected at different times of the year, Yarqon stream (*n* = sample size)

	0+	1+	2+	3+
April 1998 (*n* = 232)	–	46.5 ± 4.8	63.5 ± 3.9	76.0 ± 2.9
May 1998 (*n* = 56)	21.8 ± 4.0	46.1 ± 3.4	–	–
June 1998 (*n* = 102)	22.6 ± 4.0	49.0 ± 4.1	64.4 ± 4.3	–
July 1998 (*n* = 118)	24.3 ± 3.1 38.3 ± 2.6	52.2 ± 2.8	64.5 ± 3.4	–
February 1999 (*n* = 75)	–	40.0 ± 2.5	57.1 ± 0.4	–

size range of the larger size age 0+ group of July of the previous year (Fig. 3; Table 4). The smallest mature male and female were 40 and 41 mm, respectively (age 1+; Fig. 4). The percentage of mature males and females increased with fish size ($R^2 = 0.83$, $P < 0.001$ and $R^2 = 0.83$, $P < 0.001$, respectively). Individuals larger than 59 mm (age 2+) were all mature (Fig. 4).

Reproductive period and fecundity

Testes began to develop in November after a quiescent period of three months (August–October, Fig. 5). The gonado-somatic index of males was highest between February and April, with a maximum value in February (GSI = 2.5%). The quiescent period of females was two months longer than that of males, extending from July to November. A maximum female GSI of 10.8% was recorded in March. In May and June, only females larger than 62 mm had developed gonads. The last females (*n* = 2) to be found with developed gonads were recorded in June.

Oocytes of five different developmental stages were identified in the ovaries during the spawning period (Table 5), with at least three oocyte stages occurring simultaneously in each gonad. The proportion of oocytes in the final maturation stage (E) remained relatively constant (3.3–4.3%) throughout the spawning period.

The fecundity of the Yarqon bleak ranged between 280 and 4200 eggs in females ranging in size between 46 and 107 mm (*n* = 26). Weight specific fecundity was 276.5 ± 90.2 eggs per gram. The total length (TL in mm) and fecundity (F) regression was: $F = 0.026\ \mathrm{TL}^{2.47}$ ($R^2 = 0.77$, $P < 0.05$), with a predicted fecundity at median length (62 mm, *n* = 26) of 695 eggs.

Spawning period and juveniles

In 1999, eggs were first found in the second week of March whereas in the following year they were discovered as early as the third week of February (Table 6). In 1999 and 2000, eggs were found as late as the last week of March, and in a single site a few eggs were still found in the first week of May. Out of 14 records of presence of eggs, >85% were recorded between mid to late March (Table 6).

Eggs were found in both lentic and lotic habitats, above and below small dams. In 1999 the eggs were found at depths between 10 and 30 cm, attached to submerged branches and roots of riparian vegetation (Table 6), mostly of holy bramble, *Rubus sanctus*, and willow, *Salix acmophylla*. In 2000, eggs were found at similar depths also on rocks building or supporting the dams (within 1–3 m downstream of the dams). Up to 20 eggs were found on root clumps of ca. 180 cm^3 and rocks with an area of ca. 100 cm^2. Eggs were

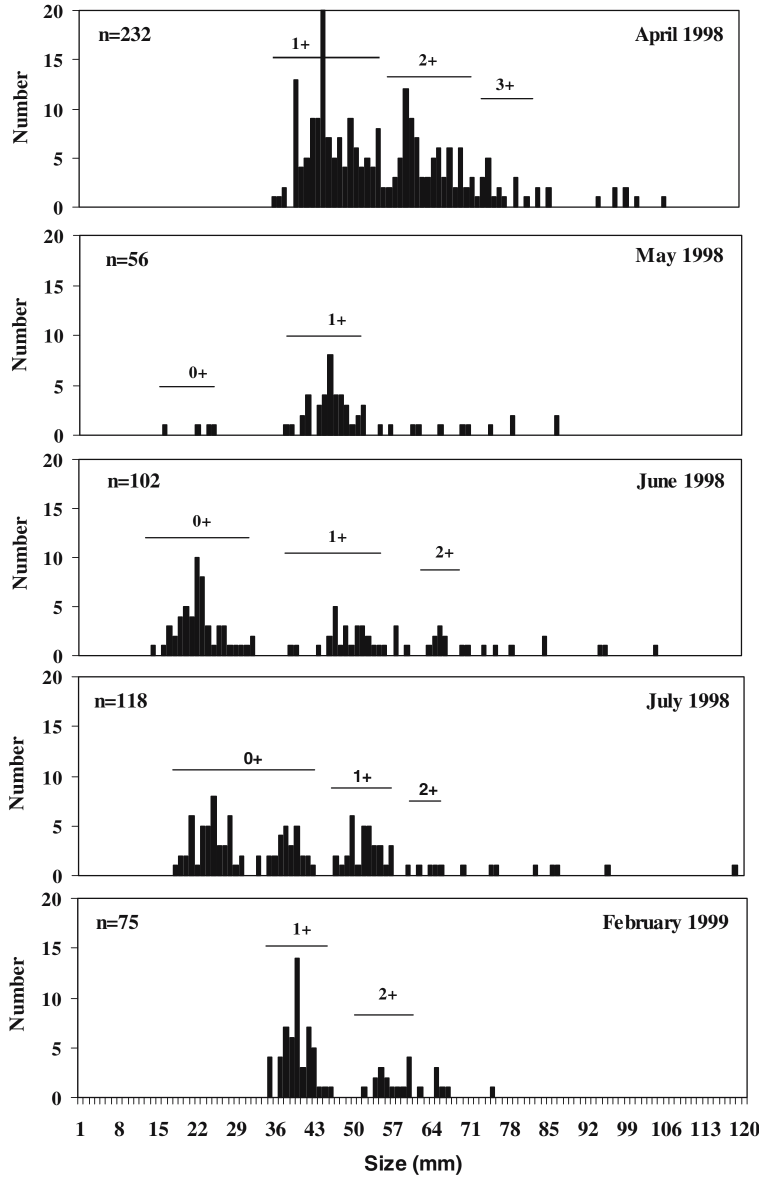

Fig. 3 Length-frequency modal progression and estimated age of the Yarqon bleak (Yarqon stream, April–July 1998 and February 1999; *n* = sample size)

never found on the artificial substrate (bricks and plastic netting) placed in the stream. However, in captivity the fish successfully spawned from mid-March to mid-May and eggs were found on bricks but not on roots. The diameter of the eggs found on bricks varied between 1540 and 1975 μm (1846 ± 131.6; *n* = 10). At 13–17°C fry hatched after 7–10 days (9.1±0.7, *n* = 39) and at 18–23°C the incubation time was about 2 days shorter (7.3 ± 1.9, *n* = 118). Fry length was 4–5 mm.

In May, June and July juveniles (mean TL < 40 mm) formed 7, 49 and 32% of the monthly catch, respectively. In July two size groups of juveniles were recorded (average size 24 and 38 mm; Fig. 3).

Discussion

Fluctuating discharge is a major disturbance and a source of temporal and spatial ecological variation in aquatic systems (Poff et al. 1997) influencing among others reproductive strategies of fish (Humphries et al. 1999; Cattaneo et al. 2001;

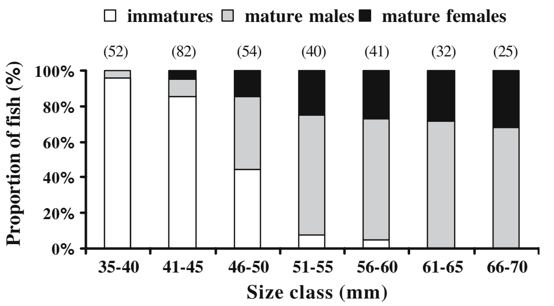

Fig. 4 Length at maturity and proportion of mature male to female of the Yarqon bleak collected during the breeding period (February–April) in relation to size class. Value in parenthesis = number of fish

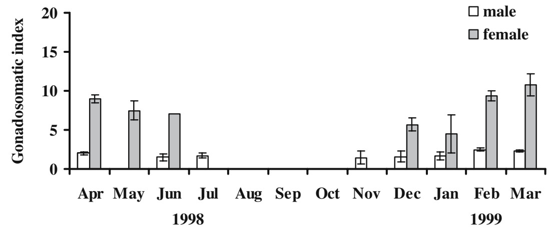

Fig. 5 Seasonal changes in gonadosomatic index of males (n = 183) and females (n = 81) of the Yarqon bleak in the Yarqon stream (April 1998–March 1999)

King et al. 2003). Adaptation to a mediterranean-type hydrologic regime is expected to select for life-history traits that favor resistance from being washed away by floods, and for survival during periods of reduced flow (Moyle 1982; Gasith and Resh 1999). Therefore, the fact that the study was conducted during two consecutive drought years has no significance when life history pattern is considered. Our findings of the reproductive biology of the Yarqon bleak support this hypothesis.

Early breeding

Contradictory to Goren's (1983) suggestion that the Yarqon bleak breeds as early as January, our findings on gonad activity, oocyte maturation, spawns and juveniles, show that breeding is initiated by mid February, with a peak in mid March, and lasts to the beginning of April.

Analysis of flood distribution in streams of the central coastal plain of Israel over a period of about 50 years indicates that on average, the mean date of the 25, 10 and 5% largest discharge events occurs before January 11 (±27 days SD; Ben-Zvi and Atzmon 1997). In about 45% of the years peak discharge in the Yarqon stream exceeded 50 m^3 s^{-1} and in 30% of the years it was two-fold higher (Ben-Zvi et al. 1995). More than 75% of the floods in the Yarqon stream occur before the third week in February, when the Yarqon bleak starts spawning, and 85% before peak spawning in mid March (Table 7, Fig. 2). Juveniles of the Yarqon bleak (10–30 mm) were recorded in May through July in the Yarqon, as well as in other perennial and intermittent streams in the central coastal plain (e.g. upper and lower Tanninim and Tut streams; A. Gasith, unpublished data). During this period both lentic and lotic habitats are plentiful (Table 1) and oxygen is not limiting (Table 2). Breeding in late February exposes the Yarqon bleak to a certain low risk of damage to early life stages by late floods, but provides a relatively long period of favorable growth conditions of increasing temperature (14–20°C), elevated water levels, high habitat diversity and abundant food resources. Moreover, in intermittent streams, early breeding enables the Yarqon bleak to reach pre-adult size (ca. 33–42 mm) prior to drying out of parts of the stream. This may explain the survival of the Yarqon bleak in intermittent streams.

Our findings on the timing of breeding of the Yarqon bleak agree with findings by others in the Iberian Peninsula (Herrera and Fernández-Delgado 1994; Fernández-Delgado and Herrera 1995; Ribeiro et al. 2000; Magalhães et al. 2003) and in California (Marchetti and Moyle 2000), and suggest that fish in mediterranean-type streams use the window of opportunity between flash floods

Table 5 Maturation stage and oocyte attributes (diameter range, diameter mean, color and appearance) of the Yarqon bleak during the spawning period (February to April; 20 fish, 10 eggs per maturation stage)

Stage	Diameter range (μm)	Mean ± SD	Egg color
A	10–40	27.1 ± 7.8	Clear-white (opaque)
B	90–200	153.3 ± 35.0	Clear-white (opaque)
C	300–400	339.6 ± 29.8	Cloudy-white (opaque)
D	490–800	613.7 ± 85.9	Pale-yellow (opaque)
E	850–1250	1055.9 ± 157.6	Yellow (yolky)

Table 6 Occurrence of eggs (+) of the Yarqon bleak recorded at different sites and on different substrate in the upper section of the Yarqon stream

Date	St. 1		St. 2		St. 3		St. 4	
	Veg	Rock	Veg	Rock	Veg	Rock	Veg	Rock
31/12/1998	NE	NE	NE	NE	NE	NE	NE	NE
17/02/1999	NE	NE	NE	NE	NE	NE	NE	NE
14/03/1999	+	NE	+	NE	+	NE	+	NE
25/03/1999	NE	NE	+	NE	+	NE	NE	NE
28/04/1999	NE	NE	NE	NE	NE	NE	NE	NE
06/05/1999	NE	NE	+	NE	NE	NE	NE	NE
28/05/1999	NE	NE	NE	NE	NE	NE	NE	NE
05/06/1999	NE	NE	NE	NE	NE	NE	NE	NE
24/12/1999	NE	NE	NE	NE	NE	NE	NE	NE
25/01/2000	NE	NE	NE	NE	NE	NE	NE	NE
20/02/2000	NE	NE	+	+	NE	+	NE	NE
16/03/2000	NE	NE	+	+	NE	+	+	+
31/03/2000	NE	NE	NE	+	NE	+	NE	NE
16/04/2000	NE	NE	NE	NE	NE	NE	NE	NE
01/05/2000	NE	NE	NE	NE	NE	NE	NE	NE

Veg = on vegetation; Rock = on rocks; NE = no eggs

and habitat drying for recruitment of the next generation. Indeed, relatives of the Yarqon bleak living in environments free of contrasting flow also reproduce at other times of the year. For example, in Keban Dam Lake (Turkey), the marmid bleak, *Acanthobrama marmid*, breeds from spring throughout summer (April–August; Çolak 1982 cited in Ünlü and Balci 1994; Table 8), in the Tigris River it breeds in spring and early summer (May–June, Ünlü and Balci 1994; Table 8). In the warm-water Lake Kinneret (Israel), the Kinneret bleak, *Mirogrex terraesanctae* (= *Acanthobrama terraesancate*) breeds throughout winter and spring (November–May). In the latter case, the spawning period is attuned with the period of rising lake level, which inundates rocky littoral areas and provides suitable spawning beds free of slimy biofilm of attached algae (Gafny et al. 1992). The breeding strategy of the Kinneret bleak may be viewed as equivalent to fish spawning in floodplains.

Multiple spawning

A single-spawning strategy at the time of seasonal uncertainty (e.g., spawning at the end of the spate period) may prove detrimental. In fluctuating environments, a late catastrophic rain-storm for example, may wipe out the entire reproductive output of that year. In contrast, spreading out annual egg production (multiple spawning) assures recruitment of at least some portion of the total spawn (Weddle and Burr 1991; Pires et al. 2000; Ribeiro et al. 2000). Several findings suggest that the Yarqon bleak is a multiple spawner. The GSI of females of the Yarqon bleak is low (10–12%) relative to that of single spawners (20% or more, e.g. *Rutilus rutilus*; Rinchard and Kestemont 1996). In addition, the ovaries of the Yarqon bleak simultaneously contain oocytes at different developmental stages and the percentage of oocytes at the final maturation stage remains relatively constant throughout the spawning season. These findings suggest the development of batches of eggs that are released over a period of time. This conclusion is supported by the bimodal size distribution pattern of age 0+ in the summer sample (July 1998, Fig. 3). Furthermore, in recent experiments in captivity we found that the number of spawns over a period of time was at least three fold higher than the number of reproducing females (M. Goren, unpublished data). Multiple spawning has been reported for other cyprinids in mediterranean-type streams (e.g., Fernández-Delgado and Herrera 1995; Pires et al. 2000; Ribeiro et al. 2000; Soriguer et al. 2000).

Growth, maturation and life span

Rapid growth and early maturity observed in fish in mediterranean-type streams increase their fitness and survival Fernández-Delgado and

Table 7 Thirteen annual flood records in the central section of the Yarqon stream and timing of spawning of the Yarqon bleak

Hydrological Year	Floods before February 21		Floods after first spawning (February 21)			Floods after peak spawning (March, 14)		
	No. of floods	Peak discharge ($m^3 s^{-1}$) Range (median)	No. of floods	% of annual floods	Peak discharge ($m^3 s^{-1}$) Range (median)	No. of floods	% of annual floods	Peak discharge ($m^3 s^{-1}$) Range (median)
1991/92	10	5–491 (84)	2	17	6–265	1	10	6
1992/93	8	3–421 (14)	2	20	8–10	1	12.5	10
1993/94	6	3.5–17 (8.5)	5	45	4.5–14 (5)	2	18	5
1994/95	13	1–72 (24)	5	28	6–7.5 (6)	3	17	5.5–7.5 (7)
1995/96	8	3–93 (8)	0	0	-	0	0	–
1996/97	7	1–230 (18)	4	36	4.5–52 (7.5)	2	18	9–52
1997/98	14	1–24 (4)	5	26	2–51 (4.5)	3	16	2–51 (4)
1998/99	8	1.5–25 (2)	3	27	1.3–2 (1.7)	3	27	1.3–2 (1.7)
1999/00	5	4–128 (74)	2	28.5	3.4–6	1	14	6
2000/01	12	1–48.5 (3)	1	8	2	1	8	2
2001/02	10	2–104 (7)	3	23	1–7 (4)	3	23	1–7 (4)
2002/03	13	1–88 (10)	3	19	3–55 (22)	2	12.5	22–54
2003/04	10	0.01–4 (1)	1	9	5.6	0	0	–
Median	10		3	23		2	14	

Hydrologic data of Hydrological Service of Israel; ‘‘10 Mills’’—Herzliyya road hydrological station no. 17135

Table 8 Comparison of reproduction traits of three cyprinids of the *Acanthobrama* complex living in habitats with different hydrologic regimes

Life history attribute	*Acanthobrama telavivensis*	*Mirogrex terraesanctae* (= *Acanthobrama terraesanctae*)	*Acanthobrama marmid*
Distribution	Coastal streams, Israel[b]	Lake Kinneret, Israel[c]	Tigris, Euphrates and Orontes river systems[h]
Hydrological regime	Mediterranean-type stream	Fluctuating Lacustrine system	Spring and early summer snowmelt floods
Maximum length	120 mm[a]	230 mm[d]	180 mm[h]
No. of age groups	5[a]	6 or 7[e]	5[h]
Size and age at maturity	40–50 mm[a] Second year	Above 80 mm[e, f] Third year	100–140 mm[h] Second year
Spawning period	Mid February to early April[a]	Mid. November to mid. May[g]	May–June[h] April–August[j]
GSI—maximum value	Male: 2–2.5%[a] Female: 9–10%[a]	Male: 1–2%[f] Female: 10–12%[g]	Male: No data Female: 10–12%[h]
Fecundity	280–4200[a]	No data	1200–8100[h] 9000–11000[j]
Spawning site	Bank vegetation and rocks[a]	Rocks near shore[f]	Bank vegetation[i]
No. of egg stages	5	6	No data
Mean egg diameter in final maturation stage	850–1250 μm[a]	820–1300 μm[f]	1100–1250 μm[h]
Egg incubation period	7–10 days (13–17°C)[a]	9–11 days (16°C)[g]	No data

[a]Present study
[b]Goren (1973)
[c]Steinitz (1954)
[d]Davidoff (1986)
[e]Ostrovsky and Walline (1999)
[f]Svislotski (1960)
[g]Gafny et al. (1992)
[h]Ünlü and Balci (1994)
[i]Erhan Ünlü—personal communication
[j]Çolak (1982, cited from Ünlü and Balci 1994)

Herrera 1995; Oliva-Paterna et al. 2003). These traits are typical to *r*-strategists, ensuring reproductive investment and maintenance of population size in stressful environments (Cowx 1990; Winemiller and Rose 1992; Wootton 1998). However, the cost of this tactic is a reduction in life span and smaller body size (Roff 1981; Mills 1991). The life history of the Yarqon bleak is in agreement with the above hypothesis. Between the first year of life and beginning of the second, more than 50% of the fish reach sexual maturity. Correspondingly, this species is smaller than its relatives that reach sexual maturity in their second year (male and female *A. marmid*, Table 8), or third year (males and female *M. terraesanctae*, Table 8) and have a relatively short life span (4–5 age groups). The relation between fecundity and the total length of the Yarqon bleak is similar to that reported for other cyprinids of up to twice its size (e.g. Ribeiro et al. 2000).

Spawning habitat

Fish that have stringent requirements of habitat features will be limited in distribution (e.g., Mills 1991). In contrast, generalist species that lay eggs on different substrate types are expected to fare better in an environment that provides variable habitats. The Yarqon bleak exhibits spawning flexibility, laying eggs on submerged branches and roots encroaching from the banks when stream level is high and on stones when it is low (Table 6). Reduced scouring flow in the vicinity of the banks (Allan 1995), and flexibility of the submerged branches and roots that move about with the running water, may explain spawning in this sheltered environment under high stream flows. However, bank vegetation becomes stranded in drought years when river level is low. Under the latter conditions fish are forced to spawn in other habitats. In the past, high water levels prevailed in the Yarqon stream throughout the year (Avitzur 1958) and habitats with submerged bank vegetation were plentiful. Under the currently reduced water regime, spawning habitat availability is reduced. Construction of riffle habitats below dams provides a rocky substrate that is used by the Yarqon bleak for spawning in drought years.

Flood cessation transitional period recruitment model

The reproductive strategy of the Yarqon bleak falls into the category of in-channel breeding but, unlike the case suggested by the low flow recruitment model (Humphries et al. 1999), the fish breed during the period of flood cessation, a transitional time between high and low flows, rather than at the time of low flow. Breeding at this time of the year in mediterranean-type streams puts early stages somewhat at risk of being washed away by late floods, but gains them a longer period of growth under favorable conditions (e.g., high water level, greater stream connectivity, high habitat availability, increasing temperature, high dissolved oxygen, variable food resources). Magalhães et al. (2003) underscored the tradeoff between reproduction and growth for fish breeding in early spring in mediterranean-type streams. During the drying period, stream connectivity is reduced and in drought years the larvae of late spawners (e.g., chub, *Squalius torgalensis*) may become stranded in spawning areas. In contrast, early spawners (e.g., nase, *Chondrostoma lusitanicum*) allow age 0+ to disperse into pool refugia, which enhances their survival during both summer droughts and spring floods. The authors point out a possible negative tradeoff for the adults of early spawners: they tend to be in poor condition after the high reproductive effort, thus unable to disperse or resist displacement during flood events. We suggest that an additional positive tradeoff for fish breeding in late winter and early spring in mediterranean-type streams is that of reduced competition with age 0+ of other fish that breed later in the season (e.g., Yarkon bleak with tropical cichlids in Israel, and Nase with Chub in south Portugal). The proposed flood cessation transitional period recruitment model seems appropriate for fish in streams with seasonal contrasting flows of high predictability but low constancy, and should be further investigated.

Conclusion

The reproductive biology of the Yarqon bleak reveals its adaptation to stream conditions prevailing in mediterranean-type streams. It initiates spawning during the flood cessation period and continues until April. Eggs and age 0+ risk being washed away by late floods but gain a longer period of larval growth under favorable conditions. The Yarqon bleak compensates for the potential loss of part of its reproductive output by multiple spawning over a period of about 2 months. Moreover, rapid growth and early maturity enable greater reproductive investment, thereby contributing to survival of this species in an environment with low constancy of flow.

On a broader scope, seasonal availability of water often leads to severe competition for this limited resource by different human sectors. Aquatic habitats usually pay the heaviest toll in altered hydrology, manifested among other by higher frequency and greater intensity of desiccation (Gasith and Resh 1999). This trend of change is expected to reduce fitness of late spawners and underscore the positive tradeoff for early spawners.

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