

PREDATION ON A CAVE FISH BY THE FRESHWATER CRAB
AVOTRICHODACTYLUS BIDENS (BOTT, 1969) (BRACHYURA,
TRICHODACTYLIDAE) IN A MEXICAN SULFUR CAVE

BY

SEBASTIAN KLAUS^{1,2}) and MARTIN PLATH^{1,3})

¹) Department of Ecology and Evolution, J.W. Goethe University Frankfurt, Siesmayerstrasse 70A,
D-60054 Frankfurt am Main, Germany

ABSTRACT

Using prey-choice experiments, we demonstrate that the freshwater crab *Avotrichodactylus bidens* (Bott, 1969) preys on cave-dwelling fish (*Poecilia mexicana* Steindachner, 1863) in a sulfidic southern Mexican cave, the Cueva del Azufre, and thus may be one of the top predators in this subterranean ecosystem.

ZUSAMMENFASSUNG

Mittels Beutewahlexperimenten können wir zeigen, dass die Süßwasserkrabbe *Avotrichodactylus bidens* (Bott, 1969) höhlenbewohnende Fische (*Poecilia mexicana* Steindachner, 1863) in einer schwefelwasserstoffhaltigen süd-mexikanischen Höhle (der Cueva del Azufre) bejagt. Möglicherweise gehören die Krabben zu den Topprädatoren in diesem unterirdischen Ökosystem.

INTRODUCTION

Freshwater crabs are thought to play a key role in tropical aquatic ecosystems. Their biomass in tropical streams can make up 58-94% of the total benthic macroinvertebrate biomass (Abdallah et al., 2004; Dobson et al., 2007). Freshwater crabs take a central position in tropical aquatic food webs: they act as prey for vertebrates, as primary and secondary consumers, and as detritivores (Williams, 1961; Gherardi et al., 1987; Dobson et al., 2002; Marijnissen et al., 2009). Furthermore, many species of freshwater crabs have an amphibious mode of life, thus linking terrestrial and aquatic energy flows (Gherardi et al., 1989). Here we

²) e-mail: klaus@bio.uni-frankfurt.de

³) e-mail: mplath@bio.uni-frankfurt.de

report on fish predation by the trichodactylid freshwater crab *Avotrichodactylus bidens* (Bott, 1969) in an extreme (sulfidic and subterranean) habitat.

Habitats are considered extreme if their physical and/or chemical characteristics are outside of the range usually experienced by an organism, thus leading to a decrease in fitness of the organism at initial exposure to this type of environment (Calow, 1989; Rothschild & Mancinelli, 2001). The type locality of *A. bidens* is the sulfidic Cueva del Azufre near Tapijulapa, in Tabasco, Mexico, a habitat that meets the definition of an extreme environment, at least for its metazoan inhabitants. This cave system is characterized by two naturally occurring abiotic stressors: (a) toxic hydrogen sulfide (H_2S) of volcanic origin and (b) darkness (Tobler et al., 2006, 2008a; Plath et al., 2007a). Due to spontaneous oxidation of H_2S in aqueous solution, the presence of H_2S leads to and aggravates hypoxia in aquatic systems, resulting in a distinct inverse correlation of H_2S and oxygen concentrations. Furthermore, its lipid solubility enables H_2S to freely penetrate biological membranes, inhibiting the cytochrome c oxidase, blocking electron transport in aerobic respiration, and thereby hampering the function of mitochondria and the production of ATP. *A. bidens* is one of very few metazoans that apparently can tolerate the toxic water combined with darkness inside the Cueva del Azufre (Gordon & Rosen, 1962).

Traditionally, it has been suggested that organisms invading extreme habitats trade-off increased costs of somatic maintenance due to the presence of physico-chemical stressors with reduced predation or parasitization risk (e.g., Robb & Abrahams, 2002; Rogowski & Stockwell, 2006). Recent studies on extremophile poeciliid fishes from the Cueva del Azufre system, however, have called this claim into question. Inside the Cueva del Azufre the widespread viviparous fish *Poecilia mexicana* Steindachner, 1863 (Cyprinodontiformes, Poeciliidae) certainly do not evade predation. Specifically, these cave fish (“cave mollies”) experience strong predation pressure by a giant water bug of the genus *Belostoma* Latreille, 1807 (Heteroptera, Belostomatidae; cf. Plath et al., 2003; Tobler et al., 2007; Tobler, 2009), which (to the best of our knowledge) was the first set of empirical studies reporting on predation on a cave fish. Water bugs capture fish with their raptorial forelegs while sitting on a rock near the edge of the water and waiting for fish passing by. Predation risk is higher in more sulfidic and, thus, hypoxic microhabitat patches, where the fish spend extended periods of time at the surface showing aquatic surface respiration (ASR; Tobler et al., 2009). Also, *Belostoma* predation is clearly male-biased (Tobler et al., 2008b), as male fish are known to have higher oxygen demands and thus spend more time showing ASR under hypoxic conditions (Plath et al., 2007b). Altogether then, it seems that the presence of H_2S forces cave mollies to the water surface, where they are exposed to elevated levels of predation. Hence, the presence of an abiotic stressor in this system clearly leads

to increased, not decreased predation by *Belostoma* (cf. Plath & Tobler, 2010). Congruent with this line of reasoning, also some species of terrestrial, large-bodied spiders were reported to prey on surfacing mollies (Horstkotte et al., 2010).

So far, all known predators of cave mollies attack them from outside of the water, i.e., while the fish are surfacing (*Belostoma* spp. are semi-aquatic and sit at the water's edge to catch fish passing by). In the present study, we examined the potential role of predation on cave mollies by the freshwater crab *Avotrichodactylus bidens*. Is *A. bidens* a top predator and does the species prey upon cave mollies? Furthermore, *Belostoma* predation appears to be size-specific, i.e., large fish are more likely to be captured (Plath et al., 2003; Tobler et al., 2007). Hence, we asked whether predation by *A. bidens*, if uncovered, would also be size-specific.

MATERIAL AND METHODS

Prey choice experiments were conducted in cave chambers V and VIII of the Cueva del Azufre (Gordon & Rosen, 1962). For comparison, experimental data on *Belostoma* predation, using the same experimental approach as for the freshwater crabs, were included in this study and were re-analysed from Plath et al. (2003). *Belostoma* predation was studied in September 2002. We introduced a large (32.7 ± 3.1 mm standard length) and a small cave molly (20.6 ± 3.2 mm) and one individual of *Belostoma* (19.0 ± 4.3 mm total length) into a plastic bottle (0.5 L), half-filled with water ($N = 20$ trials).

Experiments on *Avotrichodactylus bidens* were conducted in September 2004. In this case, we used larger (1 L) bottles to account for the larger body size of the crabs (16.5 ± 1.6 mm carapax length; large cave molly: 36.3 ± 3.3 mm; small cave molly: 15.5 ± 2.3 mm). The sample sizes was smaller ($N = 11$) because fewer crabs than water bugs could be collected.

The bottles were perforated to supply the animals with fresh water. They were placed in shallow parts of the cave in a horizontal position such that a part of the bottle remained filled with air. Therefore, heteropterans could breathe and cave mollies could perform aquatic surface respiration (Plath et al., 2007b; Tobler et al., 2009). The bottles were then covered with stones to prevent them from drifting away. We chose only places where crabs, heteropterans, and fish co-occurred. After 24 hours, all animals were removed and the fish were examined. We noted if a fish was injured or dead. All experiments were conducted with official permission and in accordance with Mexican law.

RESULTS

Belostoma predation had occurred in only eight out of 20 bottles (40% of the bottles), while in the case of predation by *Avotrichodactylus bidens*, fish were caught considerably more often (in eight out of 11 bottles, equalling 73%). This difference was statistically significant (chi-square test: $\chi^2 = 4.90$, $df = 1$, $P < 0.05$). In total, eight fish were dead or wounded in the case of *Belostoma* predation (out of 40 cave mollies; 20% of the fish), while the freshwater crabs caught 12 out of 22 fish (55%). Again, this difference was statistically significant ($\chi^2 = 12.81$, $df = 1$, $P < 0.0001$).

Our analysis of size-specific predation within the sub-set of data during which predation had occurred revealed that *Belostoma* caught more large (7 of 8) than small (1 of 8) cave mollies; this pattern deviated significantly from random ($\chi^2 = 4.50$, $df = 1$, $P < 0.05$; fig. 1). No such clear-cut pattern was observed in the case of predation by *A. bidens* (large: 5 of 12, small: 7 of 12; $\chi^2 = 0.33$, $df = 1$, $P > 0.1$).

DISCUSSION

The diet of freshwater crabs comprises a large spectrum: algae, terrestrial plant matter, fine detritus, oligochaetes, carrion, and various invertebrates (Williams, 1961; Ng, 1988; Hill & O’Keeffe, 1992; Marijnissen et al., 2009). Although freshwater crab predation on fish is known since antiquity (Brandis & Schuster, 1999), empirical studies focusing on this behaviour are rare and reports so far are restricted to the family Potamidae (cf. Erpenbeck, 1970; Schneider, 1971; Gherardi et al., 1989). Thus, our present work is the first experimental study on fish predation by freshwater crabs.

Despite the small number of individuals used for the experiments, our findings are important for at least three reasons: (1) this cave in particular is clearly not a predator-free environment for the cave fish. Although lack of predation has been assumed for other cave systems housing fishes (Romero & Green, 2005), the apparent predation by *Avotrichodactylus bidens* (this study), *Belostoma* sp. (cf. Plath et al., 2003; Tobler et al., 2007, 2008b; Tobler, 2009), and at least three different species of spiders (Horstkotte et al., 2010) clearly negate this notion.

(2) *A. bidens*, but not *Belostoma* sp., may actually be the top-predators in this subterranean ecosystem. Presumably, freshwater crabs also prey on other organisms residing in the cave, including *Belostoma* sp. As insect larvae are a well-known food source of freshwater crabs (e.g., Williams, 1961; Marijnissen et al., 2009), *A. bidens* are also likely to prey on the very abundant midge *Goeldichironomus fulvipilus* (Rempel, 1939) (Diptera, Chironomidae) (cf. Lavoie

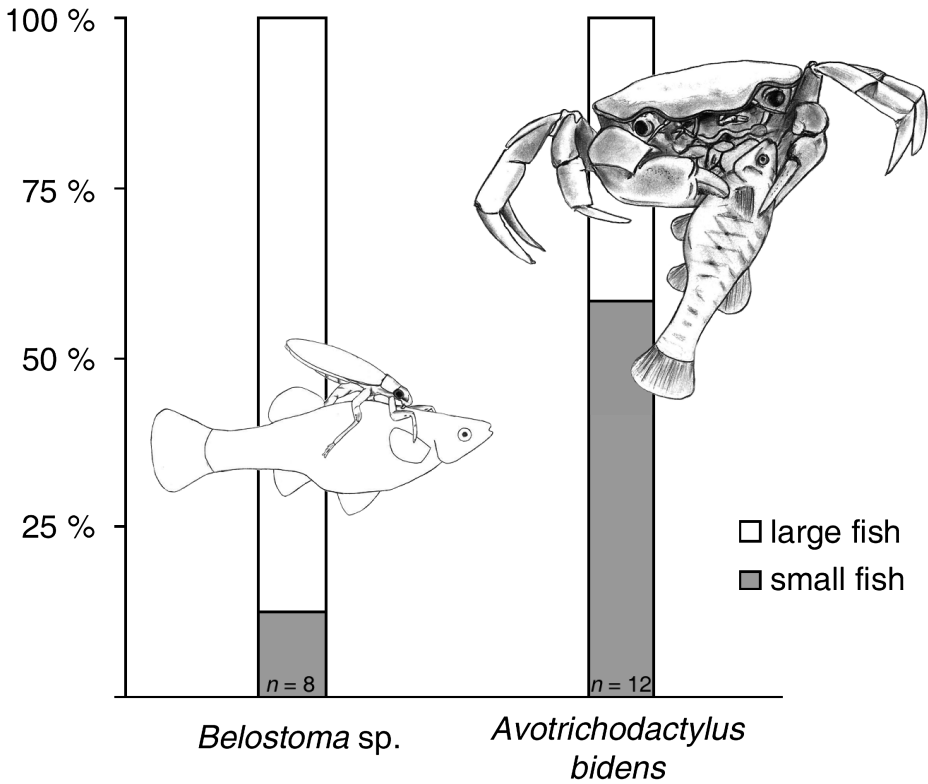


Fig. 1. Size-specific predation of *Avotrichodactylus bidens* (Bott, 1969) and *Belostoma sp.* on the cave molly *Poecilia mexicana* Steindachner, 1863 in the Cueva del Azufre. Large cave mollies in the predation experiment had a length of 36.3 ± 3.3 mm; small cave mollies of 15.5 ± 2.3 mm.

& Evans, 2002). *Belostoma sp.* occurs at high densities in the Cueva del Azufre. Using mark-recapture analysis, the population size of this sit-and-wait predator was estimated as 336 ± 130 (mean \pm S.E.) individuals in cave chamber V of the Cueva del Azufre, which results in a density of over one *Belostoma sp.* per m^2 (Tobler et al., 2007). Comparable data for *A. bidens* are as yet not available. As *A. bidens* is also observed outside the cave, and the number of individuals encountered inside the Cueva del Azufre appears to fluctuate considerably over time (M. Plath, pers. obs.), freshwater crabs are probably not permanent residents of the cave. Thus, freshwater crabs may be an important link for energy flow between extreme and non-extreme habitats.

Finally, (3) predation by species like freshwater crabs may have profound influences on behavioural and life-history traits in cave-dwelling *P. mexicana* (see Riesch et al., 2010 for discussion). For example, predation by piscivorous fishes on the related Trinidadian guppy, *Poecilia reticulata* Peters, 1859, has been shown to profoundly affect age-structure, size at maturity, and overall fecundity (e.g.,

Reznick & Endler, 1982). Even though predation by *A. bidens* was not size-specific (in contrast to *Belostoma*-predation), high predation is generally believed to select against large body size (Reznick & Endler, 1982). The question of whether and how various forms of predation affect life-history evolution and behavioural traits (e.g., escape behaviour) in the cave molly clearly warrants further research.

CONCLUSIONS

Avotrichodactylus bidens successfully preys on fish in a sulfidic cave environment and most probably represents a top-predator in this habitat. While caves have often been assumed to be predator-free sanctuaries for cave fishes (e.g., Romero & Green, 2005), our study clearly demonstrates that this view cannot be generalized: at least cave living *Poecilia mexicana* in the southern Mexican Cueva del Azufre experience strong predation pressure by species like the freshwater crab *A. bidens*.

ACKNOWLEDGEMENTS

We are grateful for the artwork done by Madlen Ziege. The Mexican Government (Permiso de Pesca de Fomento No. DGOPA.06192.240608.-1562) as well as the Municipality of Tacotalpa (SM/1133/208) kindly provided permits for the work at the Cueva del Azufre. Financial support came from the DFG (PL 470/1-2), the Hermann-Willkomm Foundation (M. P.), and the "Freunde und Förderer der Universität Frankfurt" (S. K.).

REFERENCES

- ABDALLAH, A. H., C. DE MAZANCOURT, M. M. ELINGE, B. GRAW, M. GRZESIUK, K. HENSON, M. KAMOGA, I. KOLODZIEJSKA, M. KRISTERSSON, A. KURIA, P. LEONHARTSBERGER, R. B. MATEMBA, M. MERL, B. MOSS, C. MINTO, E. MURFIT, S. N. MUSILA, J. NDAYISHINIYE, D. NUHU, D. J. ODURO, S. PROVVEDI, R. V. RASOMA, F. RATSOAVINA, R. TREVELYAN, N. TUMANYE, V. N. UJOH, G. VAN DE WIEL, T. WAGNER, K. WAYLEN & M. YONAS, 2004. Comparative studies on the structure of an upland African stream ecosystem. *Freshwater Forum*, **21**: 27-47.
- BOTT, R., 1969. Die Süßwasserkrabben Süd-Amerikas und ihre Stammesgeschichte. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **518**: 1-94.
- BRANDIS, D. & A. SCHUSTER, 1999. Süßwasserkrabben und das Sternbild des Krebs – Kulturgeschichte der Süßwasserkrabben in den mesopotamischen Hochkulturen. *Natur und Museum*, **129**: 73-82.
- CALOW, P., 1989. Proximate and ultimate responses to stress in biological systems. *Biological Journal of the Linnean Society, London*, **37**: 173-181.
- DOBSON, M. K., A. MAGANA, J. M. MATHOOKO & F. K. NDEGWA, 2002. Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? *Freshwater Biology*, **47**: 909-919.

- ERPENBECK, J., 1970. Untersuchungen zur Ökologie und Biologie von *Potamon potamios rhodium* Parisi (Decapoda, Potamidae): 1-69. (Ph.D. Thesis, Westfälische Wilhelms-Universität, Münster).
- GHERARDI, F., S. GUIDI & M. VANNINI, 1987. Behavioural ecology of the freshwater crab, *Potamon fluviatile*: preliminary observations. *Investigacion Pesquera, Barcelona*, **51** (Suppl. 1): 389-402.
- GHERARDI, F., F. TARDUCCI & F. MICHELI, 1989. Energy maximization and foraging strategies in *Potamon fluviatile* (Decapoda, Brachyura). *Freshwater Biology*, **22**: 233-245.
- GORDON, M. S. & D. E. ROSEN, 1962. A cavernicolous form of the poeciliid fish *Poecilia sphenops* from Tabasco, México. *Copeia*, **1962**: 360-368.
- HILL, M. P. & J. H. O'KEEFFE, 1992. Some aspects of the ecology of the freshwater crab (*Potamonautes perlatus* Milne Edwards) in the upper reaches of the BuValo River, eastern Cape Province, South Africa. *Southern African Journal of Aquatic Science*, **18**: 42-50.
- HORSTKOTTE, J., R. RIESCH, M. PLATH & P. JÄGER, 2010. Predation by three species of spiders on a cave fish in a Mexican sulfur cave. *Bulletin of the British Arachnological Society*, **15**: 55-58.
- LAVOIE, K. & K. EVANS, 2002. Distribution and abundance of the midge *Goeldichironomus fulvipilus*, in Cueva de Villa Luz, Tabasco, Mexico. *Journal of Cave and Karst Studies*, **64**: 181.
- MARIJNISSEN, S. A. E., E. MICHEL, D. F. R. CLEARY & P. B. MCINTYRE, 2009. Ecology and conservation status of endemic freshwater crabs in Lake Tanganyika, Africa. *Biodiversity and Conservation*, **18**: 1555-1573.
- NG, P. K. L., 1988. The freshwater crabs of peninsular Malaysia and Singapore: 1-156. (Department of Zoology, National University of Singapore, Shinglee Press, Singapore).
- PLATH, M., S. HAUSWALDT, K. MOLL, M. TOBLER, F. J. GARCÍA DE LEÓN, I. SCHLUPP & R. TIEDEMANN, 2007 (cf. a). Local adaptation and pronounced genetic differentiation in an extremophile fish, *Poecilia mexicana*, inhabiting a Mexican cave with toxic hydrogen sulfide. *Molecular Ecology*, **16**: 967-976.
- PLATH, M., J. PARZEFALL & I. SCHLUPP, 2003. The role of sexual harassment in cave- and surface-dwelling populations of the Atlantic molly, *Poecilia mexicana* (Poeciliidae, Teleostei). *Behavioral Ecology and Sociobiology*, **54**: 303-309.
- PLATH, M. & M. TOBLER, 2010. Subterranean fishes of Mexico (*Poecilia mexicana*, Poeciliidae). In: E. TRAJANO, M. E. BICHUETTE & B. G. KAPOOR, *The biology of subterranean fishes*: 283-332. (Science Publishers, Enfield).
- PLATH, M., M. TOBLER, R. RIESCH, F. J. GARCÍA DE LEÓN, O. GIÈRE & I. SCHLUPP, 2007 (cf. b). Survival in an extreme habitat: the roles of behaviour and energy limitation. *Naturwissenschaften*, **94**: 991-996.
- REZNICK, D. & J. ENDLER, 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, **36**: 160-177.
- RIESCH, R., M. PLATH & I. SCHLUPP, 2010. Toxic hydrogen sulfide and dark caves: life history adaptations in a livebearing fish (*Poecilia mexicana*, Poeciliidae). *Ecology*, **91**: 1494-1505.
- ROBB, T. & M. V. ABRAHAMS, 2002. The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*. *Behavioral Ecology and Sociobiology*, **52**: 25-30.
- ROGOWSKI, D. L. & C. A. STOCKWELL, 2006. Parasites and salinity: costly tradeoffs in a threatened species. *Oecologia*, **146**: 615-622.
- ROMERO, A. & S. M. GREEN, 2005. The end of regressive evolution: examining and interpreting the evidence from cave fishes. *Journal of Fish Biology*, **67**: 3-32.
- ROTHSCHILD, L. J. & R. L. MANCINELLI, 2001. Life in extreme environments. *Nature, London*, **409**: 1092-1101.

- SCHNEIDER, P., 1971. Zur Biologie der afghanischen Flußkrabbe *Potamon gedrosianum*. I. Lebensweise, Verbreitung, Morphologie und systematische Stellung. *Bonner Zoologische Beiträge*, **22**: 305-321.
- TOBLER, M., 2009. Does a predatory insect contribute to the divergence between cave- and surface-adapted fish populations? *Biology Letters*, **5**: 506-509.
- TOBLER, M., T. J. DEWITT, I. SCHLUPP, F. J. GARCÍA DE LEÓN, R. HERRMANN, P. G. D. FEULNER, R. TIEDEMANN & M. PLATH, 2008 (cf. a). Toxic hydrogen sulfide and dark caves: phenotypic and genetic divergence across two environmental gradients in *Poecilia mexicana*. *Evolution*, **62**: 2643-2659.
- TOBLER, M., C. FRANSSSEN & M. PLATH, 2008 (cf. b). Male-biased predation of a cave fish by a giant water bug. *Naturwissenschaften*, **95**: 775-779.
- TOBLER, M., I. SCHLUPP, K. U. HEUBEL, R. RIESCH, F. J. GARCÍA DE LEÓN, O. GIÈRE & M. PLATH, 2006. Life on the edge: hydrogen sulfide and the fish communities of a Mexican cave and surrounding waters. *Extremophiles*, **10**: 577-585.
- TOBLER, M., I. SCHLUPP & M. PLATH, 2007. Predation of a cavefish (*Poecilia mexicana*, Poeciliidae) by a giant water bug (*Belostoma*, Belostomatidae) in a Mexican sulfur cave. *Ecological Entomology*, **32**: 492-495.
- TOBLER, M., R. RIESCH, C. M. TOBLER & M. PLATH, 2009. Compensatory behavior in response to sulfide-induced hypoxia affects time budgets, feeding efficiency, and predation risk. *Evolutionary Ecology Research*, **11**: 935-948.
- WILLIAMS, T. R., 1961. The diet of freshwater crabs associated with *Simulium neavei* in East Africa. I. Crabs from West and East Uganda collected by the Cambridge East African Expedition 1959. *Annals of Tropical Medicine and Parasitology*, **55**: 128-131.

Copyright of Crustaceana is the property of Brill Academic Publishers and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.