

Temperature tolerances and southern African distribution of a tropical freshwater shrimp *Caridina nilotica* (Decapoda: Atyidae)

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Laboratory estimates of median time of survival (MTS) were used as an index of the temperature tolerance of the warm-water shrimp *Caridina nilotica*. Tolerance to high (≥ 30 °C) and low (≤ 10 °C) temperature was examined in seasonally acclimated shrimps from subtropical Lake Sibaya. The MTS decreased rapidly above 30 and below 10 °C. The MTS temperature response curve predicted a 'range for activity' extending between 11 to 11,5 °C and 31,5 to 32 °C. This tolerance range broadly matches the span of environmental temperatures which shrimps are likely to experience within their geographical range, implying that distribution may be temperature related. The physiological restrictions implied by the anomalously low upper tolerance limit may be circumvented by avoidance behaviour (e.g. diel offshore migrations) in suitable habitats.

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Laboratoriumbepalings van die mediaanoorlewings tydperk (MOT) is gebruik as 'n aanduiding van die temperatuur-toleransie van die warmwatergarnaal *Caridina nilotica*. Seisoenaal geakklimatiseerde garnale afkomstig uit die subtropiese Sibayameer is vir toleransie tot hoër (≥ 30 °C) en laer (≤ 10 °C) temperatuur ondersoek. Die MOT het bo 30 °C en onder 10 °C vinnig verminder. Die MOT-temperatuur-responskromme het 'n 'verspreiding van aktiwiteit' van 11 tot 11,5 °C en 31,5 tot 32 °C voorspel. Hierdie toleransie-verspreiding stem grootliks ooreen met die spektrum van omgewingstemperatuur wat garnale binne hulle geografiese verspreiding ondervind. Dit wil dus voorkom asof verspreiding moontlik temperatuurgebonde kan wees. Die fisiologiese beperkings soos geïmpliseer deur die onreëlmatige lae boonste toleransiegrens kan in geskikte habitate omseil word deur ontwykingsgedrag (bv. daaglikse diepseemigrasies).

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Atyid shrimps are ancient inhabitants of fresh water. Today they are widespread in fresh waters of the tropics, although some extend into cooler regions (Fryer 1977). The only southern African genus in this family is *Caridina*, with a maximum of four species recognized by Barnard (1950) and Kensley (1972). Distribution records assembled by Barnard (1950) demonstrate the restriction of *Caridina* to the north-eastern part of the subcontinent (Figure 1). The most widespread species, *C. nilotica* (Roux), was recorded only as far south as the Umzimvubu River (ca. 31°30'S) and as far west as Lake Ngami (ca. 22°33'E). I examined the low-temperature tolerance of *C. nilotica* to establish whether its southern distribution limit was likely to be temperature related, given the essentially tropical/subtropical status of this species. I also examined the upper temperature tolerance of this species following the discovery of an apparently anomalously low growth rate at 30 °C (Hart 1980b) during a study of its production ecology and bio-energetics (Hart 1980a, 1981; Hart & Allanson 1981). Considering its wide distribution and abundance in suitable habitats, surprisingly

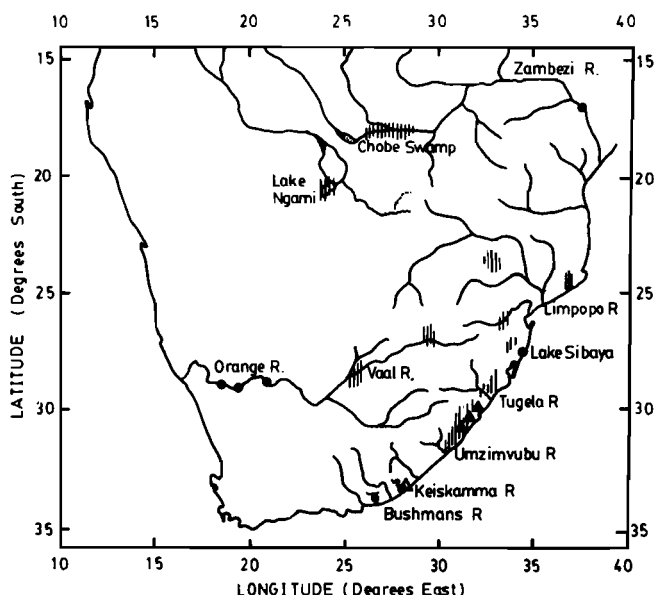


Figure 1 Distribution of *Caridina nilotica*, *C. africana* and varieties (cross hatching), and *C. typus* (shaded triangles) in southern Africa according to Barnard (1950). Additional records for *C. nilotica* shown as shaded circles, and for *C. typus* as open triangles.

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little is known of the ecology of *C. nilotica*. Some insights into its ecology are provided by a consideration of its temperature tolerances, which I report here, together with additional distribution records.

Materials and Methods

All the shrimps in this study were originally collected from vegetated littoral margins of subtropical Lake Sibaya (27°25'S/32°40'E) and exhibited the typical characteristics of *C. nilotica* (Roux). Animals freshly collected in August, the cool season, were used for the low temperature experiments. For the high temperature experiments, animals were drawn from a flourishing, longstanding laboratory culture acclimated to 30 °C for one week prior to the experiments. Details of this culture have been described by Hart (1980a,b).

Medium-sized shrimps (3–5 mm carapace length) were randomly selected and placed individually in glass jars containing ≈ 100 ml of lake water for the low temperature series and conditioned water from the parent culture vessel for the high temperature experiments. Animals were not fed during the experiments as pilot studies demonstrated the lack of any feeding response during high or low thermal stress.

Low-temperature tolerances were determined in a refrigerated incubator. Shrimps were cooled from ambient (≈ 18 °C) to the experimental temperatures of 5, 7 and 10 °C (± 0,2 °C) over periods of 6, 5 and 4 h, respectively. Control series were run at room temperature (≈ 18 °C). Test jars were covered with gas-permeable polythene sheeting to reduce evaporative losses. Water was not changed during the experiments, in view of their generally short duration.

Tolerance to high temperatures was measured in thermostatically controlled water baths. Shrimps, acclimated to 30 °C for one week, were heated to experimental temperatures of 32,5; 33,5 and 34,5 °C (± 0,2 °C) within 1 h. A control series was maintained at 30 °C. Test jars were covered with coarse nylon mesh to prevent the animals jumping out of the containers under thermal stress, while ensuring adequate gaseous interchange with the atmosphere. Evaporative losses were made good with distilled water once or twice daily, and water was completely renewed every two to three days during the longer experiments.

Shrimps were examined at intervals of 2 to 4 h during the extreme-temperature experiments, and every 8 to 24 h under more moderate experimental temperatures. Under high and low thermal stress, animals became very quiescent, and tended to collapse onto their lateral surfaces. The beat of the scaphognathite decreased slowly. Death was diagnosed when the scaphognathite failed to resume beating following gentle prodding of the shrimps with a blunt probe (Hill & Allanson 1971). Water temperatures were measured to 0,05 °C in test jars at each observation. Mean experimental temperatures were calculated from these readings. Survival times reported below refer to the interval between the start of an experiment and the diagnosis of death. Percentage survival was plotted against survival time in hours on probability paper (Finney 1952). The median time of survival (MTS) — the time taken for 50% of the animals to die — was estimated from lines fitted by eye to the probit plots. Estimates of MTS and the shape of the

survivorship curves were very similar for both arithmetic and log₁₀ transformations of survival time. Only the log₁₀ survival plots are reported below.

Results and Discussion

Low-temperature tolerance

Survivorship curves for low temperature series are shown in Figure 2, and Table 1 summarizes the MTS estimates and related experimental information for both upper and lower temperature series. Predictably, MTS decreased with decreasing temperature. In all the low temperature series apart from the 'acclimated' batch at 7 °C, probits of survival were 'split' (Finney 1952). This indicated the possibility that more than one cause of death was involved (Hill & Allanson 1971). Surprisingly, animals acclimated for 12 days at 10 °C prior to exposure at 7 °C (the 'acclimated' batch), demonstrated a lower MTS than animals transferred directly to 7 °C from ca. 18 °C (Table 1). This difference presumably reflects a depression of survival consequent to protracted low-temperature stress during the acclimation period. While this suggests that acclimation does not improve low-temperature survival for all individuals, there are indications from Figure 2 that a residual proportion of acclimated individuals survived longer than their non-acclimated counterparts. Ecologically though, this is unlikely to be significant since at these low temperatures shrimps were prostrate virtually from the outset and unlikely to survive the depredations of nature.

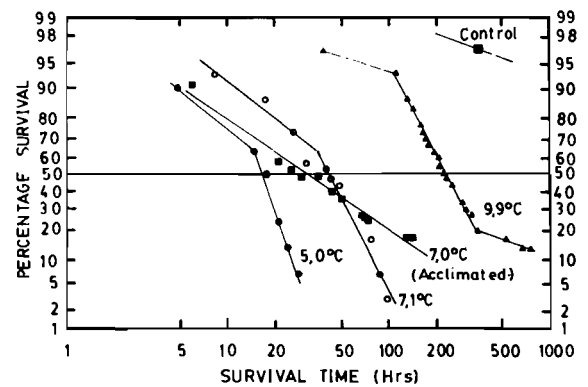


Figure 2 Survival of *Caridina nilotica* at low temperatures. Percentage survival is plotted on probit scale.

Table 1 Median time of survival (MTS) estimates for *Caridina nilotica* exposed to low and high temperatures

	Temperature (°C)	MTS (h)	Number of shrimps
Low	5,0	17	30
	7,0 (Acclimated)	30	25
	7,1	44	30
	9,9	237	55
	18,2 (Control)	∞ ^a	30
High	30,0 (Control)	∞ ^a	20
	32,4	166	20
	33,3	81	20
	34,6	14	20

^aNegligible mortality — MTS is normal physiological lifespan

High-temperature tolerance

Figure 3 shows the survivorship pattern of *C. nilotica* at high temperatures. Table 1 demonstrates the rapid decrease in survival at temperatures above 30 °C. Split probits were evident in the 32,4 and 33,3 °C series, but not at 34,6 °C. This pattern is remarkably similar to that reported for the burrowing prawn *Upogebia africana* by Hill & Allanson (1971) who observed split probits at 32 and 34 °C, but not at 35 °C. For both species, it is probable that death was too rapid at the upper temperature to allow its manifestation from different causes.

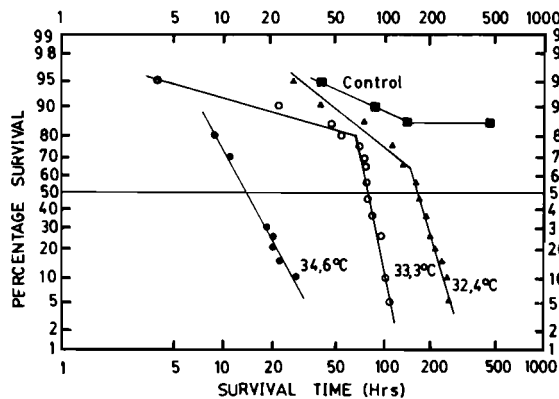


Figure 3 Survival of *Caridina nilotica* at high temperatures. Percentage survival is plotted on probit scale.

Range for activity: implications to distribution

The temperature tolerance range of *C. nilotica* is effectively summarized in Figure 4. In nature, peak seasonal maximum and minimum temperatures are unlikely to persist continuously for more than 15 to 30 days. Diel variation would further moderate temperature extremes. If the conservative value of 30 days is used as the minimum MTS commensurate with the existence of a natural population at a constant temperature, the tolerance polygon in Figure 4 predicts an activity range from 11,5 to 31,5 °C. This matches closely the minimum temperatures recorded at the ebb and flow of the Keiskamma River during 1979–1981, and the maximum water temperatures in the littoral of Lake Sibaya during 1975–1976, shown in Figure 4. Range for activity is increased by 1 °C, from 11 to 32 °C, if 15 days is used as the minimum MTS value.

C. nilotica and *C. typus* were collected recently above the ebb and flow of the Keiskamma River, and a single specimen of *C. nilotica* was taken from the Bushman's River, about 30 km upstream from the mouth. These appear to be the most southerly occurrences of *C. nilotica* in Africa. While genotypes from these southern localities conceivably tolerate lower temperatures than those from Lake Sibaya, the results reported above imply that tolerance to low temperature may be a significant factor in limiting the southern distribution of the species. However, it would be desirable to examine the low-temperature tolerances of *C. nilotica* collected from the interior highveld or southerly coastal systems where colder winter conditions prevail.

Allanson, Ernst & Noble (1962) and Solomon & Allanson (1968) have commented on an improved low-

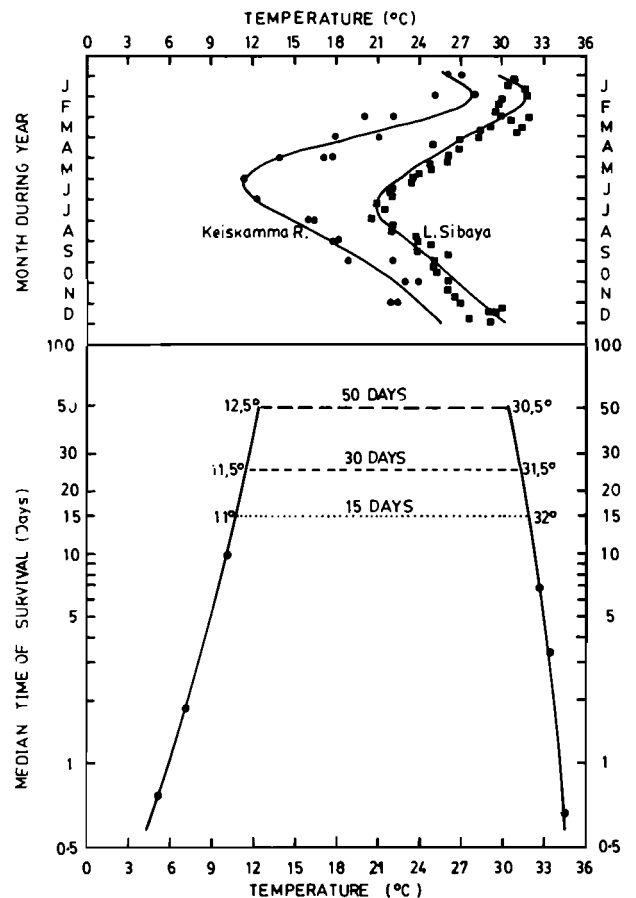


Figure 4 Median time of survival (days) of *Caridina nilotica* as a function of temperature (lower panel), in relation to early morning seasonal temperatures in the Keiskamma River and weekly maximum temperatures in Lake Sibaya (upper panel).

temperature tolerance for the freshwater cichlid fish *Oreochromis (Tilapia) mossambicus* under conditions of marginally elevated salinity. It may be significant that *C. nilotica* occurs in both fresh and brackish water (up to $\approx 4\text{‰}$) in the Keiskamma River (Read, pers. comm.) and that the Bushman's River specimen was found at a salinity of 6‰ . Further investigation is required.

The seemingly 'low' upper temperature tolerance of this tropical shrimp (Figure 4) has to be examined in relation to the thermal regime it experiences in nature. During 1975/76, the weekly maximum temperature recorded in the shallow (40 cm) littoral margins of Lake Sibaya, at a site where *C. nilotica* abounds, exceeded 30 °C on 8 occasions, and an annual maximum of 31,8 °C was recorded. Corresponding weekly minima were 5–6 °C cooler. In a detailed diel study of temperature changes at several depths in a number of marginal habitats in Lake Sibaya in March, Bruton (1973) observed water temperatures exceeding 30 °C for around 5 to 6 h per day, although diel temperatures were mostly around 26–28 °C. He recorded daily maximum temperatures between 32 and 33 °C in the littoral of the lake. Extremes of 35 °C were recorded in isolated shallow lake-side pools. Thus, while MTS drops rapidly above 30 °C (Table 1), *C. nilotica* is unlikely to have to endure temperatures exceeding 30 °C for more than a few hours per day in Lake Sibaya, and it probably escapes stressful temperatures by moving slightly offshore into deeper, cooler

waters. However, high temperatures may conceivably become a limiting factor in its local distribution in shallow areas where behavioural avoidance is not possible and may preclude its occurrence in certain other shallow tropical wetlands.

The present assessment of the geographical distribution of *C. nilotica* presupposes that juvenile and adult shrimps tolerate the same temperature range. It further presumes that a positive energy balance can be maintained over this range. The validity of these assumptions cannot presently be judged. It would also be useful to refine the analysis of both upper and lower temperature tolerances using fluctuating instead of constant experimental temperatures, to simulate more closely the situation in nature.

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