Vol. 497: 143–156, 2014
doi: 10.3354/meps10585

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 5

Trophic diversification in the evolution of predatory marine gastropods of the family Terebridae as inferred from stable isotope data

A. E. Fedosov[1,*], A. V. Tiunov[1], S. I. Kiyashko[2], Yu. I. Kantor[1]

[1]A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninski Prospect 33, Moscow 119071, Russia
[2]A. V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Palchevskogo st. 17, Vladivostok 690059, Russia

ABSTRACT: The family Terebridae includes approximately 400 species of predatory marine gastropod mollusks, commonly found in sandy bottom communities in the tropical Indo-Pacific. Like other Conoidea, Terebridae are typified by the presence of a venom gland and a highly specialized radula, which they use for hunting. Remarkably, some lineages of the family exhibit a tendency to reduction and complete loss of the radula, venom gland and proboscis. Recent studies on the mollusc community of Murray Beach (Nha Trang Bay, southern Vietnam) revealed an unusually rich and diverse fauna of Terebridae in a limited area of monotonous sandy sediments at depths of 6 to 18 m. In the present paper, mechanisms of resource partitioning between 16 syntopic Terebridae species from Murray Beach are studied using stable isotope analysis (SIA). The terebrid species studied exhibit considerable variation in isotopic signatures: mean $\delta^{13}C$ and $\delta^{15}N$ values of different species ranged between −16.9 and −9.3‰, and between 5.8 and 9.5‰, respectively. Although the isotopic niches of the species overlap considerably, the 5 most abundant species, contributing ~80% to the total abundance of the terebrid community, show little or no overlap. The studied Terebridae belong to 5 major phylogenetic lineages. By integrating phylogenetic data with the SIA results, we infer possible mechanisms of adaptive radiation in the family. Closely-related species within most phylogenetic clades, especially Clades E1 and E5, are well separated in isotopic niche space. In contrast, members of different clades overlap considerably in isotopic niche space, suggesting that trophic specialization has occurred independently in the evolution of different Terebridae lineages.

KEY WORDS: Stable isotopes · Trophic specialization · Resource partitioning · Adaptive radiation · Closely related syntopic species · Loss of radula

INTRODUCTION

Gastropods of the superfamily Conoidea (=Toxoglossa) constitute a hyper-diverse group of predatory marine snails that includes around 5000 Recent species, of which approximately 700 belong to a single genus, *Conus*. Conoideans are notable for the possession of a large venom gland and a highly modified radula, which are 2 apomorphic features underlying the complex feeding mechanism of this group. This mechanism has been best studied in members of the genus *Conus* and characterized by the use of a separate, often harpoon-like marginal radular tooth, which is detached from the rest of the radula and held at the proboscis tip, with which they stab and poison their prey (Taylor et al. 1993, Kohn et al. 1999, Kantor & Puillandre 2012). It is widely accepted that the appearance of this unique prey capture mechanism and consequent feeding specialization were the major prerequisites for extreme diversification and radiation of Conoidea (Shimek & Kohn 1981, Taylor et al. 1993, Kohn et al. 1999). Increasing interest in

*Corresponding author: fedosovalexander@gmail.com

Conoidea is largely a result of recent intensive studies of their toxins, structurally extremely diverse oligo-peptides (those of *Conus* are known as conotoxins), which constitute a rich natural resource of physiologically active components and potential drug candidates (Terlau & Olivera 2004, Olivera & Teichert 2007, Fedosov et al. 2012).

Conoidea are often abundant in tropical marine communities, and in most cases several closely related species co-occur in the same habitat. The ecology of 25 sympatric *Conus* species on the coral reefs and marine benches in Hawaii has been examined in detail (Kohn 1959). It was demonstrated that the adult ecological niches differ among the *Conus* species studied in at least 2 of the following characteristics: nature of the food, nature of and relation to the substratum, and vertical zonation. Feeding specialization in cone snails is relatively well studied, and all known species can be classified into 3 dietary groups: vermivorous (feeding on a range of vermiform invertebrates), molluscivorous (hunting other gastropods), and piscivorous (hunting fish) (Kohn & Nybakken 1975, Duda et al. 2001). At the same time, the feeding biology of other conoidean taxa is largely unknown and the assumption of their specialized feeding remains unproven.

One of the distinctive conoidean taxa is the family Terebridae (auger shells). Its members are broadly distributed in tropical areas of the world's oceans, dwelling in soft sediments from intertidal to upper bathyal depths (Bratcher & Cernohorsky 1987). The family includes about 400 Recent species (Castelin et al. 2012). Like other Conoidea, Terebridae are predators, most of them possessing a venom apparatus (Taylor 1990, Holford et al. 2009) and producing toxins, the structure of which is close to that of the toxins of cone snails (Imperial et al. 2003, 2007, Puillandre & Holford 2010). One of the most prominent features of terebrid evolution is the loss of specialized foregut structures, such as the proboscis, radular apparatus, venom gland and often the salivary glands — which has occurred independently in different lineages of the family (Taylor 1990, Puillandre & Holford 2010, Castelin et al. 2012). The venom gland has been lost at least 8 times independently in the evolutionary history of the Terebridae. Likewise, complex hypodermic teeth evolved independently 3 times from solid, non-hollow teeth (Castelin et al. 2012). It has been suggested that the loss of a specialized foregut complex is likely to be accompanied by a widening of the trophic niche, enabling predation on a wider range of prey (Kantor et al. 2012).

Unlike cone snails, members of the family Terebridae are limited to a certain substratum — sandy bottoms — where they can reach high abundance, and a number of species may occur syntopically (Kohn 1971). Recent intensive sampling in one such habitat, a sandy bottom area of ca. 150 × 150 m in Nha Trang Bay (Vietnam) near Mun Island, revealed the co-occurrence of as many as 23 terebrid species belonging to 8 genera (Kantor et al. 2012). The habitat was seemingly very homogenous — gradually sloping sandy bottom at depths of 8 to 14 m. No pronounced differences were recorded in benthic invertebrate distributions, nor in abiotic factors that could facilitate ecological isolation of the multiple Terebridae species. Co-occurrence of a number of closely related terebrid species in the same habitat implies the existence of a mechanism of resource partitioning to reduce interspecific competition; perhaps specialization on different prey (Kantor et al. 2012). However, no direct evidence of feeding specialization among terebrid species is currently available. Data on the feeding of Terebridae are very scarce, mostly inferred from the gut contents of a few species. The prey items reported were various sedentary polychaetes (mostly spionids), and enteropneusts (Marcus & Marcus 1960, Miller 1970, 1975, 1979, Taylor 1990).

Stable carbon and nitrogen isotope ratios are commonly used as indicators of organic matter source and trophic structure of animal communities (Fry 2006). There is close similarity in carbon isotope ratios ($\delta^{13}C$) between consumer and assimilated food, though a slight enrichment of consumer's tissue in ^{13}C (~1‰) is often observed (DeNiro & Epstein 1978, Post 2002). The nitrogen isotope ratio ($\delta^{15}N$) exhibits more significant stepwise enrichment of about 3.4‰ with each trophic transfer and allows estimation of the trophic level occupied by a consumer (Minagawa & Wada 1984). Stable isotope ratio analysis (SIA) is becoming a widely accepted and applied tool for determining food web structure and carbon flow in ecosystems (for review see Boecklen et al. 2011, Layman et al. 2007) and for providing an integral estimation of the trophic niche of a species (Bearhop et al. 2004, Fink et al. 2012). SIA allows quantification of trophic niche segregation among diverging, closely related species and has been applied in studies of resource partitioning in traditional model taxa undergoing intensive radiation, such as Cichlidae in the African Great Lakes (Genner et al. 1999, Anseeuw et al. 2010). To date, SIA has not been used specifically in investigations of mechanisms of radiation in species-rich and divergent groups of Gastropoda. Only a few studies on the trophic ecology of freshwater gastropods (Doi et al. 2010, Sitnikova et al. 2012) and

resource partitioning among native and alien gastropod species (Nelson & Perissinotto 2012, Meyer & Yeung 2011) based on stable isotope data have been published recently.

The present study is based on analysis of SIA data from 16 Terebridae species and aims to (1) determine whether there is any feeding specialization among syntopic terebrid species, (2) evaluate the pattern of resource partitioning in the studied terebrid community, and in particular (3) correlate SIA data with a recently published Terebridae phylogeny (Castelin et al. 2012) to evaluate patterns of trophic niche radiation in different phylogenetic lineages of Terebridae. Finally, (4) we challenge the hypothesis that the loss of a specialized foregut complex in the evolution of some Terebridae has led to a more generalist feeding mode, accompanied by widening of trophic niches. The study fosters our understanding of resource partitioning in Conoidea and provides new data on the degree of feeding specialization in the group. The latter will also help in estimation of the natural diversity of toxins produced by Conoidea.

MATERIAL AND METHODS

Sampling site

Material was collected at a dive site unofficially called Murray Beach (12° 10.084′ N, 109° 17.771′ E) near Mun Island at depths of 6 to 14 m (Fig. 1). The sampled area had a quasi-rectangular shape with a larger side of about 150 m, and surface of approximately 10 000 to 12 000 m^2. The bottom sediments are sands, gradually sloping from the shore to depths of 20 m, below 15 m becoming slightly muddy (Kantor et al. 2012). The area is fringed by corals on its southern edge. Discrete patches of seagrass are found at the northern fringe of the sands, although not in the immediate proximity of the sampling area.

Material collection

Material for the present study was collected during a series of night dives in September and October 2011. In total, 23 Terebridae species were collected, although 7 species were represented by only 1 or 2 specimens, and thus they were omitted from the present study. Specimens of the remaining 16 species, belonging to 6 genera, were relaxed in an isotonic solution of $MgCl_2 \times 6H_2O$ and pieces of foot muscle (McKinney et al. 1999) were clipped off. Foot tissue samples were dried individually for 24 h at 65°C without any prior treatment. Shells and the remaining bodies were preserved as vouchers. The list of species and numbers of specimens analyzed is provided in Table 1. Species were identified using the guide by Terryn (2007), with updates by Castelin et al. (2012). To ensure consistency of species identification with recent molecular studies, our voucher specimens were checked against sequenced voucher specimens of Castelin et al. (2012), stored at the Muséum National d'Histoire Naturelle, Paris. Voucher specimens are stored in the collection of the Laboratory of Marine Invertebrates of the A. N. Severtsov Institute.

Data on the relative abundances of the studied terebrid species on Murray Beach were obtained from Kantor et al. (2012). The total number of specimens collected in a single night was calculated for each species, and using these numbers, species were categorized as rare (1 to 4 specimens per night), uncommon (5 to 14 specimens), common and abundant (more than 15 specimens) (Table 1).

To collect potential prey items of terebrids, 40 l of sediment were collected from the same site in a seperate dive (performed in the same collection trip) and sieved, first through a fine mesh (mesh size 3 mm) and then through plankton gauze (mesh size 0.5 mm); the collected infaunal invertebrates (mostly polychaetes) were identified to family level and dried in the same way as gastropods. These polychaetes were assigned to known trophic guilds according to Fauchald & Jumars (1979).

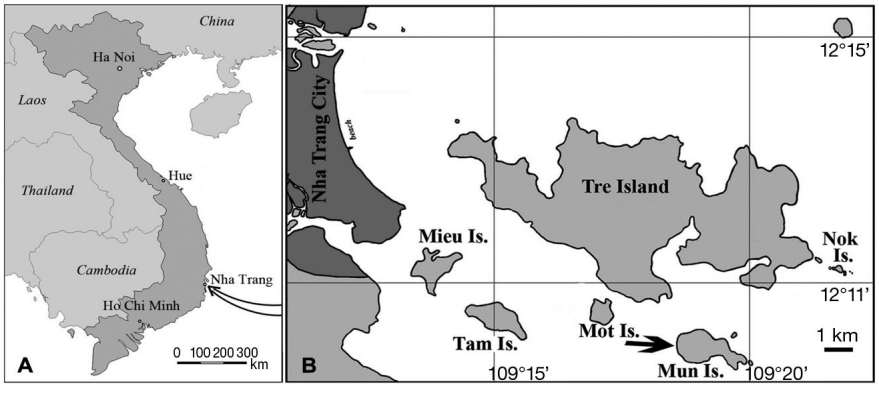

Fig. 1. Location of the sampling area in (A) the South China Sea and (B) the archipelago of Nha Trang Bay

Table 1. Summary of shell sizes, carbon and nitrogen stable isotope values, relative abundance, phylogenetic clade and presence/absence (+/–) of radulae in the studied Terebridae species. Abundance data from Kantor et al. (2012); clade assignment from Castelin et al. (2012)

Species	Code	n	Shell height (mm), avg. (min–max)	$\delta^{13}C$ Avg. (SD)	$\delta^{13}C$ min to max (‰)	$\delta^{15}N$ Avg. (SD)	$\delta^{15}N$ min to max (‰)	C/N Avg. (SD)	Abundance	Clade	Radula
Myurella kilburni	kil	5	24.2 (20.5–29.5)	–9.3 (0.3)	–9.8 to –9.0	5.8 (0.6)	5.1 to 6.5	3.7 (0.2)	3	E5	+
Myurella columellaris	col	5	38.4 (26–46.3)	–14.2 (0.8)	–15.5 to –13.5	8.4 (0.7)	7.3 to 9.1	3.6 (0.1)	3	E5	–
Myurella undulata	und	5	33.7 (28.1–38.8)	–15.3 (1.0)	–15.9 to –13.6	9.1 (0.2)	8.9 to 9.4	3.8 (0.1)	2	E5	–
Myurella affinis	aff	5	41.5 (38.7–47.9)	–11.2 (0.5)	–11.5 to –10.4	8.0 (0.4)	7.4 to 8.6	3.7 (0.1)	3	E1	–
Hastulopsis amoena	amo	5	31.9 (27.3–35.0)	–16.6 (0.5)	–17.0 to –15.9	8.5 (0.3)	8.4 to 9.0	3.6 (0.1)	1	E1	–
Myurella nebulosa	neb	5	33.9 (25.9–40.6)	–14.2 (1.9)	–17.0 to –11.9	9.5 (0.2)	9.2 to 9.9	3.8 (0.3)	3	E1	–
Hastula lanceata	lan	5	47.6 (36.4–57.5)	–12.8 (0.8)	–13.7 to –11.9	8.2 (0.8)	7.4 to 9.5	3.6 (0.1)	2	D	+
Oxymeris dimidiata	dim	5	92.5 (43.3–113.1)	–13.2 (0.6)	–13.8 to –12.3	8.6 (0.2)	8.2 to 8.8	3.5 (0.1)	1	B	–
Oxymeris cerithina	cer	5	46.7 (41.9–52.0)	–10.8 (0.3)	–11.1 to –10.3	8.4 (0.2)	8.1 to 8.7	3.7 (0.1)	1	B	–
Oxymeris maculata	mac	4	112.1 (6.7–133.1)	–10.8 (0.5)	–11.5 to –10.2	8.5 (0.3)	8.1 to 8.8	3.6 (0.1)	1	B	–
Terebra subulata	sub	5	70.2 (51.9–78.6)	–12.2 (0.8)	–13.1 to –11.1	7.9 (0.5)	7.4 to 8.6	3.6 (0.1)	3	C	+
Terebra funiculata	fun	4	37.4 (32.0–40.0)	–16.9 (0.3)	–17.1 to –16.5	8.5 (0.2)	8.4 to 8.8	3.6 (0.2)	1	C	+
Triplostephanus triseriata	tri	5	48.2 (36.5–54.6)	–13.4 (0.8)	–14.2 to –12.3	9.2 (0.2)	9.0 to 9.5	3.7 (0.1)	2	C	+
Terebra cingulifera	cin	4	57.9 (47.9–64.1)	–12.7 (0.7)	–13.3 to –11.8	7.0 (0.5)	6.3 to 7.5	3.7 (0.1)	1	C	+
Terebra babylonia	bab	5	57 (38.6–65.2)	–13.7 (0.7)	–14.2 to –12.6	8.3 (0.3)	8.0 to 8.8	3.7 (0.2)	2	C	+
Terebra quoygaimardi	quo	5	41.2 (37.9–44.7)	–12.6 (1.3)	–14.0 to –10.6	7.3 (0.5)	6.6 to 7.7	3.8 (0.1)	1	C	+

Phylogenetic and morphologic background

Data on phylogenetic relationships of the 16 Terebidae species were obtained from Castelin et al. (2012); they belong to 5 major phylogenetic clades: Clade B: *Oxymeris cerithina*, *O. maculata* and *O. dimidiata*; Clade C: *Terebra babylonia*, *T. cingulifera*, *T. funiculata*, *T. quoygaimardi*, *T. subulata* and *Triplostephanus triseriata*; Clade D: *Hastula lanceata*; Clade E1: *Hastulopsis amoena*, *Myurella affinis*, and *M. nebulosa*; Clade E5: *Myurella columellaris*, *M. kilburni* and *M. undulata* (Figs. 2 & 3). Generic assignments here are according to Castelin et al. (2012) and the current version of WoRMS (www.marinespecies.org, accessed 10 Apr 2013) and reflect the state-of-the-art in Terebridae taxonomy. However,

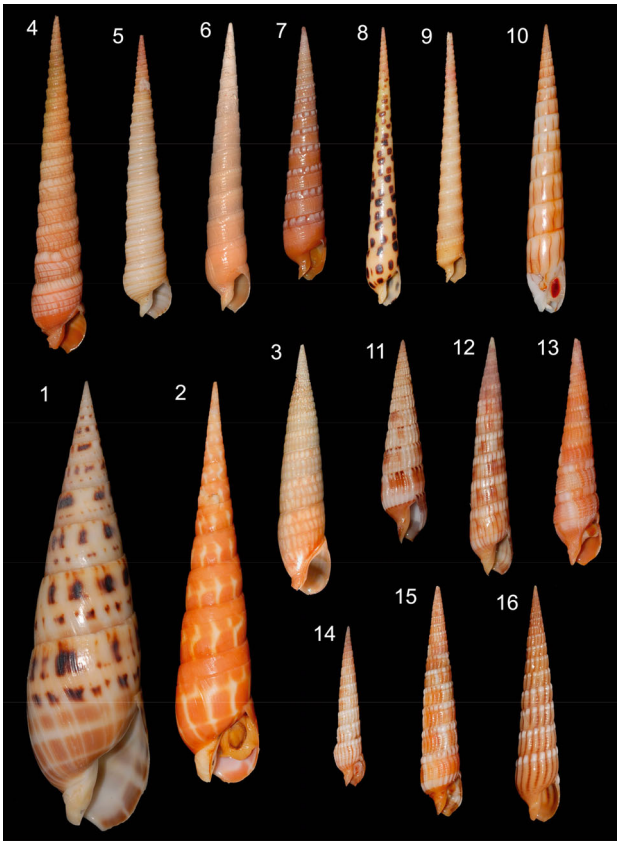

Fig. 2. Shells of the studied species of Terebridae, collected at dive site Murray Beach off Mun Islands, Nha Trang Bay in September 2010. Specimens 1–3 = Clade B (1 = *Oxymeris maculata*, 2 = *O. dimidiata*, 3 = *O. cerithina*); Specimens 4–9 = Clade C (4 = *Terebra babylonia*, 5 = *T. funiculata*, 6 = *T. cingulifera*, 7 = *T. quoygaimardi*, 8 = *T. subulata*, 9 = *Triplostephanus triseriata*); Specimen 10 = Clade D (*Hastula lanceata*); Specimens 11–13 = Clade E1 (11 = *Hastulopsis amoena*, 12 = *Myurella affinis*, 13 = *M. nebulosa*); Specimens 14–16 = Clade E5 (14 = *Myurella kilburni*, 15 = *M. columellaris*, 16 = *M. undulata*)

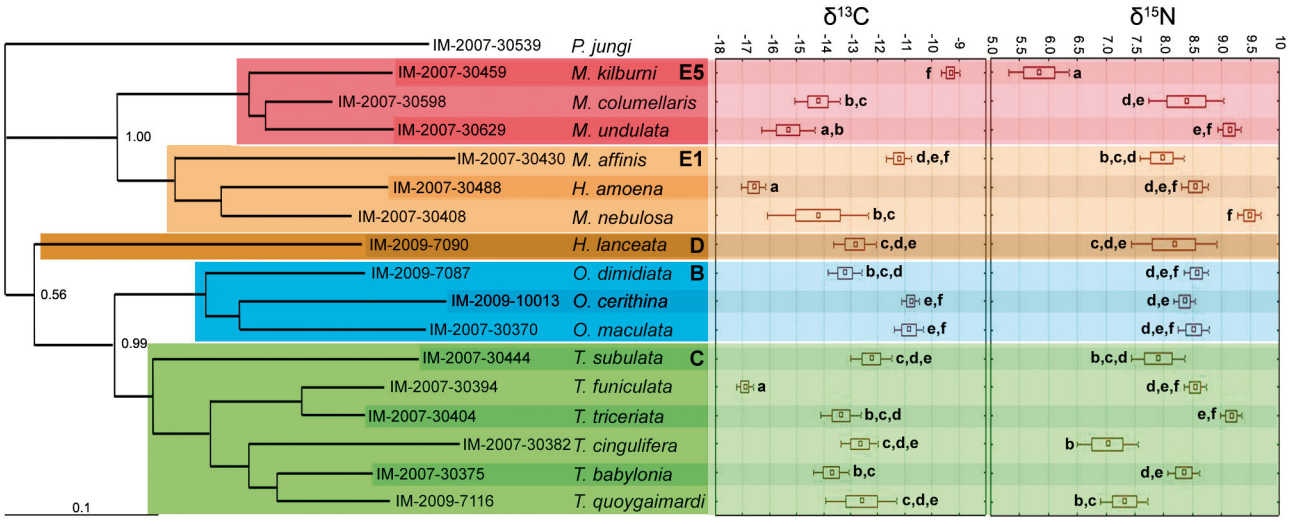

Fig. 3. Bayesian phylogenetic tree obtained with the concatenated dataset of CO1, 12S rRNA and 16S rRNA sequences (reduced dataset from Castelin et al. 2012; see 'Materials and methods'). Major phylogenetic clades identified by Castelin et al. (2012). Scale corresponds to 10 % difference in nucleotide composition. Carbon and nitrogen isotope ratios for each species shown in boxplots on the right (mean, SE and SD). Lower case letters a–f indicate homogenous groups inferred from ANOVA with post-hoc Tukey HSD test ($p < 0.05$)

the family requires major revision in order that generic assignments in the family correspond to the monophyletic groupings revealed in the phylogenetic analysis. In particular, the genus *Myurella*, which includes species from unrelated phylogenetic Clades E1 and E5, is obviously polyphyletic (Castelin et al. 2012).

To reconstruct the relationships among the studied terebrid species, the molecular dataset of Castelin et al. (2012) was reduced and reanalyzed (see Table 2). *Pellifronia jungi*, from the most basal terebrid Clade A (Castelin et al. 2012), was selected as an outgroup. Sequences were aligned for each gene independently with Muscle (Edgar 2004), with the hypervariable regions of 12S rRNA and 16S rRNA genes excluded from the analysis. The best fitting model of nucleotide substitution was identified for each gene independently using Modeltest (Posada & Crandall 2001); the general time-reversible model with invariable sites and a gamma-distributed rate heterogeneity parameter (GTR+G+I) was selected for the concatenated dataset. Phylogenetic reconstructions were conducted by Bayesian analysis, consisting of 2 Markov chains, 10 000 000 generations each, run in 6 parallel analyses in MrBayes (Huelsenbeck et al. 2001). When log-likelihood scores were found to sta-

Table 2. Molecular data used for the phylogenetic analysis in the present study

Species	Voucher ID number	GenBank CO1	GenBank 12S	GenBank 16S
Myurella kilburni	MNHN-IM-2007-30459	EU685511	EU685355	EU685647
Myurella columellaris	MNHN-IM-2007-30598	EU685584	EU685438	EU685730
Myurella undulata	MNHN-IM-2007-30629	EU685542	EU685393	EU685684
Myurella affinis	MNHN-IM-2007-30430	EU685506	EU685351	EU685642
Hastulopsis amoena	MNHN-IM-2007-30488	JQ809070	JQ808579	JQ808788
Myurella nebulosa	MNHN-IM-2007-30408	EU685516	EU685361	EU685653
Hastula lanceata	MNHN-IM-2009-7090	JQ809061	JQ808568	JQ808777
Oxymeris dimidiata	MNHN-IM-2009-7087	JQ809127	JQ808633	JQ808843
Oxymeris cerithina	MNHN-IM-2009-10013	JQ809119	JQ808625	JQ808836
Oxymeris maculata	MNHN-IM-2007-30370	EU685496	EU685341	EU685632
Terebra subulata	MNHN-IM-2007-30444	EU685501	EU685346	EU685637
Terebra funiculata	MNHN-IM-2007-30394	EU685565	EU685416	EU685707
Triplostephanus triseriata	MNHN-IM-2007-30404	EU685497	EU685342	EU685633
Terebra cingulifera	MNHN-IM-2007-30382	JQ809144	EU685443	EU685735
Terebra babylonia	MNHN-IM-2007-30375	JQ809135	EU685445	EU685737
Terebra quoygaimardi	MNHN-IM-2009-7116	JQ809176	JQ808676	JQ808892

bilize, consensus trees were calculated after omitting the first 10% of trees as burn in.

Data on the presence or absence of a radula were obtained from Castelin et al. (2012). For the species not described in that work (*Myurella columellaris*, *M. undulata*, *Oxymeris cerithina*, *Terebra quoygaimardi*), voucher specimens were studied. Shells of voucher specimens were drilled a few whorls above the aperture, and the bodies were extracted and dissected. All members of phylogenetic Clades C and D possess a radula. In contrast, species of Clades B, E1 and E5 typically do not have a radula — with the exception of *Myurella kilburni*, which has morphologically peculiar hollow hypodermic teeth, acquired independently from Terebridae of other lineages (Castelin et al. 2012).

Stable isotope analysis

For C and N isotope measurements, dried tissue samples of 0.5 to 0.8 mg were filled into 5 × 8 mm tin capsules and analyzed using a Thermo-Finnigan Delta V Plus continuous-flow IRMS coupled with an elemental analyzer (Thermo Flash 1112) in the Joint Usage Center at the Institute of Ecology and Evolution RAS. The isotopic composition of N and C was expressed in the δ-notation relative to the international standard (atmospheric nitrogen or VPDB): $\delta X(‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$, where R is the ratio of the heavier isotope to the lighter isotope. Samples were analyzed with reference gas calibrated against IAEA reference materials USGS 40 and USGS 41 (glutamic acid). The drift was corrected using an internal laboratory standard (acetanilide). The standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values in USGS 40 (n = 8) was <0.15‰.

Along with isotopic analyses, nitrogen and carbon content (as %) was determined in all samples. The C/N (mass/mass) ratio in the studied samples averaged 3.7 and did not differ among species (Table 1). This indicates that lipid concentration was uniformly low, and no lipid normalization of $\delta^{13}C$ values was required (Post et al. 2007).

Data analysis

Accurate quantification of the isotopic niche widths of the studied species was not possible, given our restricted dataset with less than 10 specimens per species analyzed. However, isotopic niche widths were assessed using the standard ellipses function incorporated in SIAR package for R (Jackson et al. 2012). Standard ellipses provide an estimate of the mean population core isotopic niche, based on a maximum likelihood approach. Use of the (n – 2) correction in calculation of standard ellipses is believed to make the estimate less sensitive to the sample size (Jackson et al. 2012).

To assess the overlap of isotopic niches among species, we employed analysis of similarity (ANOSIM; Clarke 1993), which is a distribution-free analog of 1-way ANOVA (Clarke 1993). Practically, it deals with the matrix of pairwise comparisons between individual observations within and between groups, with the mean within group distance (calculated as an intermediate argument in ANOSIM) being basically close to NND (mean nearest neighbor distance), one of the community metrics introduced by Layman et al. (2007) and representing the density of species packing (Vaudo & Heithaus 2011). The resulting parameter R scales from −1 to +1, and indicates the degree of difference among certain predefined groups; R = 0 indicates completely random grouping, whereas higher R values indicate higher dissimilarity between groups. The significances of pairwise comparisons were inferred from uncorrected p-values with Euclidian distances used as a dissimilarity measure, and α set to 0.05. The analyses were performed in PAST version 2.17 (Hammer et al. 2001).

To assess isotopic niche similarities among the 16 species, their individual $\delta^{13}C$ and $\delta^{15}N$ values were assigned to 16 corresponding groups, regardless of their phylogenetic relationships. To estimate similarities between different phylogenetic clades, mean $\delta^{13}C$ and $\delta^{15}N$ values of each species were treated as individual observations and assigned to 4 groups, corresponding to Clades B, C, E1 and E5. For calculating general characteristics of similarity within each phylogenetic clade, separate datasets for Clades B, C, E1 and E5 were created.

To quantify the isotopic niche overlap among clades, we calculated mean numbers of non-significant pairwise comparisons per species for each clade, and the proportions of non-significant comparisons with species belonging to the same and different clades.

RESULTS

Stable C and N isotope ratios in syntopic Terebridae

The carbon and nitrogen stable isotope compositions of the 16 species (Table 1, Figs. 3 & 4) exhibited considerable interspecific variability. Species aver-

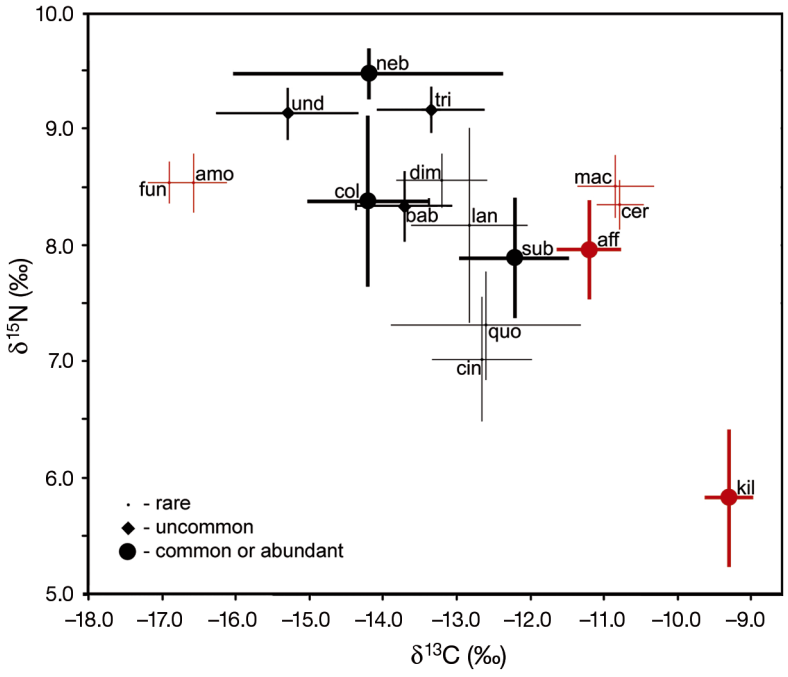

Fig. 4. $\delta^{13}C/\delta^{15}N$ biplot (mean ± SD) of studied Terebridae species in relation to their comparative abundances in the community of Murray Beach. Fine bars = rare species; strong bars with diamonds = uncommon species; strong bars with solid circles = common and abundant species. Species with $\delta^{13}C$ range ≤1.1 are marked with red. See Table 1 for species abbreviations

age $\delta^{13}C$ values ranged from –16.9‰ in *Terebra funiculata* to –9.3‰ in *Myurella kilburni*; species average $\delta^{15}N$ values ranged from 5.8‰ in *M. kilburni* to 9.5‰ in *M. nebulosa* (Table 1). The intraspecific variability in stable isotope ratios was considerably lower; average within-species ranges were 1.8‰ for $\delta^{13}C$ and 1‰ for $\delta^{15}N$, though they varied considerably among species.

Of the 16 species, 13 fell in the central area of the isotopic niche space biplot with $\delta^{13}C$ ranging from –16‰ to –10.5‰, and $\delta^{15}N$ from 6.7‰ to 9.7‰ (Fig. 4). Ten species had similar mean $\delta^{15}N$ values, between 7.9‰ and 8.6‰, that indicated feeding at the same trophic level.

Six species — *Terebra funiculata* (fun), *Oxymeris cerithina* (cer), *Myurella kilburni* (kil), *M. affinis* (aff), *Hastulopsis amoena* (amo) and *O. maculata* (mac), marked in red in Fig. 4 — exhibited relatively low intraspecific variability in $\delta^{13}C$ values (SD ≤1.3‰). These 6 species stand apart from the most crowded area of the isotopic niche biplot, with either relatively low (*T. funiculata*, *H. amoena*) or high (*O. cerithina*, *M. kilburni*, *M. affinis* and *O. maculata*) $\delta^{13}C$ values. In contrast, the 3 species with the highest intraspecific $\delta^{13}C$ variation (SD > 3‰), *Myurella nebulosa* (neb), *M. undulata* (und) and *Terebra quoygaimardi* (quo), fall in the most crowded area of the biplot.

Overlap of the isotopic niches was generally high. The matrix of pairwise comparisons (see Appendix) indicated only 1 species, *Myurella kilburni*, with an isotopic niche significantly distinct from all the other species ($p < 0.05$ for all pairwise comparisons). The remaining species showed from 1 (*Hastulopsis amoena*, *Terebra funiculata*) to 7 (*Myurella columellaris*, *Hastula lanceata*) non-significant pairwise comparisons (ANOSIM; $p \geq 0.05$) with an average of 3.5 non-significant comparisons per species (Table 3).

Nevertheless, the 5 most abundant species, which contribute 80% of total terebrid abundance on Murray Beach (Kantor et al. 2012), had minimal overlap in their isotopic niches (mean $\delta^{13}C$ and $\delta^{15}N$ values shown in bold in Fig. 4; individual measurements and standard ellipses shown in Fig. 5). The pairwise comparison matrix suggested a high level of isotopic niche space segregation among these 5 species (ANOSIM; R = 0.715). Only 2 out of 10 pairwise comparisons using ANOSIM failed to separate the dominant species, indicating slight overlap of isotopic niches in the pairs *Terebra subulata–Myurella affinis* and *M. collumelaris–M. nebulosa*, though the latter 2 species are well separated along the $\delta^{15}N$ axis (Fig. 5).

Isotopic signatures, phylogenetic position and anatomical traits

Comparison of isotopic signatures between phylogenetic clades of Terebridae revealed only 1 signifi-

Table 3. Pairwise comparisons for different phylogenetic clades of the studied Terebridae; sp = number of species in clade; n_w = no. of non-significant comparisons between members of the same clade; N_w = total no. of pairwise comparisons within clade; n_o = no. of non-significant comparisons with species from other clades

	sp	n_w/N_w	n_w/sp / n_o/sp
Clade B	3	1/3	0.66/2
Clade C	6	4/15	1.33/2.66
Clade E1	3	0/3	0/2.33
Clade E5	3	1/3	0.66/3

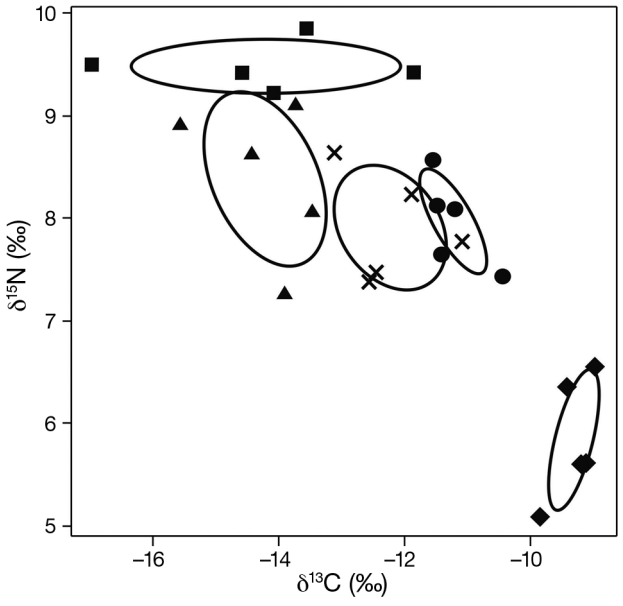

Fig. 5. $\delta^{13}C$ / $\delta^{15}N$ scatter plot of the 5 most abundant Terebridae species in the community of Murray Beach. The lines enclose the standard ellipse area (SEAc) for each species. Solid circles = *Myurella affinis*; triangles = *M. columellaris*; diamonds = *M. kilburni*; squares = *M. nebulosa*; X-crosses = *Terebra subulata*

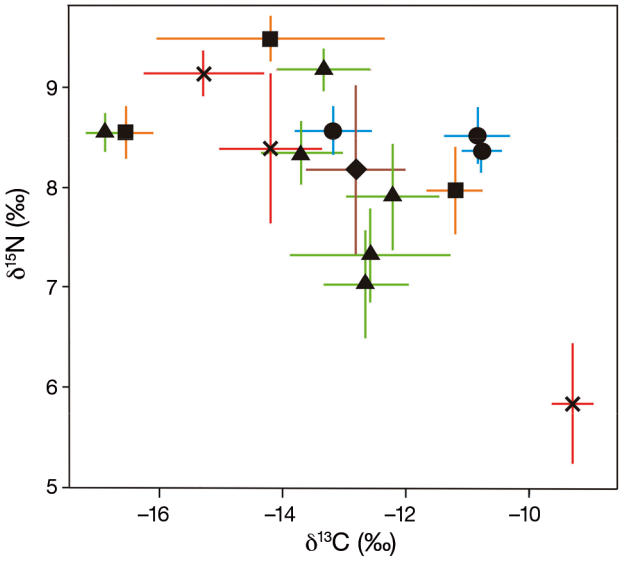

Fig. 6. $\delta^{13}C$ / $\delta^{15}N$ biplot (mean ± SD) of studied Terebridae species with regard to their clade assignments. Solid circles = Clade B; triangles = Clade C; diamond = Clade D; squares = Clade E1; X-crosses = Clade E5

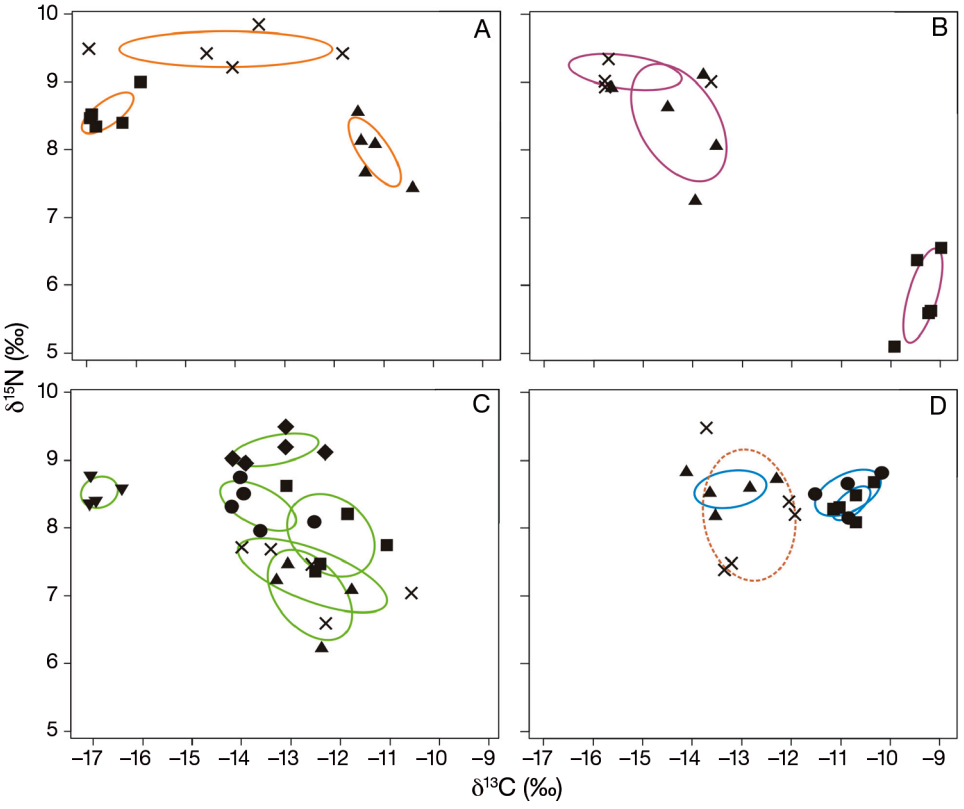

Fig. 7. $\delta^{13}C$/$\delta^{15}N$ scatter plots of studied Terebridae species in regard to their clade assignments. The lines enclose the standard ellipse area (SEAc) for each species. (A) Clade E1: triangles = *Myurella affinis*; squares = *Hastulopsis amoena*; X-crosses = *M. nebulosa*; (B) Clade E5: triangles = *M. columellaris*; squares = *M. kilburni*; X-crosses = *M. undulata*; (C) Clade C: solid circles = *Terebra babylonia*; triangles = *T. cingulifera*; upturned triangle = *T. funiculata;* diamonds = *Triplostephanus triseriata*; squares = *T. subulata*; X-crosses = *T. quoygaimardi*; (D) Clades B and D: solid circles = *Oxymeris maculata*; triangles = *O. dimidiata*; squares = *O. cerithina*; X-cross = *Hastula lanceata*

cant difference (between Clades E1 and D) in 10 pairwise comparisons, suggesting lack of isotopic niche space segregation among clades.

In contrast, closely related species within clades often differed notably from each other in their location in isotopic niche space (Figs. 3, 6 & 7), and in most cases exhibited significant differences in the pairwise distances matrix (ANOSIM; $p < 0.05$, Appendix).

Within-clade divergence of isotopic niches was most pronounced in Clade E1, 3 species of which were well separated along both isotopic axes (Figs. 3 & 7A); ANOSIM indicated significant differences in all pairwise comparisons between species (Table 3, Appendix). The intraspecific variation in isotopic signatures of *Myurella affinis* and *Hastulopsis amoena* was modest, while the third species, *M. nebulosa* showed the greatest variation in $\delta^{13}C$. *M. affinis* and *M. nebulosa* are the most abundant terebrids in the studied community.

Of the 3 studied species in Clade E5 (ANOSIM; R = 0.79), *Myurella columellaris* and *M. undulata* did not differ significantly in the pairwise comparison, while *M. kilburni* occupied the opposite corner of the isotopic niche space biplot (Figs. 3 & 7B), apart not only from the 2 other Clade E5 species, but from all other studied species. The isotopic niches of the Clade E5 species had 3.66 overlaps on average, but only 0.66 were with species from the same clade (Table 3).

Five species of Clade C (ANOSIM; R = 0.6) had similar mean values of δ^{13} (−13.7‰ to −12.2‰) but differed in $\delta^{15}N$ (Figs. 3 & 7C); the sixth species, *Terebra funiculata*, diverged from the others with a lower δ^{13} value. On average, each Clade C species had 4 isotopic niche overlaps and only 1.33 of them were with other Clade C species (Table 3). Standard ellipses, constructed for Clade C species in particular suggested strong overlaps between *T. babylonia*, *T. qouygaimardi* and *T. subulata*.

Only in Clade B (ANOSIM; R = 0.61) did all species have similar mean values of $\delta^{15}N$ (8.4 to 8.6‰, see Table 1, Figs. 3 & 7D). *Oxymeris maculata* and *O. cerithina* had greatly overlapping isotopic niches, while the third species, *O. dimidiata,* differed from them with lower δ^{13} values. All 3 species exhibited low intraspecific variability in isotopic signatures and occupied a relatively compact area of the isotopic niche space biplot, unlike species of Clades E1 and E5.

Finally, *Hastula lanceata*, the only member of Clade D in the studied community, displayed the highest intraspecific variation of isotope signatures, occupying the central area of the isotope niche space biplot (Figs. 3 & 7D).

Comparison of stable isotope values between Terebridae and possible prey items

This study did not sample enough potential prey to infer possible dietary differences among terebrid species. Of the few polychaetes collected in the sampling area, species of Sabellidae (filter-feeders) had the lowest mean $\delta^{13}C$ value (−19.1‰) and a $\delta^{15}N$ value of 5.8‰ (Fig. 8). Polychaetes of some other families had $\delta^{15}N$ values similar to those of Sabellidae, but higher ^{13}C content in their tissues: Spionidae (mostly surface deposit feeders; mean $\delta^{13}C$ = −16.1‰, mean $\delta^{15}N$ = 6.2‰), Amphinomidae (carrion feeders or carnivores; $\delta^{13}C$ = −15.2‰, $\delta^{15}N$ = 6.0‰) and Glyceridae (detritivores or carnivores; mean $\delta^{13}C$ = −12.1‰, mean $\delta^{15}N$ = 6.2‰). Polychaetes, which are exclusively carnivorous (i.e. Nephtyidae and Aphroditiidae) exhibited higher values of $\delta^{15}N$ (from 7.6‰ to 8.9‰), suggesting that they occupy a similar trophic level to the studied terebridae species. The differences in $\delta^{13}C$ and $\delta^{15}N$ between some of the polychaetes and the terebrid species suggest that spionid, amphinomid and glycerid polychaetes may be preyed upon by members of the terebrid community. However, establishment of trophic linkages of this community requires a much larger dataset, with a wider range of potential prey items analyzed, and best of all supplemented by direct observations.

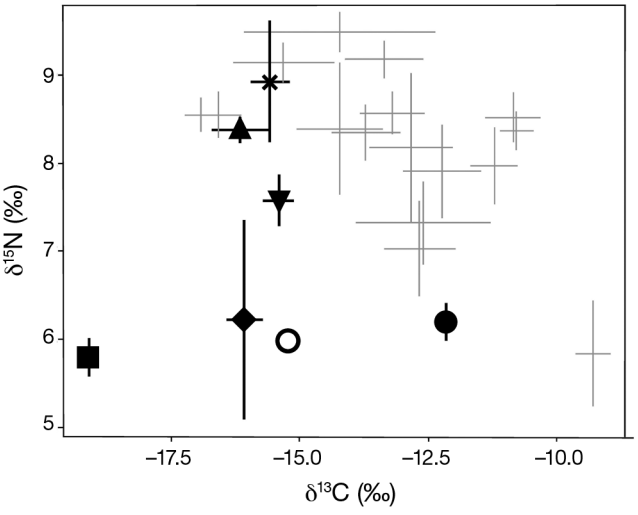

Fig. 8. $\delta^{13}C/\delta^{15}N$ biplot (mean ± SD) of potential food items of Terebridae. ○ = Amphynomidae gen. sp.; ● = Glyceridae gen. sp.; X-cross = Nephtidae gen. sp.; ■ = Sabellidae gen. sp.; ◆ = Spionidae gen. sp.; ▲ = Aphroditiidae gen. sp. 1; ▼ triangle = Aphroditiidae gen. sp. 2. Isotope signatures of studied Terebridae species are shown in grey (Fig. 6)

DISCUSSION

Feeding specialization and resource partitioning among Terebridae in the studied community

For a compact taxonomic group, expected to be uniform in feeding biology, the terebrid species studied showed a considerable interspecific range of isotopic signatures (7.6‰ for $\delta^{13}C$ and 3.7‰ for $\delta^{15}N$), and at the same time generally moderate intraspecific variability in both stable isotope ratios. High interspecific variability in isotopic signature implies that (1) a variety of carbon sources supports the studied terebrid community and (2) they feed at different trophic levels.

Our results suggest that the studied Terebridae rely on diverse sources of primary production. The isotopic niches of the 6 species that showed little variation in $\delta^{13}C$ were situated apart from the most crowded part of the isotopic niche space biplot. The central area of the biplot in turn was occupied by species with higher $\delta^{13}C$ variation (Fig. 4). One possible explanation of such a distribution of $\delta^{13}C$ ranges is that those species forming the main core on the biplot are supported by multiple carbon sources, while the isotopic niches of other species that fringe the main core on both the left and right are specialized on a particular carbon source.

The data on polychaete isotopic signatures may be of use, as it allows estimation of $\delta^{13}C$ in primary production resources of the Murray Beach community — based on the isotopic signatures of the analyzed polychaetes that belong to known trophic guilds — providing an indirect estimate of what resources may support the terebrid community. Sabellid worms are filter-feeders supported mainly by phytoplankton (Fauchald & Jumars 1979); in our data one species of this family may represent a first level consumer, reflecting the carbon isotopic signature of phytoplankton. Published $\delta^{13}C$ values of marine phytoplankton usually range between −24 and −18‰ (Dauby 1989, Davenport & Bax 2002). If we assume ^{13}C enrichment per trophic level of about 0 to 1‰, none of the terebrid species is likely to feed exclusively on filter-feeding sabellids, although it is possible that the 2 terebrid species with the lowest $\delta^{13}C$ values, *Terebra funiculata* and *Hastulopsis amoena*, are largely supported by consumers of phytoplankton-derived primary production. It can be suggested that other terebrid species with higher $\delta^{13}C$ values are partly or mostly supported by the food webs based on organic matter derived from benthic sources: benthic algae ($\delta^{13}C$ values in tropical waters are usually −19 to −10‰; Hsieh et al. 2000, Lepoint et al. 2004), or sea-grass ($\delta^{13}C$ usually around −10‰; Lepoint et al. 2004). The very narrow intra-population $\delta^{13}C$ range of *Myurella kilburni* and its uniquely high mean $\delta^{13}C$ value imply its specialization to a single source of carbon, different from those supporting the other studied Terebridae. Presuming that this species shares the terebrid predatory lifestyle (i.e. represents a secondary consumer), we conclude that the primary production source which supports *M. kilburni*, in addition to having a uniquely high $\delta^{13}C$ value, has a very low $\delta^{15}N$ signature — possibly about zero. Among all sources of primary production in marine communities, only seagrass fits these criteria; apart from having the highest $\delta^{13}C$ values, some species of seagrass have a $\delta^{15}N$ signal of 0‰ or even −2‰ (Lepoint et al. 2004).

The indirect interaction between consumer species mediated by a shared resource is known as exploitative competition (Wootton 1994, Elias et al. 2013). Its effect on competing species may force a resource shift, or result in competitive exclusion (Elias et al. 2013). A shift in resource may be realized through either mutual compression of trophic niches in competing species, leading to their further specialization, or through a mechanism whereby the less competitive species may be forced to expand its niche to include a secondary resource (Codron et al. 2011). Both scenarios imply appearance of efficient resource partitioning between species to allow their co-occurrence within a single habitat.

Though the studied terebrid species display multiple overlaps in isotopic niches, isotopic niche space seems to be well separated (1) among species with high abundance and (2) among the most closely related species, at least within some phylogenetic clades. It is logical to expect a higher degree of exploitative competition between co-occurring abundant species with high densities (Watanabe 1984, Cotgreave 1994). The segregation of the isotopic niches of the 5 most abundant terebrid species suggests minimal or no overlap of their actual trophic niches. The isotopic niches of 4 species, *Terebra subulata*, *Myurella nebulosa*, *M. columellaris* and *M. affinis* seem to be contiguous, which may suggest that mutual compression of their trophic niches took place during their co-evolution. Following the same logic, the outlying isotopic niche of *M. kilburni* may reflect a shift to a secondary resource. Comparison of isotopic niches of *M. kilburni* and *M. nebulosa* suggests a remarkable difference in their feeding biology and trophic strategies. The mean $\delta^{15}N$

value of *M. kilburni* (the lowest among the studied species) indicates its relatively low trophic position, whereas low interspecific variability in $\delta^{13}C$ values suggests strong trophic specialization (see above). In contrast, the isotopic niche of *M. nebulosa* is characterized by high $\delta^{15}N$ values and the widest range of $\delta^{13}C$ values (5.2‰) — features typical of a higher level consumer with wide intraspecific $\delta^{13}C$ range — suggesting multiple carbon sources supporting the consumer.

Trophic diversification in different phylogenetic lineages of Terebridae

Our study revealed that the isotopic niche overlap among closely related species (belonging to the same clade) is significantly smaller than the overlap between species from different clades. The isotopic niches of species in at least 2 phylogenetic lineages, E1 and E5, are well separated suggesting trophic diversification with the appearance of alternative feeding specializations in each of these clades. The advantage of the trophic diversification is obvious: it reduces exploitative competition among closely related sympatric species, allowing co-occurrence of a number of related species in the same community (Schluter 1994, Ingram 2011). The pattern of isotopic niche distribution in the different clades suggests that late evolutionary radiation in Terebridae was accompanied by trophic diversification, which happened independently in different clades. Indeed, recent studies have demonstrated that the most closely related species tend to exhibit the strongest exploitative competition because they 'tend to interact with their shared resource species in a similar way' (Elias et al. 2013, p. 1355). This pattern of interspecific interaction was referred to as a 'negative phylogenetic signal' and has already been documented in some groups of marine predators (Rezende et al. 2009, Rutschmann et al. 2011).

More distantly related Terebridae species had greater overlap of isotopic niches, which may suggest convergence of their actual trophic niches. It is likely that more distantly related lineages had traveled along different pathways of specialization such that a partial overlap of trophic niches does not cause strong competition. A study of adaptive radiation in Antarctic notothenioid fishes (Rutschmann et al. 2011) also integrated phylogenetic data with stable isotope analyses and their results are similar to ours. Great variation within, and substantial overlap between different phylogenetic lineages were found, indicating that ecological diversification has occurred several times in parallel in different notothenioid families. The adaptive radiation in notothenioid fishes also suggested diversification along the benthic–pelagic axis, i.e. a partitioning of habitat together with the diversification of trophic niches. In our case, all Terebridae species share a similar lifestyle and no distinct trend of ecological diversification was revealed, thus narrowing the possibilities for adaptive radiation in the group.

Alternatively, it is possible that, for species from different phylogenetic clades, the overlap in isotopic niches is less indicative of actual trophic niche overlap (Bearhop et al. 2004). All known Terebridae are predators, and therefore the width of their isotopic niche reflects not only the level of the trophic specialization of a predator, but is also affected by the level of trophic specialization of its prey. In other words, the wide isotopic signature range in a given terebrid species does not necessarily reflect the wide spectrum of prey consumed, but may also be a result of feeding on a single generalist prey species (Post 2002, Bearhop et al. 2004, Cummings et al. 2012). In turn, the overlap in isotopic niches among terebrid species suggests either their actual trophic niche overlap, or may reflect an overlap of isotopic niches of their prey species. In the second case, 2 prey species may belong to different taxonomic groups and differ strikingly in feeding biology, but have similar trophic level and be supported by similar carbon source(s). For example, the isotopic niches of 2 species of Clade B, *Oxymeris maculata* and *O. cerithina*, overlap considerably, yet it is unlikely that they feed on the same prey species. The shell height of adult specimens of *O. maculata*, the biggest known terebrid, reaches 274 mm (Bratcher & Cernohorsky 1987), while in *O. cerithina* it usually does not exceed 50 mm. Body size has been identified as a major factor determining predator-prey interactions (Petchey et al. 2008, Rezende et al. 2009); the huge size difference between *O. maculata* and *O. cerithina* presumes dietary differences, and trophic competition between them seems unlikely. The co-occurrence of multiple Terebridae species with different shell size in the same habitat has also been noticed by Kohn (1971), who suggested that different size implies general differences in ecology and a lack of interspecific competition.

The most distinctive isotopic niche divergence was demonstrated among species of phylogenetic Clades E1 and E5. Considerable differences in stable isotope ratios between closely related species of these clades suggest not only a specialization on different prey

species, but also imply that they are supported by different carbon sources, and therefore have minimal overlap (if any) in the food chains they rely on. This may give a clear advantage to a group of closely related species, as it spreads their predation pressure across the prey community. Potentially, it permits each of the closely related species to achieve considerable abundance, by excluding within-clade exploitative competition. This suggestion agrees well with the data on species abundances, as 4 of the 5 most abundant terebrids in the studied community belong to Clades E1 and E5. Therefore, we suggest that the key mechanism in the microevolution of this lineage was the high degree of resource partitioning with specialization on different sources of primary production.

Loss of radula and isotopic niche width

There seems to be no connection between the presence or absence of the radula and the width of the isotopic niche. All studied species of Clades B, E1 and E5, with the exception of *Myurella kilburni*, lack a radula and venom gland. Of these 8 species, 4 (*Hastulopsis amoena* and all *Oxymeris* spp.) display low intraspecific variation of isotope signatures, suggesting a limited spectrum of prey species. On the other hand, the intraspecific variation in the isotope signatures of radula-less *Myurella* species (*M. nebulosa* and *M. columellaris*) were relatively high. Even within the same clade, some radula-less species may vary considerably in isotopic signatures, while others show little variation. Apparently, loss of the radula and other specialized foregut structures cannot itself be regarded as a prerequisite of generalist feeding in Terebridae and should be considered in a more general evolutionary context.

Acknowledgements. Material for the present study was collected during field work in Vietnam that was supported by the Coastal Branch of the Russian-Vietnamese Tropical Center. We are thankful to the staff of the Russian-Vietnamese Tropical Center for assistance in organization of the field sampling and loan of some laboratory equipment. We thank our friend and colleague I. Marin for his help during the collection of material. We also thank I. Pokrovsky (Max Planck Institute for Ornithology, Seewiesen) and A. Gonchar (Research Institute of Applied Acoustic, Dubna) for help in statistical analysis and, in particular, some tips on using R. We are grateful to the anonymous referees and responsible editor for comprehensive analysis of our manuscript and to R. Cowie (University of Hawaii) for help in editing the final version of the manuscript. This study was supported by the Russian Foundation for Basic Research Grant RFBR-11-04-01284-a.

LITERATURE CITED

Anseeuw D, Guelinckx J, Snoeks J (2010) Differences in stable isotope composition within and among zooplanktivorous Utaka cichlid populations from Lake Malawi. Afr J Ecol 48:378–385

Bearhop S, Adams CE, Waldron S, Fuller RA, MacLeod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73: 1007–1012

Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. Annu Rev Ecol Evol Syst 42:411–440

Bratcher T, Cernohorsky W (1987) Living terebras of the world: a monograph of the recent Terebridae of the world. American Malacologists, Melbourne, FL

Castelin M, Puillandre N, Kantor YI, Modica MV and others (2012) Macroevolution of venom apparatus innovations in auger snails (Gastropoda; Conoidea; Terebridae). Mol Phylogenet Evol 64:21–44

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Codron D, Hull J, Brink JS, Codron J, Ward D, Clauss M (2011) Effect of competition on niche dynamics of syntopic grazing ungulates: contrasting the predictions of habitat selection models using stable isotope analysis. Evol Ecol Res 13:217–235

Cotgreave P (1994) The relation between body size and abundance in a bird community: the effects of phylogeny and competition. Proc R Soc Lond 256:147–149

Cummings DO, Buhl J, Lee RW, Simpson SJ, Holmes SP (2012) Estimating niche width using stable isotopes in the face of habitat variability: a modelling case study in the marine environment. PLoS ONE 7:e40539

Dauby P (1989) The stable carbon isotope ratios in benthic food webs of the Gulf of Calvi, Corsica. Cont Shelf Res 9: 181–195

Davenport SR, Bax NJ (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Can J Fish Aquat Sci 59: 514–530

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

Doi H, Yurlova NI, Kikuchi E, Shikano S, Yadrenkina EN, Vodyanitskaya SN, Zuykova EI (2010) Stable isotopes indicate individual level trophic diversity in the freshwater gastropod *Lymnaea stagnalis.* J Molluscan Stud 76:384–388

Duda TF, Kohn AJ, Palumbi SR (2001) Origins of diverse feeding ecologies within *Conus*, a genus of venomous marine gastropods. Biol J Linn Soc 73:391–409

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32:1792–1797

Elias M, Fontaine C, van Veen FJF (2013) Evolutionary history and ecological processes shape a local multilevel antagonistic network. Curr Biol 23:1355–1359

Fauchald K, Jumars PA (1979) The diet of worms: a study of Polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Fedosov AE, Moshkovskii SA, Kuznetzova KG, Olivera BM (2012) Conotoxins: from the biodiversity of gastropods to new drugs. Biochemistry (Mosc) (Suppl B) 6:107–122

Fink P, Reichwaldt ES, Harrod C, Rossberg AG (2012) Deter-

mining trophic niche width: an experimental test of the stable isotope approach. Oikos 121:1985–1994

Fry B (2006) Stable isotope ecology. Springer, Heidelberg

Genner MJ, Turner GF, Barker S, Hawkins SJ (1999) Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. Ecol Lett 2: 185–190

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electronica 4:1–9

Holford M, Puillandre N, Terryn Y, Cruaud C, Olivera BM, Bouchet P (2009) Evolution of the Toxoglossa venom apparatus as inferred by molecular phylogeny of the Terebridae. Mol Biol Evol 26:15–25

Hsieh HL, Kao WY, Chen CP, Liu PJ (2000) Detrital flows through the feeding pathway of the oyster (*Crassostrea gigas*) in a tropical shallow lagoon: $\delta^{13}C$ signals. Mar Biol 136:677–684

Huelsenbeck JP, Ronquist F, Hall B (2001) MrBayes: bayesian inference of phylogeny. Bioinformatics 17: 754–755

Imperial JS, Watkins M, Chen P, Hillyard DR, Cruz LJ, Olivera BM (2003) The augertoxins: biochemical characterization of venom components from the toxoglossate gastropod *Terebra subulata*. Toxicon 42:391–398

Imperial JS, Kantor YI, Watkins M, Heralde FM and others (2007) Venomous auger snail *Hastula* (*Impages*) *hectica* (Linnaeus, 1758): Molecular phylogeny, foregut anatomy and comparative toxinology. J Exp Zool B Mol Dev Evol 308B:744–756

Ingram T (2011) Evolution of the trophic niche and food web structure. PhD Dissertation, University of British Columbia, Vancouver

Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLoS ONE 7:e31757

Kantor YI, Puillandre N (2012) Evolution of the radular apparatus in Conoidea (Gastropoda: Neogastropoda) as inferred from a molecular phylogeny. Malacologia 55: 55–90

Kantor YI, Fedosov AE, Marin IN (2012) An unusually high abundance and diversity of the Terebridae (Gastropoda: Conoidea) in Nha Trang Bay, Vietnam. Zool Stud 51: 663–670

Kohn AJ (1959) The ecology of *Conus* in Hawaii. Ecol Monogr 29:47–90

Kohn AJ (1971) Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. Limnol Oceanogr 16:332–347

Kohn AJ, Nybakken JW (1975) Ecology of *Conus* on eastern Indian Ocean fringing reefs: diversity of species and resource utilization. Mar Biol 29:211–234

Kohn AJ, Nishi M, Pernet B (1999) Snail spears and scimitars: a character analysis of *Conus* radular teeth. J Molluscan Stud 65:461–481

Layman CA, Arrington DA, Montana CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Lepoint G, Dauby P, Gobert S (2004) Applications of C and N stable isotopes to ecological and environmental studies in seagrass ecosystems. Mar Pollut Bull 49:887–891

Marcus E, Marcus E (1960) On *Hastula cinerea*. Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo 260:25–66

McKinney RA, Lake JL, Allen M, Ryba S (1999) Spatial variability in mussels used to assess base level nitrogen isotope ratio in freshwater ecosystems. Hydrobiologia 412: 17–24

Meyer WM III, Yeung NW (2011) Trophic relationships among terrestrial molluscs in a Hawaiian rain forest: analysis of carbon and nitrogen isotopes. J Trop Ecol 27: 441–445

Miller B (1970) Studies on the biology of Indo-Pacific *Terebra*. PhD Dissertation, University of New Hampshire, Durham, NH

Miller BA (1975) The biology of *Terebra gouldi* Deshayes, 1859 and a discussion of life history similarities among other terebrids of similar proboscis type. Pac Sci 29: 227–241

Miller BA (1979) The biology of *Hastula inconstans* (Hinds, 1844) and a discussion of life history similarities among other *Hastula*s of similar proboscis type. Pac Sci 33: 289–306

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140

Nelson AFM, Perissinotto R (2012) Stable isotope evidence for dietary overlap between alien and native gastropods in coastal lakes of Northern KwaZulu–Natal, South Africa. PLoS ONE 7:e31897

Olivera BM, Teichert RW (2007) Diversity of the neurotoxic *Conus* peptides: a model for concerted pharmacological discovery. Mol Interv 7:251–260

Petchey OL, Beckerman AP, Riede JO, Warren PH (2008) Size, foraging, and food web structure. Proc Natl Acad Sci USA 105:4191–4196

Posada D, Crandall KA (2001) Selecting models of nucleotide substitution: an application to human immunodeficiency virus 1 (HIV-1). Mol Biol Evol 18:897–906

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703–718

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152: 179–189

Puillandre N, Holford M (2010) The Terebridae and teretoxins: combining phylogeny and anatomy for concerted discovery of bioactive compounds. BMC Chem Biol 10:7

Rezende EL, Albert EM, Fortuna MA, Bascompte J (2009) Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecol Lett 12:779–788

Rutschmann S, Matschiner M, Damerau M, Muschick M, Lehmann MF, Hanel R, Salzburger W (2011) Parallel ecological diversification in Antarctic notothenioid fishes as evidence for adaptive radiation. Mol Ecol 20:4707–4721

Schluter D (1994) Experimental evidence that competition promotes divergence in adaptive radiation. Science 266: 798–801

Shimek RL, Kohn AJ (1981) Functional morphology and evolution of the toxoglossan radula. Malacologia 20:423–438

Sitnikova T, Kiyashko SI, Maximova N, Pomazkina GV, Roepstorf P, Wada E, Michel E (2012) Resource partitioning in endemic species of Baikal gastropods indicated by gut contents, stable isotopes and radular morphology. Hydrobiologia 682:75–90

Taylor J (1990) The anatomy of the foregut and relationships in the Terebridae. Malacologia 32:19–34

Taylor JD, Kantor YI, Sysoev AV (1993) Foregut anatomy, feeding mechanisms, relationships and classification of Conoidea (=Toxoglossa) (Gastropoda). Bull Nat Hist Mus London (Zool) 59:125–169

Terlau H, Olivera BM (2004) *Conus* venoms: A rich source of novel ion channel-targeted peptides. Physiol Rev 84: 41–68

Terryn Y (2007) A collectors guide to recent Terebridae: (Mollusca: Neogastropoda). ConchBooks & Natural Art, Hackenheim

Vaudo JJ, Heithaus MR (2011) Dietary niche overlap in a nearshore elasmobranch mesopredator community. Mar Ecol Prog Ser 425:247–260

Watanabe JM (1984) The influence of recruitment, competition and benthic predation on spatial distributions of three species of kelp forest gastropods (Trochidae, *Tegula*). Ecology 65:920–936

Wootton J (1994) The nature and consequences of indirect effects in ecological communities. Annu Rev Ecol Syst 25:443–466

Appendix. Matrix of uncorrected p-values of ANOSIM pairwise comparisons between isotopic signatures of the studied Terebridae species. Non-significant comparisons shown in bold. Within-clade comparisons enclosed in boxes

Species	Code	kil	col	und	aff	amo	neb	lan	dim	cer	mac	sub	fun	tri	cin	bab	quo
Myurella kilburni	kil	**E5**	0.007	0.008	0.008	0.008	0.009	0.007	0.009	0.007	0.007	0.009	0.008	0.008	0.008	0.007	0.008
Myurella columellaris	col		**E5**	**0.074**	0.008	0.008	**0.208**	**0.093**	**0.177**	0.007	0.007	0.016	0.033	**0.088**	0.017	**0.765**	**0.091**
Myurella undulata	und			**E5**	0.009	0.016	**0.130**	0.017	0.016	0.007	0.007	0.007	0.058	0.021	0.008	0.033	0.007
Myurella affinis	aff				**E1**	0.009	0.008	0.009	0.007	0.038	**0.141**	**0.064**	0.009	0.007	0.007	0.008	0.031
Hastulopsis amoena	amo					**E1**	0.018	0.010	0.009	0.008	0.007	0.008	**0.758**	0.009	0.009	0.009	0.009
Myurella nebulosa	neb						**E1**	0.032	0.030	0.008	0.016	0.018	**0.082**	**0.608**	0.016	0.009	0.010
Hastula lanceata	lan							**D**	**0.290**	0.009	0.024	**0.852**	0.007	**0.172**	**0.337**	**0.151**	**0.507**
Oxymeris dimidiata	dim								**B**	0.008	0.009	**0.055**	0.007	**0.157**	0.008	**0.288**	0.025
Oxymeris cerithina	cer									**B**	**0.722**	0.009	0.008	0.006	0.009	0.008	0.008
Oxymeris maculata	mac										**B**	0.023	0.007	0.029	0.031	0.007	0.014
Terebra subulata	sub											**C**	0.008	0.022	**0.290**	0.024	**0.341**
Terebra funiculata	fun												**C**	0.026	0.015	0.023	0.009
Triplostephanus triseriata	tri													**C**	0.028	0.043	0.009
Terebra cingulifera	cin														**C**	0.030	**0.960**
Terebra babylonia	bab															**C**	**0.062**
Terebra quoygaimardi	quo																**C**

Editorial responsibility: Philippe Borsa, Montpellier, France

Submitted: May 8, 2013; Accepted: October 7, 2013
Proofs received from author(s): December 23, 2013