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Selective predation by the zoarcid fish *Thermarces cerberus* at hydrothermal vents

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Abstract

This study investigates predation by the vent zoarcid fish *Thermarces cerberus* through gastrointestinal analyses of 27 specimens collected with the submersible ALVIN at vents at 9°50′N on the East Pacific Rise. *T. cerberus* fed most frequently on gastropod mollusks (mainly *Lepetodrilus elevatus*) and amphipod crustaceans (mainly *Ventiella sulfuris*). Species found occasionally in high abundance included the swarming amphipod *Halice hesmonectes* and the snail *Cyathermia naticoides*. Other items also found in gastrointestinal tracts, but in very low numbers, included polychaete worms, crustaceans and unidentified tissue clumps. The comparison between the size distribution of *L. elevatus* limpets ingested by *T. cerberus* and those found attached to vestimentiferan tubes suggest that the fish may selectively prey on large limpets. If the selective removal of large *Lepetodrilus* spp. limpets by *T. cerberus* does occur, then it would have potential community-level consequences at hydrothermal vents, since these mobile gastropods appear to inhibit the settlement of sessile vent species, including tube-building worms. Our results suggest possible direct and indirect effects of *T. cerberus* on benthic community structure at hydrothermal vents on the East Pacific Rise.
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1. Introduction

Deep-sea hydrothermal vents commonly have low diversity of physiologically specialized predators and experience few visits by opportunistic

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predators from surrounding habitats, likely because of the toxicity of hydrogen sulfide found at vents to non-specialized organisms (Voight, 2000). Zoarcid fishes are specialized predators commonly found in sulfide-rich habitats such as hydrothermal vents, cold seeps and whale skeletons (Desbruyères and Segonzac, 1997; Sibuet and Olu, 1998; Biscoito et al., 2002). Zoarcids of the genus *Thermarces* are conspicuous members of deep-sea hydrothermal vent communities of the East Pacific Rise (Cohen et al., 1985; Rosenblatt and Cohen, 1986; Biscoito et al., 2002). The taxonomy of the species inhabiting the hydrothermal vents near 9°N at the East Pacific Rise (EPR) has been debated among ichthyologists (Rosenblatt and Cohen, 1986; Geistdoerfer and Seuront, 1995; Biscoito et al., 2002), but we will follow the recommendations by Biscoito et al. (2001), and refer to all the specimens we collected at this site as *Thermarces cerberus*. None of the fish collected for this study had the dusky brown coloration typical of the other *Thermarces* species found at the 9°N East Pacific Rise site (Biscoito et al., 2001).

T. cerberus lives among the vestimentiferan worm communities (vestimentiferans are now considered to be members of the polychaete family Sibloglinidae, but will be referred to herein as vestimentiferans to differentiate them from other sibloglinids; Rouse, 2001) and near high-temperature vents along the East Pacific Rise, in 8–12 °C waters (Geistdoerfer and Seuront, 1995). Geistdoerfer and Seuront (1995) described the diet of *T. cerberus* as dominated by amphipods, with limpets as the second most abundant prey items. Fragments of vestimentiferans have been reported in *T. cerberus* stomachs (Rosenblatt and Cohen, 1986; Geistdoerfer and Seuront, 1995), but these reports remain ambiguous because disturbance events caused by research submersibles could make broken vestimentiferan remains available to fish (Rosenblatt and Cohen, 1986).

Though predation has been shown to directly and indirectly influence natural aquatic communities through complex webs of species interactions (Paine, 1969; Menge et al., 1994; Hixon and Brostoff, 1996), biological interactions have been generally considered to play relatively minor roles in determining the structure of hydrothermal vent communities (Tunnicliffe and Juniper, 1990; Van Dover, 1995). But recent predatory exclusion experiments at the East Pacific Rise vents (Micheli et al., 2002) suggest that *T. cerberus* influences the structure of hydrothermal vent benthic communities by consuming mobile gastropods and indirectly reducing their grazing on recruits of mobile and sessile invertebrates, including vestimentiferans. The present study analyzes the composition and size of prey items in guts of *T. cerberus* individuals caught using the submersible ALVIN in order to understand the fish's role as a predator in potentially structuring hydrothermal vent animal communities on the East Pacific Rise.

2. Methods

T. cerberus specimens were collected at two hydrothermal vent sites ('East Wall' and 'Biovent') along the axial valley on the East Pacific Rise (9°50′N, 104°17′W) at depths that ranged between 2490 and 2520 m. Detailed description of the physical and chemical characteristics of this vent field can be found elsewhere (Detrick et al., 1987; Haymon et al., 1991; Lutz et al., 1994). Fish were caught from among or near megafaunal communities dominated by vestimentiferan tubeworms (mainly *Riftia pachyptila*) or vent mussels (*Bathymodiolus thermophilus*).

A total of 27 *T. cerberus* specimens was collected and analyzed, eight specimens in 1998, 13 in 1999, and six in 2000. Specimens were captured at the 'East Wall' ($n = 24$) and 'Biovent' ($n = 3$) sites. Samples were pooled between the two sites for subsequent analyses because of the similar invertebrate communities and close proximity (800 m) of these sites (Mullineaux et al., 2003), and the potentially high mobility of *T. cerberus* (G. Sancho, personal observation). Fish were captured alive with a multi-chambered suction sampler attached to the submersible ALVIN. On reaching the surface they were transferred immediately to a cold room in order to minimize decomposition of the gut contents. Within 2 h, each fish was measured (total length, and when possible standard length and weight), sexed and dissected, with preservation of the stomach and intestines sepa-

rately in 95% ethanol. In the laboratory all recognizable food items from the guts were identified to the species level (or the lowest taxonomic category possible) and measured using a binocular microscope. Total shell length (L_{tot}) was measured in gastropods as the maximum linear length, always with the anterior opening of the shell as a reference. Amphipod length was measured from the frontal edge of the cephalothorax to the most distant point of the curved abdomen, without manual stretching of the specimens. Copepod length was measured from the cephalothorax edge to the distal end of the abdomen.

In 1998 collections, sub-samples of food items were extracted for isotopic analyses making direct comparisons of prey abundance impossible. In fish collected in 1999 and 2000, all stomach and intestinal contents were preserved, identified and measured for analyses of relative prey abundance, frequency and size. Because of the extreme difficulty and high economic cost of capturing these abyssal fish, the maximum possible numbers of specimens were included in different analyses (e.g. calculation of frequency of occurrence of prey items employed data from all 27 fish), even though the effects of size, sex, collection site and date could not be evaluated statistically.

Description of prey items in guts of *T. cerberus* followed methods described in Hyslop (1980) and Costello (1990). Prey items were lumped into four general food categories: crustaceans, gastropods, polychaetes and unidentified tissue clumps. The total number of individual items in a certain food category was recorded for all fish (C_n; expressed as the percentage of the total number of items in all food categories), and the mean number of individual prey per gastrointestinal tract (N). The percentage of all fish that contained one or more prey items of a food category (f) was also employed as a measure of frequency of occurrence.

Size distributions of ingested *Lepetodrilus elevatus* were compared with data from limpet samples collected independently (May 8, 1999) from vestimentiferan tubes at 'East Wall' by Sadosky (2001) as part of the French cruise 'HOPE 99'. Unfortunately, our length measurement of limpets was not directly comparable to the curvilinear

length (measured along the external side of the shell between the anterior and posterior ends) of Sadosky et al. (2002). To compensate, we transformed our total shell linear lengths (L_{tot}) from ingested limpets into curvilinear lengths (L_{curv}) using a calibration obtained by measuring both lengths on 10 specimens covering the relevant size range (3.6–13.5 mm L_{tot}). The resulting transformation function was

$$L_{curv} = 1.16 \times L_{tot} + 0.85; \quad R^2 = 0.99.$$

Differences in shell size-distributions were tested by a Kolmogorov–Smirnov two-sample test (Sokal and Rohlf, 1995).

3. Results

The 27 fish analyzed ranged in total length from 127 to 397 mm (mean = 297 mm, SD = 69 mm). The specimens captured included 17 females, six males and four immature individuals of indeterminate sex (Table 1).

The mean number of prey items found in the gastrointestinal tracts of *T. cerberus* (only from the 19 fish collected in 1999 and 2000) was 26.4 (range 1–118, SD = 59.6) (Table 2). The diet of *T. cerberus* was clearly dominated by gastropods ($C_n = 50.1\%$) and crustaceans ($C_n = 47.1\%$), while polychaete worms ($C_n = 2.0\%$) and unidentified tissue clumps ($C_n = 0.8\%$) were much rarer (Fig. 1). The analysis of the frequency of occurrence of prey item in gastro-intestinal tracts (f) from all 27 fish specimens also confirmed the dominance of gastropods ($f = 66.7\%$) and crustaceans ($f = 77.8\%$) and the occasional occurrence

Table 1
Total length of the *Thermarces cerberus* (average, maximum, minimum and standard deviation) used in stomach content analyses ($N = 27$)

Sex	N	Total length (mm)			
		Mean	Max	Min	SD
Female	17	329	397	260	66
Male	6	304	340	268	51
Immature	4	138	170	127	87

Table 2
Frequency, abundance and sizes of prey items found in *Thermarces cerberus*. Percentage of gastrointestinal tracts containing a prey item (*f*) from all 27 fish collected. Overall total number of prey items (*N*). and abundance per individual fish (mean and maximum) measured from 19 fish collected in 1999 and 2000. Prey size (mean, standard deviation, maximum and minimum values) measured as stated in Methods section

	f	*N*	Abundance		Prey size (mm)		
	%		Mean	Max	Mean	SD	Max–min
ANNELIDA							
Polychaetes[a]	22.2	9	0.47	3			
MOLLUSCA							
Lepetodrilus elevatus	59.3	118	6.16	31	7.0	2.8	12.9–0.9
Lepetodrilus pustulosus	14.8	2	0.11	2	9.3	2.8	11.3–7.3
Lepetodrilus cristatus	3.7	1	0.05	1	4.4		
Lepetodrilus ovalis	3.7	1	0.05	1	5.6		
Cyathermia naticoides	33.3	130	6.84	102	4.0	0.9	6.2–1.3
CRUSTACEA							
Halice hesmonectes	18.5	117	6.16	91	4.1	1.3	8.8–1.6
Ventiella sulfuris	66.7	108	5.68	19	3.9	1.5	11.2–0.8
Copepods	11.1	6	1.20	3	1.2	0.1	1.3–1.1
Bythograea spp.[b]	11.1	4	0.80	1	—		
Unidentified tissue[c]	14.8	4	0.21	2			

[a]Diverse unidentified polychaete worm remains.
[b]Two megalopa larvae, one whole crab and a separate pair of claws.
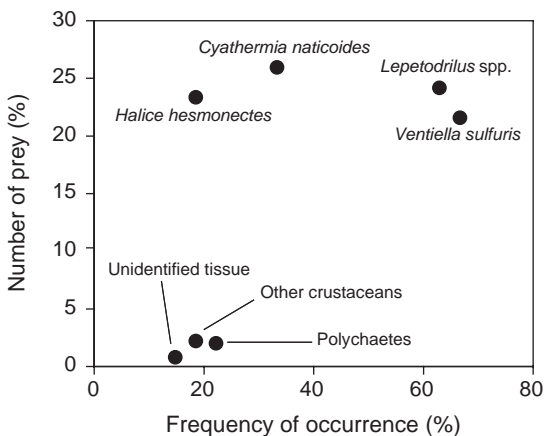[c]Unidentified tissue clumps, possibly from *Riftia pachyptila*.

Fig. 1. Relationship between the number (C_n, number of individual items in a prey category expressed as a percentage of all items found) and frequency of occurrence (*f*, percentage of fish containing prey items of a specific prey grouping) of the prey categories in *Thermarces cerberus* diet. Only fish collected in 1999 and 2000 were considered.

of polychaete worms (*f* = 22.2%) and unidentified tissue (*f* = 14.8%) (Fig. 1).

Two mobile species dominated the gastropod mollusk category, a limpet (*L. elevatus*, C_n = 23.3%, *f* = 59.3%) and a snail (*Cyathermia naticoides*, C_n = 25.9%, *f* = 33.3%). Other gastropods consumed by *T. cerberus* included the limpets *Lepetodrilus ovalis*, *L. pustulosus* and *L. cristatus* (Table 2). Crustacean prey mainly consisted of amphipods, *Ventiella sulfuris* (C_n = 21.5%, *f* = 66.7%) and *Halice hesmonectes* (C_n = 23.3%, *f* = 18.5), and also included copepods and brachyuran crabs (Table 2).

Polychaete worm remains were easily recognizable by characteristic bristles and body structures, but were not identifiable to the species level, except for one *Archinome rosacea* specimen. The unidentified tissue category consisted of large clumps of dark amorphous and partially digested tissue.

Similar findings in *T. cerberus* stomach contents have been identified as respiratory plume and trophosome tissues from vestimentiferan worms, most likely of *R. pachyptila* (Rosenblatt and Cohen, 1986; Geistdoerfer and Seuront, 1995), but a definitive identification was not possible.

The size class distribution (L_{curv}) of *L. elevatus* found in the gastro-intestinal tracts of *T. cerberus* collected in 1999 and 2000 was significantly different (Kolgomorov–Smirnov parameter = 1.461; $p = 0.028$) from the size distribution of individuals sampled from *R. pachyptila* tubes at the same vent site in 1999 (Fig. 2). The mean size (L_{curv}) for ingested limpets was 9.0 mm

(range 1.9–15.8 mm, $n = 118$), greater than the mean value of 6.9 mm from limpets found on vestimentiferan tubes (range 1.6–12.5 mm, $n = 476$) at the same location (Sadosky, 2001).

4. Discussion

The diet of *T. cerberus* was dominated by mobile gastropod and amphipod species closely associated with vigorous flow areas, dominated by vestimentiferan and mussel communities at EPR vents. The two most frequent prey species were *L. elevatus* and *V. sulfuris*. This result confirms the limited observations from other studies (Rosenblatt and Cohen, 1986; Geistdoerfer and Seuront, 1995; Geistdoerfer, 1996). Other crustaceans (copepods, adult and larval crabs) and polychaetes were also found, indicating that *T. cerberus* is a benthic predator feeding on a wide assortment of potential prey.

T. cerberus preyed mainly on two gastropod species, the limpet *L. elevatus* and the snail *C. naticoides*, which are commonly found on *R. pachyptila* worm tubes (Mullineaux et al., 2003). The distribution of gastropods in the diet of *T. cerberus* varied: *L. elevatus* was found in the majority of fish guts ($f = 59.3\%$), as opposed to *C. naticoides*, which was ingested by a third of the fish analyzed ($f = 33.3\%$), one of which contained 102 snails (78% of all *C. naticoides* counted). The other gastropods preyed upon by *T. cerberus* (*L. pustulosus*, *L. cristatus* and *L. ovalis*) constituted only 3.3% of the limpets ingested and were all species found mainly within the vestimentiferan faunal zone characterized by vigorous flows and elevated temperatures (Mullineaux et al., 2003). This clear dominance by *L. elevatus* within the ingested limpets is similar to the limpet community found on vestimentiferan tubes at the 'East Wall' vent site (Sadosky, 2001), where *L. elevatus* accounted for 99.3% of all limpet species sampled. Thus we have no evidence that *T. cerberus* preferentially selects *L. elevatus* over other limpet species found at the vestimentiferan faunal zone of the EPR vents.

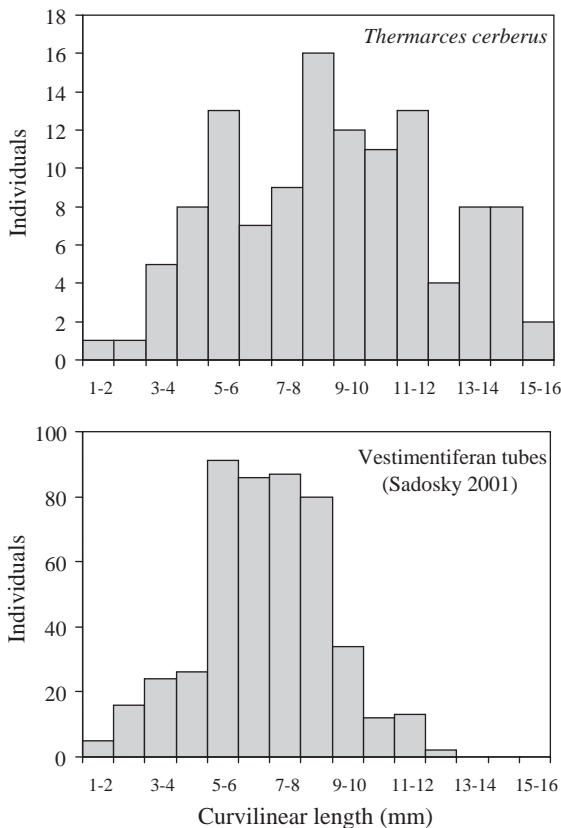Focusing on *L. elevatus*, the distribution of size classes of limpets ingested by *T. cerberus* was

Fig. 2. Size frequency distributions for *Lepetodrilus elevatus* specimens ingested by *Thermarces cerberus* ($n = 118$; only from fish collected in 1999 and 2000) and found on vestimentiferan tubes collected at the 'East Wall' site (re-drawn from Sadosky 2001; $n = 476$).

markedly different from the size distribution of limpets found attached to vestimentiferan tubes. *T. cerberus* ingested limpets of all sizes, but seemed to preferentially select larger individuals: 39.0% of the *L. elevatus* found in gastrointestinal tracts were larger than 10 mm in curvilinear length, even though individuals this large accounted for only 5.7% of this species found on vestimentiferan tubes (Sadosky, 2001). The largest limpet found in natural populations sampled from vestimentiferan tubes at the 9 N° 'East Wall' vent had a maximum curvilinear length of 12.9 mm (Sadosky, 2001). Of the 118 *L. elevatus* ingested by *T. cerberus* at the same location, 18 limpets (15.25%) were larger than 12.9 mm and the maximum size recorded was 15.8 mm. The capture of *T. cerberus* specimens from 'East Wall' in 1999 occurred only 7–12 days before limpets were collected from worm tubes (Sadosky, 2001), negating the possibility that observed size differences were the result of sampling at different times. Limpets collected from vestimentiferan tubes at 13°N East Pacific Rise vent showed bimodal size distributions (Sadosky et al., 2002), and were also smaller (maximum length of 13.3 mm) than limpets ingested by fish in our study.

The discovery of large limpets in *T. cerberus* guts raises the question of why these sizes were not found in tubeworm aggregations sampled by Sadosky (2001) or Sadosky et al. (2002). It is possible that fish are finding the largest limpets in vent microhabitats that were not sampled by these authors, such as in bivalve beds where *L. elevatus* densities can be quite high (Van Dover and Trask, 2000; Van Dover, 2002) or within rock cracks. Feeding by *T. cerberus* outside the vent habitat is unlikely since *L. elevatus* recruitment is restricted to vent habitats, with recruits found primarily on vestimentiferan clumps, with reduced abundances in bivalve beds and rarely observed in suspension feeder or periphery areas (Mullineaux et al., 2003). Video analysis of *T. cerberus* feeding behaviors is underway to address this issue, but has not yet yielded conclusive results (G. Sancho, personal observation). A second possible explanation for these findings is that the random sampling of tubeworms and associated fauna might have missed rare large limpets. Finally, abundant *T.*

cerberus populations strongly targeting large limpets might be effective at reducing the populations of large limpets through intense predation among the vestimentiferan tubes, especially if large limpets are relatively rare in this habitat.

The higher digestion rates of small crustaceans (amphipods and copepods) compared to mollusks may result in the underestimation of their importance in the diet of *T. cerberus* in comparison to gastropod mollusks with thick shells, which likely remain for longer periods in the gastrointestinal tract. The two amphipod species found in the gastrointestinal tracts were both abundant prey items, but greatly differed in their distribution: *V. sulfuris* was homogeneously distributed among the fish analyzed ($f = 66.7\%$), while *H. hesmonectes* was found only in five fish ($f = 18.5\%$), one of which contained 91 individuals (78% of all *H. hesmonectes* counted). This pattern indicates that *T. cerberus* regularly preyed on benthic *V. sulfuris*, the most abundant amphipod in East Pacific vents and commonly found close to the substrate in the vestimentiferan zone (Desbruyères and Segonzac, 1997). Yet occasionally *T. cerberus* consumed *H. hesmonectes*, which form dense monospecific aggregations in the water column near vent openings (Van Dover et al., 1992) and probably constitute an opportunistic, but also important, food resource.

Other prey items found in the gastrointestinal tracts of *T. cerberus* were rare and did not seem to constitute an important part of the diet of this predator. All identifiable organisms consisted of vent-associated organisms found in the vestimentiferan zone (Desbruyères and Segonzac, 1997). Vestimentiferans were not definitively detected in the diet of *T.cerberus*. If the clumps of 'unidentified tissue' were vestimentiferan remains, their importance in the diet of *T. cerberus* would still be minimal, corroborating previous observations (Rosenblatt and Cohen, 1986; Geistdoerfer and Seuront, 1995). It has been suggested that the vestimentiferan *R. pachyptila* becomes available to the fish only after being "crushed" by submarine maneuvering in the vent area (Rosenblatt and Cohen, 1986). It is unclear if *T. cerberus* preys on live vestimentiferans. Accidental ingestion of *Riftia* tissue could conceivably occur during

attacks on moving amphipods, and feeding within the capture chamber of the suction sampler on *Riftia* remains collected during the capture of fish is also a possibility.

The importance of mobile grazing gastropods in the diet of *T. cerberus* described in this study suggests a likely effect on the gastropod populations through predation-induced mortality. In addition, predation on gastropods by *T. cerberus* can also have indirect consequences for other organisms. In the absence of large predators, i.e. when predators were experimentally excluded with cages, higher abundances of limpets and lower abundances of sessile benthic invertebrates (including vestimentiferan tubeworms, vent mussels and tubiculous polychaetes) colonized rocky substrates (Micheli et al., 2002), a finding consistent with the hypothesis that grazing activities by limpets and snails may dislodge newly recruited organisms and reduce the effective settlement of larvae. The feeding activity of *T. cerberus* likely reduces the abundance of limpets, indirectly promoting the successful settlement and growth of juvenile vestimentiferans and other sessile benthic invertebrates (Micheli et al., 2002).

In the absence of size–frequency data for *L. elevatus* over its entire potential feeding area (including bivalve beds as well as tubeworm aggregations), it is not possible to be certain that size-selective predation on limpets is occurring. Nevertheless, the greater abundance of large limpets in the guts of *T. cerberus* than in tubeworm aggregations does provide evidence that prey are being selected by size. If true, this might have significant, direct effects on the population structure of these mollusks. For example, it might permit the recruitment and early growth of small limpets and reduce the number of large individuals with the highest potential to disrupt the settlement and colonization of benthic invertebrates through 'bulldozing' (Dayton 1971) while moving and grazing along the substrate. The dietary characteristics of *T. cerberus* therefore indicate the potential importance of this predator in determining the structure of vent invertebrate communities through complex ecological relationships.

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