

Habitat-associated evolutionary rates in deep-sea invertebrates

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Abstract

In environments where resources occur as ephemeral patches within a matrix of resource scarcity, patch characteristics can strongly affect organisms' life-history traits. Depending on patch longevity, life histories may evolve to match the availability of resources, potentially resulting in deterministic patterns of evolution. In the deep sea, organic falls, hydrothermal vents, and cold seeps create patches of high productivity that persist over different lengths of time, ranging from decades to millennia. Using publicly available data for mitochondrial CO1, we examined the relationship between habitat type and rates of molecular evolution among mussels (Mytilidae: Bathymodiolinae) and tubeworms (Siboglinidae), two clades that have diversified in these deep-sea environments. We observed an inverse relationship between habitat longevity and rates of mitochondrial sequence evolution, supporting the hypothesis that resource longevity structures life-history variation. Contrary to expectation, animal size does not correlate with rates of molecular evolution after accounting for phylogeny. Within both clades, species that specialize on organic falls exhibit faster substitution rates than related species at vents and seeps. The similar patterns recovered in two deeply diverged phyla suggest that the proposed relationship between resource longevity and rates of molecular evolution may be widespread.

Keywords: Siboglinidae, Bathymodiolinae, deep sea, molecular evolution, life-history traits

Introduction

In environments where resources occur asynchronously as patches within a matrix of resource scarcity, the longevity of each patch may affect organisms' life-history traits. Depending on the environmental context, life histories can evolve to match and exploit different patterns of resource variability (Schwinning & Ehleringer, 2001). Where resources are short-lived but occur frequently, taxa may experience multiple short-duration pulses within a lifetime and may evolve traits associated with starvation resistance to survive periods between pulses or pulsed growth and reproduction when resources become available (Chesson et al., 2004; Poulson, 2001). Alternatively, if resource duration is less than potential lifespans, resource consumers may evolve accelerated life histories to reproduce before resources are extinguished (Mu et al., 2021). By contrast, when resource longevity is comparatively long and other external sources of adult mortality remain low, organisms may experience relaxed selection for accelerated life histories or may even evolve decelerated senescence (Durkin et al., 2017). While mobile organisms can move among transient resource patches, the life histories of sessile taxa are constrained by the longevity of their required resource.

The deep sea is a classic example of severe resource limitation. While most of the deep-sea benthos is limited by the

transport of organic carbon from surface waters, patches of chemosynthetic primary production create localized hotspots of high productivity. Analogous to photosynthesis, chemosynthesis is a carbon fixation pathway that derives energy from reduced chemical compounds (e.g., hydrogen sulfide) rather than light. Such hotspots in the deep sea generally occur in three types of environments—cold seeps, hydrothermal vents, and organic falls—substrates that persist over different timescales. Cold seeps occur where brine or hydrocarbons (generally methane) rise from buried reservoirs through sediments to the seafloor. Seeps typically occur along continental margins and tend to be stable over thousands of years (Aharon et al., 1997; Cordes et al., 2009; Roberts & Aharon, 1994). Hydrothermal vents occur along spreading margins and volcanic hotspots where heated, mineral-rich fluids below ground pass through fissures into the water column. The longevity of individual vent habitats is highly variable and correlates with regional seafloor spreading rates (Baker et al., 1995). Vent longevity can range from a few years along the ultra-fast Southern East Pacific Rise to centuries along the super-slow Mid-Atlantic Ridge (Baker et al., 1995; Grassle, 1985; Juniper & Tunnicliffe, 1997; Sarrazin et al., 1997; Shank et al., 1998; Vrijenhoek, 2010). Organic falls occur when large quantities of organic matter (e.g., animal, wood, or kelp) sink from shallow waters to the deep sea. Anaerobic

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decomposition produces reduced compounds, which—especially at large organic falls, such as baleen whales—can sustain chemosynthetic communities for years to decades (Braby et al., 2007; Fujiwara et al., 2007; Lundsten et al., 2010; Smith & Baco, 2003).

Disparate invertebrate clades have radiated into and across deep-sea chemosynthetic environments, including mussels (Lorion et al., 2013), crustaceans (Shank et al., 1999), annelids (Black et al., 1997), gastropods (Kano et al., 2016), and others. Within some groups, such as tubeworms (Siboglinidae) and mussels (Mytilidae: Bathymodiolinae), closely related lineages occur across vents, seeps, and organic falls, but individual species can be highly specialized and occur only on a single habitat type. For organisms constrained to ephemeral resources (organic falls and some vents), there may be stronger selection for rapid growth and reproduction to occur before resources are extinguished (Génio et al., 2012; Grassle, 1985). By contrast, organisms living in more stable habitats may benefit from slower growth and delayed reproduction. For example, siboglinid tubeworms at vents and seeps exhibit highly variable growth rates across habitats, including closely related species that exhibit among the fastest growth and oldest age reported for any invertebrates in the world (Bergquist et al., 2000; Durkin et al., 2017; Lutz et al., 1994). However, the high toxicity of vent environments may accelerate rates of DNA damage, potentially increasing susceptibility to disease and reducing average lifespans of vent inhabitants (Dixon et al., 2000). Vent specialists might therefore compensate for high toxicity by evolving r-strategy life-history traits like small body size and early reproduction (Wilson & MacArthur, 1967) (subsequently referred to herein as the mutagen avoidance hypothesis; Dixon et al., 2000; Pruski & Dixon, 2003). Mussels and tubeworms span orders of magnitude in shell and tube length, with the smallest species found at organic falls and the largest at vents and seeps (Durkin et al., 2017; Lorion et al., 2013; Lutz et al., 1994; Rouse et al., 2018).

Variation in life-history traits along a slow-to-fast spectrum (Montiglio et al., 2018; Promislow & Harvey, 1990; Stearns, 1983) often corresponds with variation in the rate of genome evolution (Bromham, 2020; Gillman & Wright, 2013). Overall rates of DNA substitution have been linked to specific life-history characteristics such as body mass or size, generation length, and metabolic rates (e.g., Berv & Field, 2018; Berv et al., 2024; Bromham, 2011; Field et al., 2020; Gillooly et al., 2005; Hua et al., 2015; Lanfear et al., 2013; Santos, 2012; Thomas et al., 2010; Weller & Wu, 2015). In particular, invertebrates with shorter life spans and generation lengths tend to have faster rates of molecular evolution in both synonymous and nonsynonymous nucleotide sites of mitochondrial proteins (Thomas et al., 2010). Therefore, ephemeral environments that differentially constrain consumer life histories may generate divergent patterns of molecular evolution.

Here, we explore a novel resource longevity hypothesis where temporal variability in resource supply mediates consumer life-history strategies and rates of molecular evolution. By acting as a maximum constraint on an individual's lifespan, resource longevity may induce a relationship between habitat type, life-history variation, and patterns of molecular evolution in deep-sea invertebrates. If resource longevity is the dominant force constraining life histories, we predicted that constraints for rapid growth and early reproduction in short-lived habitats such as organic falls would favor r-selected

specialists with shorter generation lengths and smaller adult sizes, imparting a signature of accelerated rates of molecular evolution. Likewise, we expected the opposite in comparatively stable habitats such as cold seeps, where constraints on life-history strategies may be relaxed or even reversed (Durkin et al., 2017). Further, under this conceptual framework, we expected hydrothermal vent-associated species to exhibit variable life histories and rates of molecular evolution due to the variability in vent longevity (Baker et al., 1995). By linking ecological variability with patterns of molecular substitution, we document a relationship between environmental stability and consumer evolution that may be relevant across ecosystems and biomes.

Methods

Overview

We tested the resource longevity hypothesis by examining the relationships among habitat type, life-history variation, and rates of molecular evolution in mussels (Mytilidae: Bathymodiolinae) and tubeworms (Siboglinidae) from the deep sea. We analyzed mitochondrial DNA substitution rates using Cytochrome c oxidase subunit 1 (CO1) sequence data from the literature. Using CO1, we first estimated gene trees and calculated root-to-tip branch lengths as proxies for the relative rates of molecular evolution within each clade. To analyze patterns in rate variation, we applied phylogenetic ANOVA (Garland et al., 1993) and the traitRate method (Levy Karin et al., 2017a, 2017b), which uses a model-based approach to estimate trait-dependent substitution rate variation. We explored potential mechanisms underlying relationships between habitat stability and evolutionary rates by compiling empirical animal body size data from the literature. Using univariate (mussels) and multivariate (tubeworms) models to estimate missing size data, we then examined how patterns in animal body size may covary with substitution rates among habitat types. Finally, we validated our results through multiple sensitivity analyses.

Study organisms

Bathymodiolin mussels (Mytilidae: Bathymodiolinae) and siboglinid tubeworms (Siboglinidae) are foundational groups in deep-sea chemosynthetic environments. With a few exceptions (Ockelmann & Dinesen, 2011; Rouse et al., 2004), both clades function as primary producers through symbiosis with chemoautotrophs. Bathymodiolinae likely used organic falls as stepping-stones to colonize deep-sea-reducing habitats from shallow ancestors (Distel et al., 2000; Samadi et al., 2007; Smith et al., 1989). The evolutionary history of Siboglinidae has been the subject of substantial debate (Glover et al., 2005, 2013; Li et al., 2019; Rouse et al., 2004, 2015; Taboada et al., 2015; Worsaae et al., 2016). Siboglinidae contains four lineages: Vestimentifera, which occurs primarily at vents and seeps; *Sclerolinum*, which is comprised of a single cosmopolitan species that occurs in sediments associated with organic falls as well as vents and seeps; *Osedax*, which are organic fall specialists; and Frenulata, which occurs in a variety of organic-rich sediments and is the sister clade to all other siboglinids.

Frenulata is the most speciose subfamily in Siboglinidae. It contains over 130 recognized species (Halanych, 2005) across a variety of environments, including deep-sea trenches, continental slopes, and estuaries (Karaseva et al., 2021). However, only a small minority of taxa have been reported from vents,

seeps, or organic falls, and even fewer are thought to occur exclusively in these habitats (Dando et al., 2008). Due to the lack of habitat specificity across Frenulata and the scarcity of ecological information available for this group, there is uncertainty about the degree to which frenulates reported from vents, seeps, or organic falls are truly specialized on those habitat types. We therefore excluded Frenulata from our analysis, and subsequent discussion of Siboglinidae refers to the *Osedax*-Vestimentifera-*Sclerolinum* clade.

Molecular data, estimates of genetic distance, and evolutionary timescales

To examine the relationship between habitat type and rates of molecular evolution, we estimated and compared substitution rates of mitochondrial DNA using published datasets of Cytochrome *c* oxidase subunit 1 (CO1) available on Genbank as of December 31, 2021. Mitochondrial CO1 is a standard barcode sequence for a wide range of taxa (Hebert et al., 2003). The CO1 protein product is involved in aerobic metabolism, which is a critical pathway in the electron transport chain and may be a direct target of selection for H₂S resistance in deep-sea chemosynthetic environments (McMullin et al., 2003). Our sample includes most Bathymodiolin mussel and siboglinid tubeworm species (except for Frenulata) that are habitat specialists and have CO1 sequences available from the literature (Supplementary Tables S1 and S2). As outgroups, we used *Modiolus* for mussels, and *Cirratulus*, *Sabella*, and *Sternaspis* for tubeworms (Supplementary Tables S1 and S2).

We aligned CO1 sequences for mussels, tubeworms, and their associated outgroups using the MAAFT online alignment server with automatic algorithm detection (Standley & Katoh, 2013). We visually inspected alignments for typical anomalies (e.g., poorly aligned indels) using Sequencher (Gene Codes Corporation, 2010) but did not detect any. We estimated CO1 gene trees for mussels and tubeworms using the maximum likelihood method implemented in IQ-Tree 2.1.1 (Minh et al., 2020; Nguyen et al., 2014). We selected an optimal partition model with the MFP + MERGE approach (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017), with each codon position (CP) defined as the unit for partitioning. We generated alternative tree inferences with and without topological constraints to assess whether estimated root-to-tip branch lengths were sensitive to the tree topology. For Bathymodiolinae, we applied a comprehensive topological constraint from Lorion et al. (2013), matching 53 taxa in the dataset. For Siboglinidae, we applied a constraint derived from a transcriptome-based phylogeny (Li et al., 2019) that matched 16 taxa (see Supplementary Material for constraint trees and IQ-TREE output files).

To further evaluate the uncertainty in our proxy for genetic distance, we applied a bootstrapping approach to estimate branch length variability in the ML phylogram inference. We generated 100 nonparametric bootstrap resamples of the molecular datasets and re-estimated the branch lengths using IQ-TREE as described above. We used the standard bootstrap option (“-b”) to generate full ML branch length estimates for each resampled dataset and then summarized the resulting variance across bootstrap resamples. In addition, we separately estimated pairwise distance matrices for CO1 using the *dist.dna* function in the *ape* R package (Paradis et al., 2004) with the F81 substitution model (Felsenstein, 1981). We then compared those estimates to pairwise distances estimated

from the constrained IQ-TREE phylograms to independently check the sensitivity of our branch length estimates to topological inference.

We generated evolutionary timescales (chronograms) by scaling our branch length estimates from IQ-TREE with *treePL* (Smith & O’Meara, 2012), using “congruification” (Eastman et al., 2013). This technique enabled us to apply the divergence time estimates from published chronograms to new phylogram estimates of expanded taxonomic scope. This approach automatically identifies all phylogenetically equivalent, corresponding nodes, constrains their ages exactly, and then applies a rate-smoothing algorithm across the remaining branches (see Supplementary code). For mussels, we used a time-scale reference from Lorion et al. (2013), and for tubeworms, we used a time-scale reference from Li et al. (2019), as with topology constraints. We used these chronograms for all downstream phylogenetic comparative analyses.

Habitat occupancy

We scored each lineage in the molecular dataset as occupying vents, seeps, organic falls, other, or a combination thereof based on occupancy records in the literature. We combined animal falls and wood falls into a single category because they are similarly ephemeral, many organic fall specialists occur across multiple types of falls, and taxa restricted to different organic substrates exhibit similar life-history traits (Génio et al., 2012). There are no known mussel or tubeworm kelp fall specialists, so this category is not represented in our analysis. Species reported from multiple habitat types were classified as polymorphic for habitat occupancy. Available methods cannot consider the evolution of polymorphic character data in this analytical context, so the final molecular data set was restricted to taxa specializing on particular habitat types. This approach assumes that habitat occupancy evolves as a discrete monomorphic trait.

Although reconstructing the history of habitat occupancy is not our primary focus, we visualized estimates of ancestral states across a summary of 1,000 stochastic character mapping simulations (Bollback, 2006) generated with *phytools* (Figure 1) (Revell, 2012). For each case, we optimized an “all-rates-different” (ARD) model that allows unequal transition rates. ARD models were also used in the *traitRate* approach below. We assigned a root state prior using the approach in FitzJohn et al. (2009) where each possible root state is weighted according to its probability of giving rise to the observed data, given the model parameters and the phylogenetic tree.

Animal size data

We examined patterns of life-history variation across habitat types by compiling animal body size data from the literature. For mussels, we collected each species’ maximum recorded shell length (Supplementary Table S1). Using the phylogenetic chronogram, we estimated missing shell size values (~30% of the dataset) under Brownian motion (BM) (Cavalli-Sforza & Edwards, 1967) and Ornstein-Uhlenbeck (OU) (Hansen, 1997) models of evolution in the R programming language (R Core Team, 2018) with the *Rphylopars* package (Goolsby et al., 2017). Estimates of missing mussel shell sizes were similar under BM and OU models ($R^2 \sim 0.63$). Δ AIC favored imputations under OU by ~180 units relative to BM, so subsequent analyses of mussel body size utilize estimates from OU (Supplementary Table S1).

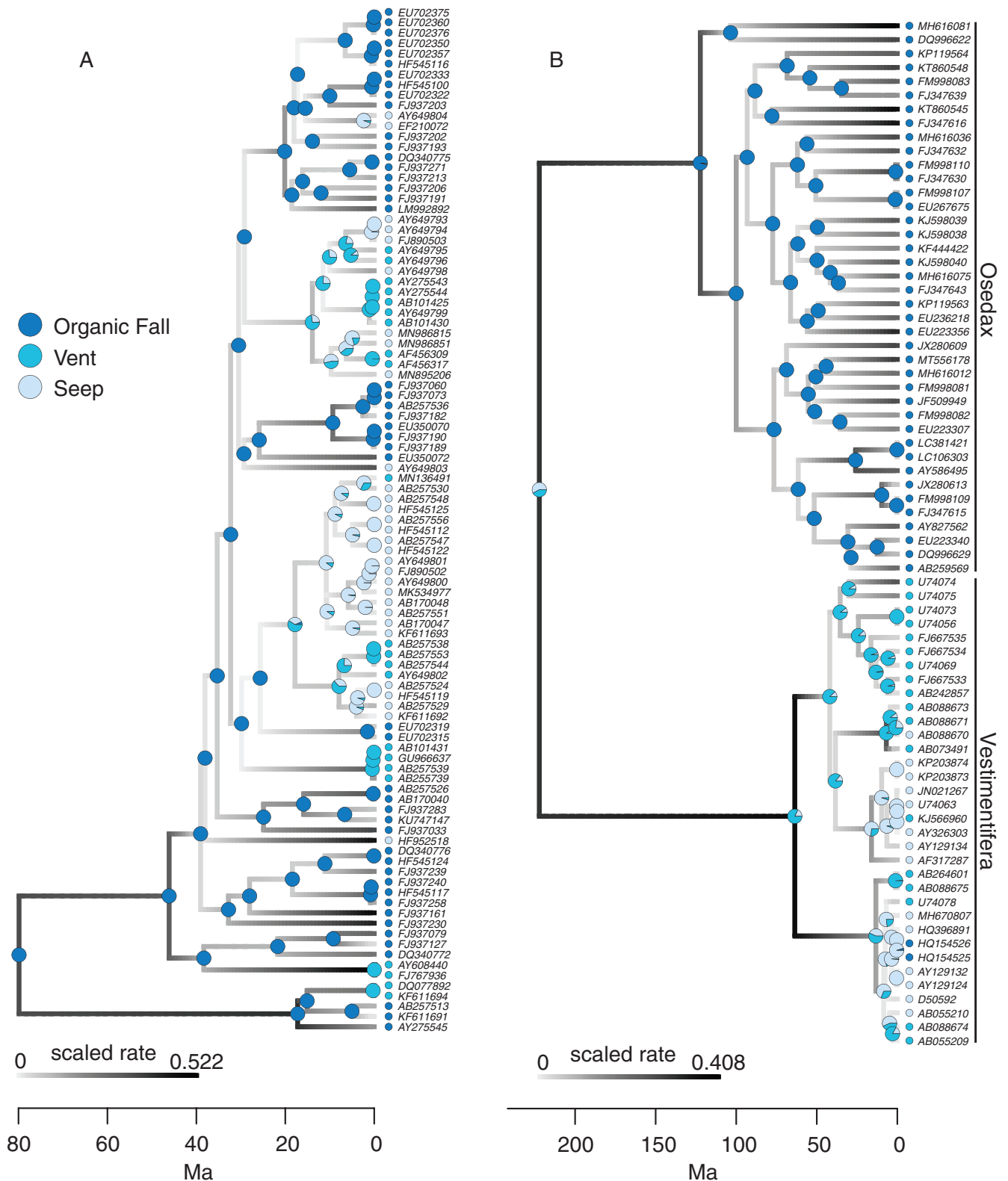


Figure 1. Variation in CO1 substitution rates across mussels (A) and tubeworms (B). Branch shading illustrates scaled branch length estimates, with the fastest rates shown in dark gray and the slowest in light gray. Pie charts at nodes indicate the posterior probability of being in a particular habitat state, applying stochastic character mapping (Bollback, 2006) under an ARD model (Revell, 2012). For both mussels (A) and tubeworms (B), estimated substitution rates are fastest (dark gray branches) in lineages from organic falls (dark blue markers) and slowest (light gray branches) in lineages from cold seeps (light blue markers).

For tubeworms, we sought to collect data on the most reasonable proxy for organism size. However, ongoing debate regarding anatomical homologies across Siboglinidae (Bright et al., 2013; Rouse, 2001; Southward et al., 2005; Worsaae et al., 2016) coupled with extremely limited data availability complicates comparative analyses. To consider some anatomical data from this group, we compiled species' maximum reported tube length from the literature (Supplementary Table S2). Due to limited data availability, analyses of tube length are preliminary and likely underestimate the sizes of large species. Large tubes may be more likely to break during collection, and in some cases, length data are only available from tube fragments. In addition, the relationship between tube length and body length is likely nonlinear because while some species occupy their entire tubes, others only occupy a portion, and yet others extend beyond the length of their tubes (Fisher et al., 1997; Rouse et al., 2018). Nevertheless, we suggest the tube length data summarized herein represent the best available proxy for tubeworm size.

Due to substantial gaps in available tubeworm size data (~70% of the dataset), we reconstructed missing values using a multivariate approach that leverages evolutionary covariances among multiple traits to more accurately estimate missing values. For this approach, we compiled available data from the literature for maximum tentacle length and the length of the anterior body segment just below the tentacles, which corresponds to the vestimentum in Vestimentifera and the upper trunk in *Osedax* (Supplementary Table S2; Worsaae et al., 2016). We then compared estimates of missing tube length values under multivariate BM (mvBM) and multivariate OU (mvOU) stochastic process models using mvMORPH (Clavel et al., 2015). Δ AIC favored imputations under mvOU by ~31 units relative to mvBM, so we used these estimates for downstream analyses (Supplementary Table S2). Notably, univariate imputations (only considering empirical tube size data) under BM were very similar to those under mvOU ($R^2 > 0.9$), suggesting a strong phylogenetic signal underlying tubeworm body size.

Comparative analysis of substitution rates

While there are sophisticated models for evaluating the evolutionary covariance among continuous multivariate traits and substitution rates (Lartillot & Delsuc, 2012; Lartillot & Poujol, 2011), similarly flexible general models are not yet available for multinomial discrete traits (though see Hu et al. (2019) and Mayrose and Otto (2010); Levy Karin et al. (2017b) for the binary case). Without a model-based approach for multinomial characters, substitution rates (e.g., “tip-rates”) can be estimated from molecular clock models and regressed against a discrete factor while accounting for potential phylogenetic nonindependence (e.g., Yonezawa et al., 2016). Alternatively, root-to-tip branch lengths are a simple metric representing the sum of path lengths from the root to each tip in a phylogram and have been used to estimate the amount of molecular evolution since the most recent common ancestor of a clade (Asar et al., 2023; Bromham et al., 2002; Omland, 1997). While root-to-tip branch lengths can be sensitive to node-density artifacts (Venditti et al., 2006), they outperformed an independent sister-pairs approach in recent simulations of molecular and morphological branch rates (Asar et al., 2023).

Here, we tested the resource longevity hypothesis by first investigating patterns of variation in root-to-tip path lengths

using an ANOVA approach. Then, we applied an integrated, model-based approach (“traitRate”; Mayrose & Otto, 2010; Levy Karin et al., 2017a) that estimates a mixture of local molecular clocks and the evolution of an associated binary character. Unlike branch length or tip rates approaches, traitRate leverages information about molecular clock variation across the entire phylogeny to test if substitution rates are related to character state transitions. By examining congruence among multiple approaches, we reduce the likelihood of coincidence, error, or analytical bias yielding spurious conclusions.

Analysis of root-to-tip path lengths

All analyses were conducted in the R programming language (R Core Team, 2018), predominantly using the *phylolm* (Tung Ho & Ané, 2014), *Rphylopars* (Goolsby et al., 2017), and *phytools* (Revell, 2012) R packages, unless otherwise noted. We checked for the presence of a node-density effect in root-to-tip path lengths by fitting simple linear models; ‘total path length’ ~ ‘count of nodes along a path’. The slope was near zero for both mussels and tubeworms (−0.003 and 0.01, respectively), suggesting node density did not have substantial effects. We then applied the Phylogenetic ANOVA method in *phytools* (Revell, 2012) with post hoc tests described by Garland et al., (1993) to assess differences in the mean of the natural log of root-to-tip path lengths across habitat types. We used 10,000 simulations to determine statistical significance and applied the Benjamini-Hochberg correction (Benjamini & Hochberg, 1995) for multiple hypothesis testing at an alpha threshold of 0.05.

In addition, we used phylogenetic generalized least squares (pGLS) to assess the relationships among relative rates of molecular evolution and habitat type, animal size, and their interaction terms. We included the natural log of the number of nodes along each root-to-tip path to account for potential node-density effects (Venditti et al., 2006), though, as noted above, we did not observe any. For pGLS models, we evaluated the impact of a residual correlation structure approximated by a BM or OU process (Harmon and Harmon, 2018). This procedure generated four alternative models under each assumption of phylogenetic covariance, which we ranked with AIC scores corrected for small sample sizes (Supplementary Tables S3 and S4) (Burnham & Anderson, 2002). We computed a coefficient of determination, R^2_{pred} , to assess the overall amount of variance explained by the models (Supplementary Tables S3 and S4) (Ives, 2018).

Finally, we evaluated the sensitivity of body size analyses by rerunning all models without imputed size values. We estimated bootstrapped 95% confidence intervals of model slopes under pGLS and under a simple implementation of an independent sister-pairs approach in R (see “analyze_sister_pairs” in “functions.R”). Our sister-pairs approach assesses trait differences between pairs of closely related species using linear regression and bootstrapped confidence intervals to evaluate evolutionary associations while accounting for phylogenetic nonindependence.

Integrated model-based analysis of molecular and habitat evolution

To the best of our knowledge, there is not yet an integrated framework that can estimate the evolution of a multinomial discrete trait (e.g., vent, seep, and organic fall) and its co-evolution with molecular substitution rates. However, the traitRate

method can assess a binary case where a discrete character evolves between one of two states (Levy Karin et al., 2017b; Mayrose & Otto, 2010). traitRate estimates the evolutionary history of a discrete binary trait using stochastic mapping (Huelsenbeck et al., 2003) along with a scaled tree and two clocks reflecting the rate of molecular evolution in each state. It uses a joint-likelihood framework to compare models that assume independent or dependent rates of molecular evolution and also computes site-specific Bayes factors for a given sequence alignment under an HKY model (Hasegawa et al., 1985). Because this framework is limited to binary comparisons, we compared alternative models that evaluated each pairwise combination of habitat types (vent vs. seep, vent vs. organic fall, and seep vs. organic fall). Within each clade, we subset the relevant lineages from the corresponding phylogenetic framework and alignments described above. We ran the analysis using the TraitRateProp web server (Levy Karin et al., 2017a) with default parameters to estimate the relative rate of molecular evolution for each comparison. We also estimated site-specific Bayes factors across each paired comparison to assess patterns of habitat association among the first, second, and third CPs across the CO1 sequence alignments. Since mutations in nonsynonymous sites (first and second CPs) often alter amino acid products, they are commonly thought to be more affected by selection than synonymous sites (third CPs). We therefore estimated proportions of significant (BF > 3) nonsynonymous and synonymous sites, averaged across each paired comparison.

Results

Dataset and branch lengths

Molecular datasets filtered for lineages with unique habitat affiliations contained 99 mussel (663 bp) and 74 tubeworm (1,524 bp) ingroup CO1 sequences (Supplementary Tables S1 and S2). The mussel dataset contained 47 organic fall, 30 seep, and 22 vent sequences (Figure 1A). The tubeworm dataset contained 42 organic fall, 14 seep, and 18 vent sequences (Figure 1B). For constrained and unconstrained topologies of both clades, the mean root-to-tip path lengths from bootstrapped and empirical datasets had correlation coefficients >0.98, indicating that stochastic error in estimates of genetic distance had negligible effects on branch length estimates. Pairwise genetic distances estimated under an F81 substitution model (no topology) were similar to those estimated by IQ-TREE (mussels $R^2 = 0.76$, tubeworms $R^2 = 0.91$), suggesting topology does not strongly affect estimates of genetic distance. Therefore, our sample of CO1 sequences appears sufficient to generate stable estimates of branch lengths. IQ-TREE estimated that each CP was best modeled with a unique substitution model for both mussels and tubeworms (Supplementary Table S5).

Comparing molecular substitution rates across habitat types

Phylogenetic ANOVA results were consistent with our prediction that substitution rates differ among habitat types. When comparing root-to-tip path lengths estimated under a topological constraint, mussels from organic falls appear to have faster substitution than species from vents and seeps after correcting for multiple hypothesis tests (Figure 2A: $t = 5.57$, $p = 0.02$; $t = 7.89$, $p = 0.01$, respectively). Organic fall tubeworms also appear to exhibit faster substitution

than vent and seep tubeworms, but only in analyses using root-to-tip path lengths inferred without a topological constraint (Figure 2D: $t = 12.54$, $p = 0.05$; $t = 12.85$, $p = 0.04$, respectively). Phylogenetic ANOVA of mussel branch lengths estimated without a topological constraint (Figure 2B) and tubeworm branch lengths with a topological constraint (Figure 2C) do not differ significantly across habitat types at an alpha threshold of 0.05.

Phylogenetic ANOVA was sensitive to topological constraint due to slight differences in rooting position between constrained and unconstrained analyses, which impact the relative branch lengths for clades subtending the most recent common ancestor despite stable estimates of pairwise genetic distances. In addition, the presence/absence of topological constraints alters the relative variability of branch length estimates within trees. In mussels, root-to-tip branch lengths estimated without a topological constraint have increased variability (SD ~1.3x), potentially obscuring a signal of differentiation by habitat type after considering phylogeny (Figure 2B). Despite noise derived from uncertainty in the placement of the root, every statistically significant Phylogenetic ANOVA test statistic was consistent with predictions from the resource longevity hypothesis (Figure 2).

Further, every pairwise comparison using an integrated model of molecular and habitat evolution in traitRate (Levy Karin et al., 2017b) detected significant associations between the rate of molecular evolution and habitat affinity (Table 1). In all cases, the estimated relative rates between habitat states were consistent with predictions from the resource longevity hypothesis (organic fall > vent > seep). All tests were significant at an alpha threshold of 0.05 after controlling for the false discovery rate (Benjamini & Hochberg, 1995) and the family wise error rate (Holm, 1979). On average, about 28% (17%–39%) of the nucleotide sites in each comparison have substitution rates associated with habitat type. Among sites with moderate support (Bayes Factor > 3; Jeffreys, 1961), ~85% of sites in both mussel and tubeworm analyses reflect putatively neutral synonymous third CPs, whereas ~15% of sites are located in first or second positions (Supplementary Figure S1). Overall, analyses comparing substitution rates across habitat types using the traitRate approach strongly support the resource longevity hypothesis.

Phylogenetic generalized linear models

For both mussels and tubeworms, the model with the fewest parameters had the highest relative AICc weight (64% and 42%, respectively) and only included habitat type as a factor predictor of mitochondrial substitution rate variation under a BM evolutionary model (Supplementary Tables S3 and S4). The top-ranked models for mussels and tubeworms had high predictive power (R^2_{pred} : 0.65, 0.72, respectively), though the lowest-ranked models also performed well (R^2_{pred} : 0.60, 0.65, respectively). Contrary to expectation, animal size was not a significant predictor in the top-ranked models. To examine this pattern in greater detail, we generated additional pGLS models that directly compared our proxy of substitution rate and animal size (Figure 3). In every case, the apparent negative relationship between substitution rate and animal size observed in the empirical data disappears in analyses that account for phylogenetic nonindependence (Figure 3). Sensitivity analyses that excluded imputed size values yielded slopes (β) that were not significantly different from zero (95% bootstrapped confidence intervals); mussels: pGLS β

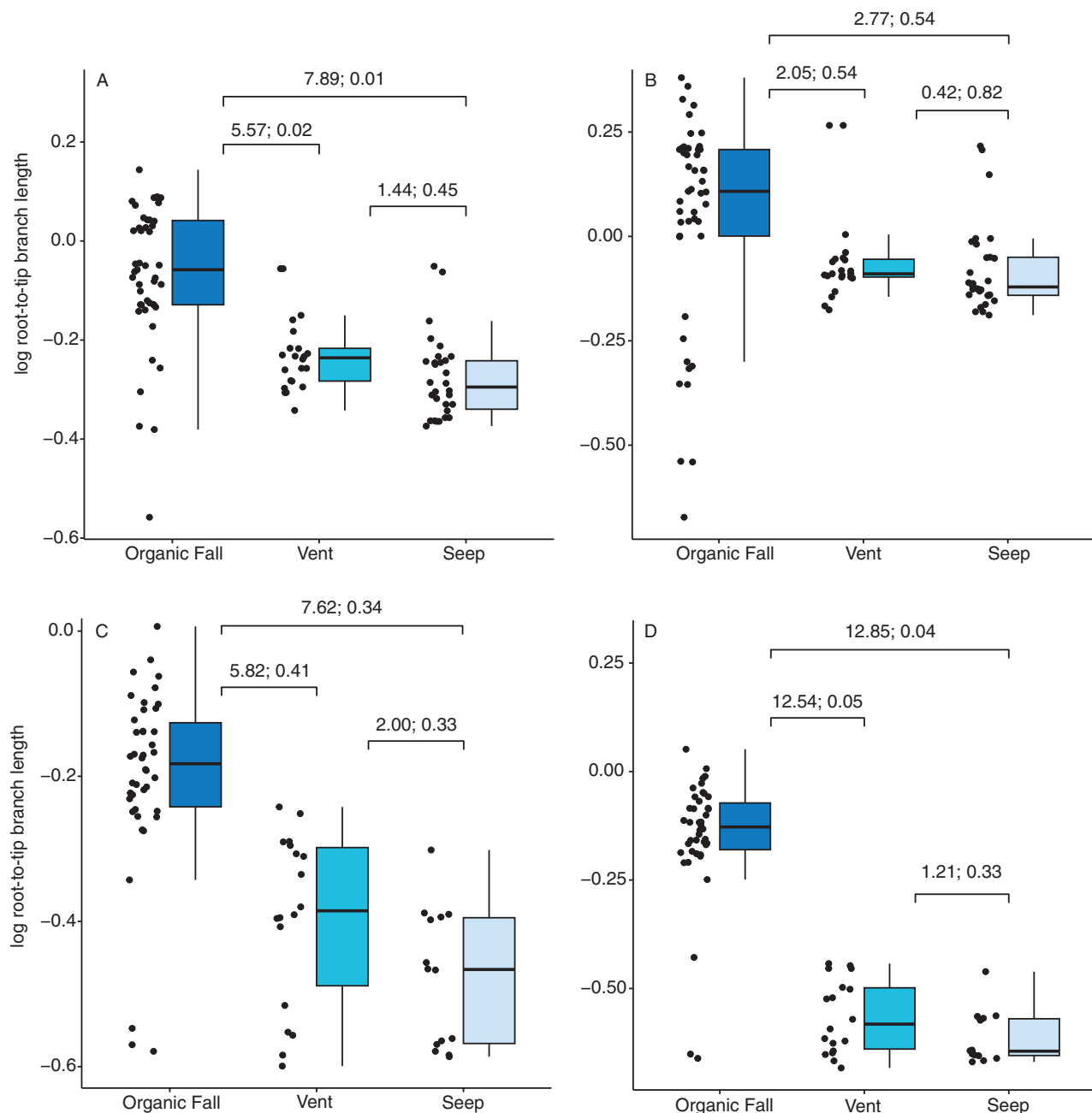


Figure 2. Variation in substitution rates among habitat types for mussels (A, B) and tubeworms (C, D). Plots on the left (A, C) depict root-to-tip branch lengths estimated under a topological constraint, whereas plots on the right (B, D) depict branch length estimates from unconstrained gene trees. Results from Phylogenetic ANOVA (Harmon et al., 2008; Revell, 2012) and subsequent post hoc tests (Garland et al., 1993) are depicted for each comparison as t -value; p -value. All four comparisons indicate that root-to-tip path lengths are longest in organic fall taxa and shortest in seep taxa. Two analyses (A, D) show statistically significant differences among habitat types after accounting for multiple tests (Benjamini & Hochberg, 1995). These patterns are recapitulated in the model-based approach estimated with traitRate (Table 1; Supplementary Figure S1).

$[-8e-04, 8e-04]$, sister-pairs β $[-2.829, 12.783]$; tubeworms: pGLS β $[-0.012, 0.012]$, sister-pairs β $[-4.830, 13.483]$. Thus, differences in animal size across habitat types (Figure 4) appear unrelated to covarying patterns of substitution rates (Figure 3).

Discussion

Our resource longevity hypothesis proposes that in environments structured by strong bottom-up control, where

resources occur as ephemeral patches, patch longevity may constrain axes of life-history variation, leading to an inverse relationship between resource longevity and rates of molecular evolution. Multiple independent analyses of mitochondrial CO1 in mussels and tubeworms failed to reject the resource longevity hypothesis (Figure 5A). Organic fall taxa have longer root-to-tip path lengths (t -values in Figure 2A and D) and significantly faster relative substitution rates when evaluated in pairwise tests under the traitRate model (~ 3.5 – $4\times$ faster than vent or seep taxa; Table 1). Likewise, vent taxa show

Table 1. Summary of traitRate model comparisons.

Taxon	Substrate 1	Substrate 2	D statistic	DF	<i>p</i>	Prop	Relative rate
Siboglinidae	Vent	Organic Fall	103.6	2	3.2×10^{-23}	0.29	0.25
Siboglinidae	Vent	Seep	7.96	2	1.9×10^{-2}	0.24	3.50
Siboglinidae	Seep	Organic Fall	75.2	2	4.7×10^{-17}	0.32	0.25
Bathymodiolinae	Vent	Organic Fall	17.48	2	1.6×10^{-4}	0.27	0.25
Bathymodiolinae	Vent	Seep	347.96	2	2.8×10^{-76}	0.39	4.00
Bathymodiolinae	Seep	Organic Fall	34.6	2	3.1×10^{-8}	0.26	0.28

Note. traitRate compares alternative models in which the rate of sequence evolution either depends on or is independent of a binary character state. We partitioned a three-state habitat preference into three pairwise comparisons. For all comparisons, *p*-values reject the null hypothesis that the dependent model (i.e., substitution rates depend on habitat state) is equivalent to the independent model. We report uncorrected *p*-values, as all tests remain significant at an alpha threshold of 0.05 after controlling for the false discovery rate (Benjamini & Hochberg, 1995) or the family wise error rate (Holm, 1979). The “prop” column shows the estimated proportion of sites in each alignment whose individual rates are associated with evolutionary transitions between habitat states. The relative rate reflects the overall rate of sequence evolution associated with Substrate 1 relative to Substrate 2. Values greater than 1 indicate that taxa associated with Substrate 1 have proportionally faster sequence evolution than taxa associated with Substrate 2 and vice versa. For example, in the first comparison, the relative rate of 0.25 means the overall rate of sequence evolution is four times faster in tubeworms from organic falls than from hydrothermal vents. Every comparison produced relative rate estimates that are consistent with predictions from the resource longevity hypothesis.

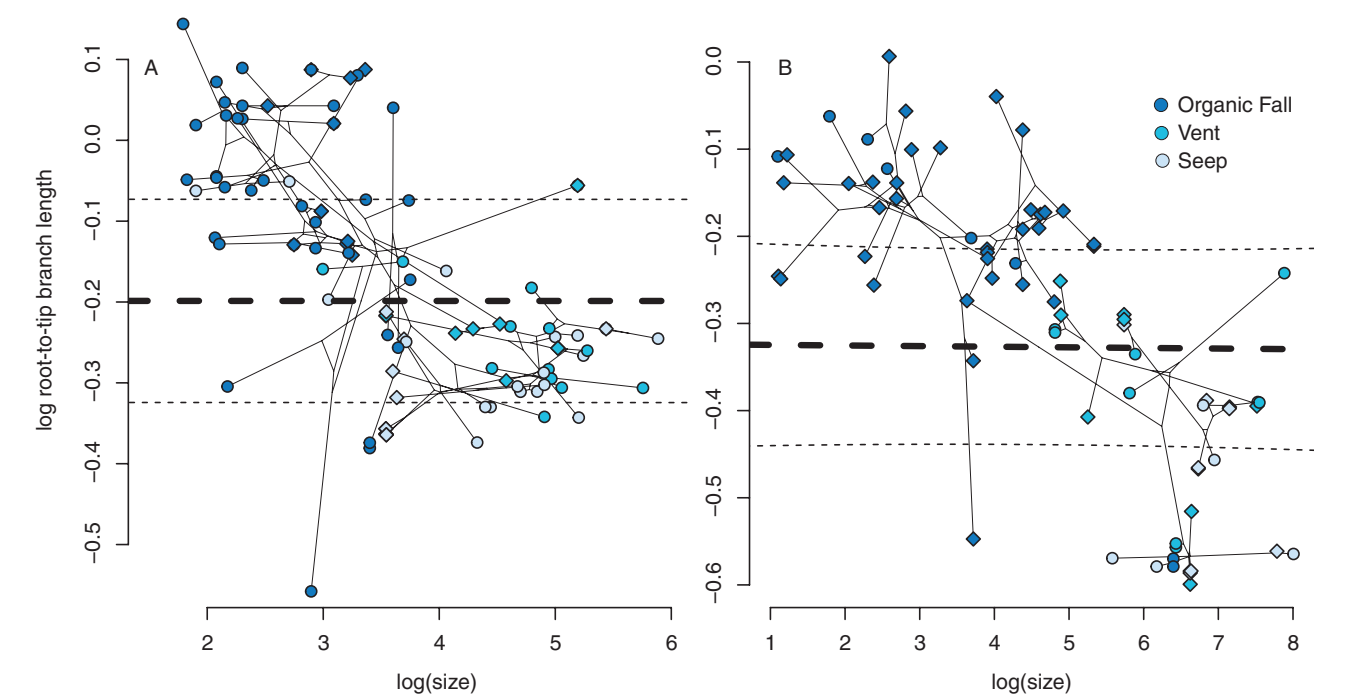


Figure 3. Phylogenetic correlations between substitution rate and animal size for mussels (A) and tubeworms (B). Solid lines in each plot illustrate phylogenetic branches among taxa. In mussels (A), multiple branches overlap across the size range, demonstrating multiple evolutionary transitions between small and large shell sizes. In tubeworms (B), the single branch connecting small species on the left to larger species on the right indicates that small tubeworms form a single monophyletic group. Circular markers represent measurements from the literature, while diamond markers denote estimated animal sizes. Colors correspond to habitat association. Dashed regression lines and associated 90% CIs from phylogenetic generalized least squares regression (Tung Ho & Ané, 2014) illustrate the relationships between animal size and substitution rate after accounting for phylogeny, assuming a BM model for residual variation. The ~0 slope in both mussels and tubeworms indicates that accounting for phylogenetic nonindependence eliminates apparent correlations between animal size and substitution rate suggested by the empirical data. Patterns were similar when estimated under constrained (depicted here) and unconstrained topologies (not shown).

intermediate root-to-tip path lengths and are also ~3.5–4× faster than seep taxa under the traitRate model (Table 1). The small size of our genetic datasets affords limited statistical power to detect subtle effects of habitat type on evolutionary rate. Any single analysis would likely only detect a trend if the signal were strong. Therefore, the congruence across distinct analytical approaches—and disparate invertebrate clades—lends robust support for a relationship between habitat type and evolutionary rate.

Site-specific analyses with traitRate revealed that most individual nucleotide sites with rates of molecular evolution strongly associated with habitat occupancy are synonymous third codon positions, suggesting a predominantly neutral process driving these associations. In a few cases, nonsynonymous sites are strongly associated with habitat occupancy (BF > 10), implying robust associations that may impact protein phenotype (e.g., positions 187 and 247 in Supplementary Figure S1A [mussels] and 325 in Supplementary Figure S1B

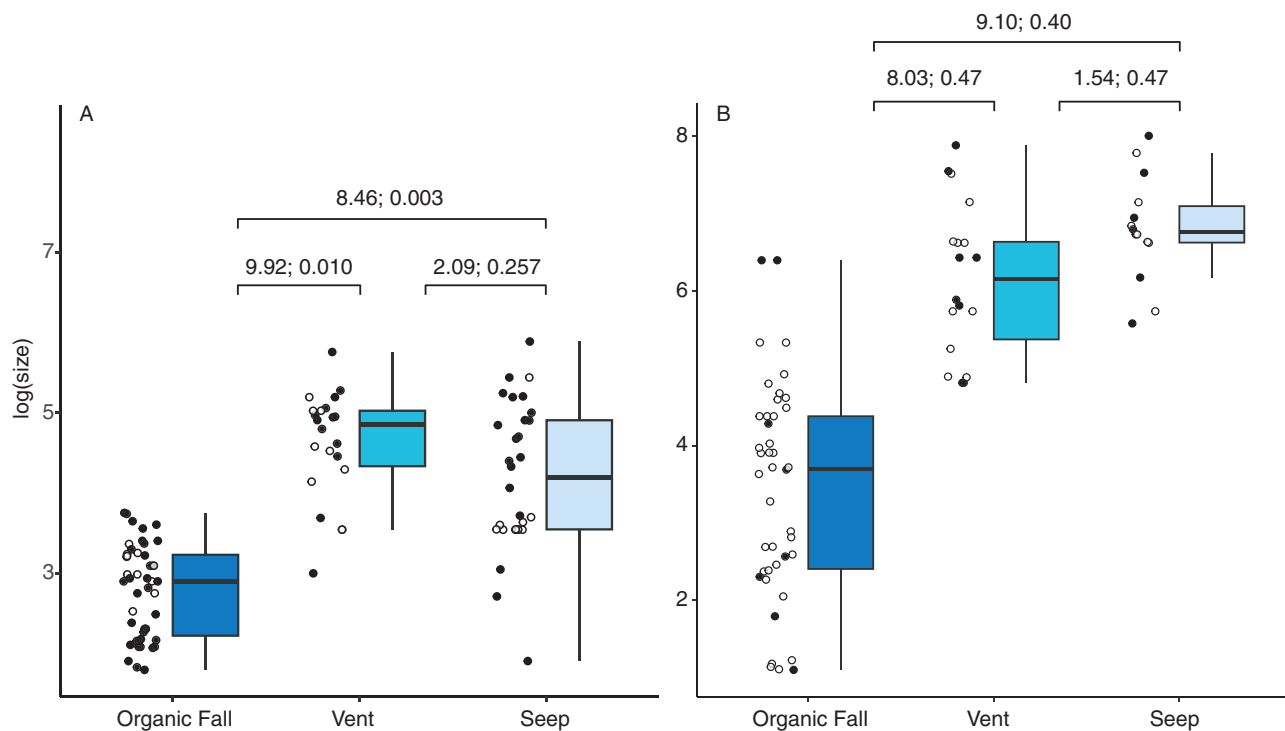


Figure 4. Variation in animal sizes among habitat types for mussels (A) and tubeworms (B). Organic Fall mussels have significantly smaller shell sizes than vent or seep mussels (A), while tubeworm tube sizes do not differ significantly among habitat types after accounting for phylogeny (B). Results from Phylogenetic ANOVA (Harmon et al., 2008; Revell, 2012) and subsequent post hoc tests (Garland et al., 1993) are depicted for each comparison as t -value; p -value. Black markers represent log size data compiled from the literature, while white markers depict estimated sizes derived from BM (mussels) and mvOU (tubeworms) imputation. Boxplots summarize completed datasets that include estimated sizes.

[tubeworms]). Notably, in tubeworms, sites 325 and 1048 are implicated in multiple pairwise comparisons (Supplementary Figure S1B). These sites represent candidate polymorphisms for future investigations of the functional implications of CO1 evolution across deep-sea environments.

Habitat occupancy in tubeworms is strongly clustered phylogenetically (Figure 1), with few apparent transitions between habitat states (after necessarily excluding species that are polymorphic for habitat occupancy). Phylogenetic signal in habitat occupancy thus reduces the effective sample size, challenging efforts to distinguish between the effects of habitat and phylogeny on tubeworm substitution rates in Phylogenetic ANOVA. This simplified approach is sensitive to rooting of the estimated gene trees because measures of root-to-tip branch length assume that the root position is correctly inferred. Nevertheless, the ANOVA framework allows us to evaluate differences among all three habitat states simultaneously, and every statistically significant comparison indicates test statistics consistent with the resource longevity hypothesis (Figures 2 and 5). Importantly, since the traitRate approach does not rely on root-to-tip branch lengths, it is not affected by the caveats associated with Phylogenetic ANOVA or estimates of root-to-tip branch lengths.

Patterns of mussel and tubeworm size variation are also consistent with the resource longevity hypothesis. Mussel shell sizes differ among habitat types, with the smallest mussels occurring at organic falls, intermediate at vents, and largest at seeps, a pattern that holds after accounting for phylogeny (Figure 4; Lorion et al., 2013). Organic fall mussels also exhibit pedomorphic traits in shell microstructure relative to species at vents and seeps, suggesting a repeated pattern of

mussel life-history acceleration associated with organic fall specialization (Génio et al., 2012). Even though shell sizes differ across habitat types, these differences do not significantly predict CO1 substitution rates after accounting for phylogeny (Figure 3). Despite substantial missing data on siboglinid tube length, our analysis across habitat types generated similar patterns to those in mussels. Sampling and analytical bias in tubeworms may have led us to underestimate the sizes of large species, so our analyses of tubeworm tube length are necessarily preliminary. Given the strong phylogenetic signal underlying tubeworm body size evolution, the accuracy of our estimates depends on the accuracy of the underlying phylogenetic framework (Li et al., 2019).

The decoupling between animal size and substitution rates suggested by our results appears consistent with the life histories of Siboglinidae. For example, vent tubeworms along the East Pacific Rise exhibit some of the fastest growth rates reported for any marine invertebrate (Lutz et al., 1994), while closely related species from seeps in the Gulf of Mexico achieve similar tube lengths but have lifespans that can exceed three centuries (Durkin et al., 2017). Organic fall tubeworms in the subfamily Osedax exhibit life-history traits unique within Siboglinidae, including a reproductive strategy wherein females maintain harems of microscopic males within their tubes. Osedax also contains heterotrophic, rather than autotrophic, symbionts. These traits in Osedax coincide with organic fall specialization, and it is unclear how they may impact the relationships between animal size, habitat type, and rates of molecular evolution in Siboglinidae. However, the fact that organic fall taxa are generally smaller does not appear to explain their overall faster rates of molecular evolution. Given

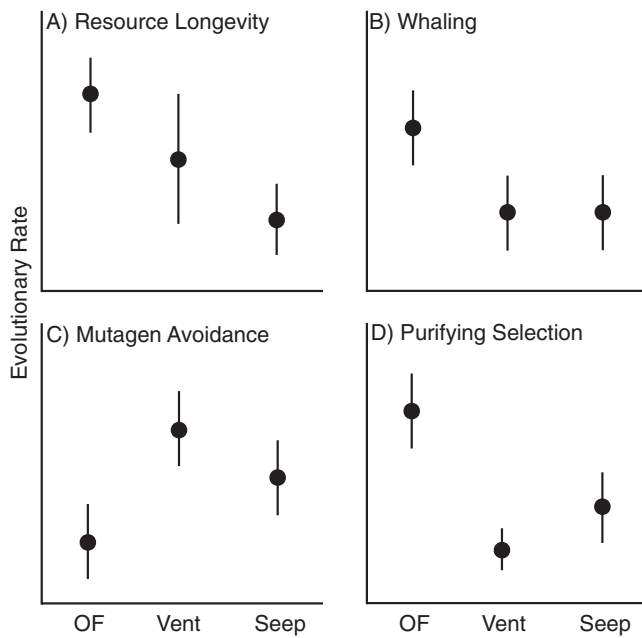


Figure 5. Predicted relationships between habitat type and rates of molecular evolution according to relevant hypotheses. The resource longevity hypothesis (A) proposes that habitats that persist for contrasting lengths of time differentially constrain consumers' life-history strategies, leading to an inverse relationship between habitat longevity and consumers' rates of molecular evolution. This hypothesis predicts the fastest evolutionary rates in organic falls, which are ephemeral; slowest rates in seeps, which are comparatively stable; and intermediate but variable rates at vents, which have variable longevities. The whaling hypothesis (B) predicts that bottlenecks in whale populations from commercial whaling caused bottlenecks in populations of whale fall specialist consumers (Smith et al., 2019). This hypothesis predicts faster evolutionary rates at organic falls due to genetic drift in whale fall populations, in contrast to vent and seep taxa that were unaffected by the whaling industry. The mutagen avoidance hypothesis (C) argues that because high environmental toxicity should increase mutation rates, specialist consumers in highly toxic environments may exhibit compensatory r-selection to avoid accumulating mutations over individuals' lifespans (e.g., mutations to germline or DNA repair machinery; Dixon et al., 2000). This hypothesis predicts reduced generation lengths and therefore faster rates of molecular evolution in highly toxic environments (vents) than in less toxic ones (organic falls). Purifying selection (D) filters out mutations, thus decelerating rates of molecular evolution in areas of the genome under selection. Since CO1 is vulnerable to sulfide toxicity (McMullin et al., 2007), one might expect the strength of purifying selection on this gene to vary between environments with different sulfide levels. This hypothesis predicts the slowest CO1 evolution in vents, where high sulfide concentrations should impose strong purifying selection, and faster CO1 evolution at organic falls and seeps, which have variable but generally lower sulfide concentrations and should therefore impose weaker purifying selection.

this pattern, all the available evidence is consistent with an outsized role for habitat affinity as a driver of molecular rate variation, with little apparent relationship with animal sizes.

Organic fall, vent, and seep habitats persist over different timescales, ranging from just a few years to millennia, and have long been hypothesized to impose different constraints on the evolution of consumers' life-history strategies (Craddock et al., 1995; Génio et al., 2012; Lutz et al., 1994; von Cosel & Olu, 1998). The long-term stability of cold seep environments has been invoked to explain the diversity of seep fauna (Sibuet & Olu, 1998), the large size (up to 360 mm) of the seep mussel *Bathymodiolus boomerang* (von Cosel & Olu,

1998), and lifespan estimates for seep tubeworms that exceed 250 years in *Lamellibrachia luymeri* (Bergquist et al., 2000) and 300 years in *Escarpiella laminata* (Durkin et al., 2017). In addition, McMullin et al. (2003) found that a small sample of vent-associated vestimentiferans have faster rates of molecular evolution in CO1 compared to seep-associated lamellibrachids. However, this pattern was not strongly recapitulated for their sample of escarpids, a group of primarily seep-associated tubeworms (McMullin et al., 2003). Halanych et al. (1998) observed an apparent deceleration in CO1 substitution rates in Vestimentiferan tubeworms and lower genetic diversity than expected relative to other annelids. To our knowledge, no subsequent studies have directly revisited the hypothesis that patterns of molecular rate variation in deep-sea invertebrates may reflect habitat affinities.

Deep-sea research is constrained by substantial financial and logistical obstacles to collecting and observing specimens. Some species in this analysis are only known from a single locality, so additional specimen collection efforts may reveal individuals of those species at multiple habitat types, which would disqualify them from our analysis. In addition, excluding species with polymorphic habitat associations is a potential source of analytical bias (Wiens, 1999). While our ancestral state reconstructions are broadly consistent with prior work indicating organic falls as ancestral for mussels (Lorion et al., 2013) and vents as ancestral for the tubeworm subfamily Vestimentifera (McCowan et al., 2023), additional work is needed to comprehensively evaluate ancestral habitat evolution across Siboglinidae. Our analyses also assume that effective population sizes are similar across habitat types, an assumption that could be tested explicitly as additional population data become available in the future. Phylogenomic or population genomic inference of more complex demographic processes or selection will require substantially more investment in specimen collection from deep-sea environments. As additional genetic data become available in the future, more parameter-rich techniques like Bayesian analyses of tip rates may elucidate more nuanced patterns of molecular evolution.

As summarized in Vrijenhoek (2013), some researchers have hypothesized that exposure to hostile, mutagenic conditions at hydrothermal vents might directly influence mutation rates, thereby leading to a relationship between habitat affinity and rates of DNA damage (Dixon et al., 2000; Pruski & Dixon, 2003). This hypothesis predicts an association between patterns of molecular evolution and habitat occupancy, perhaps in DNA repair machinery or susceptible regions of the genome. However, Dixon et al. (2000) suggested overall compensatory r-selection (Wilson & MacArthur, 1967) at vents could favor survivorship of short-lived fast-growing tubeworms, in contrast to seep specialists, which grow slowly and generally experience lower concentrations of sulfides and heavy metals than those produced at vents (McMullin et al., 2007; Scott & Fisher, 1995). The toxicity hypothesis predicts that the whole genomes of these organisms should be affected by selection for life histories compatible with an environment toxic to DNA.

In general, the hypothesis of r-selection for mutagen avoidance in the deep sea predicts that the fastest rates of molecular evolution should be observed at hydrothermal vents (Figure 5C), where DNA toxicity due to sulfide and heavy metals is generally expected to be strongest relative to organic falls and cold seeps (McMullin et al., 2007; Scott & Fisher, 1995). Our analyses of CO1 show the fastest rates at organic falls for both mussels and tubeworms and are, therefore, inconsistent with

the mutagen avoidance hypothesis (Figure 2). Nevertheless, examining other genes, such as those directly involved in DNA repair or with differing susceptibility to sulfide toxicity, could provide a more direct and comprehensive test of the mutagen avoidance hypothesis. Alternatively, one might also expect strong purifying selection for sulfide resistance at vents, decelerating molecular evolution in genes related to sulfide adaptation or vulnerability (Figure 5D). Selective processes may be stronger in some environments, such as vents, whereas neutral processes may be stronger in others, like organic falls. Future work modeling the strength of selection across multiple genes could elucidate the relative contributions of selective and neutral processes in driving substitution rate variation across deep-sea environments. The resource longevity hypothesis does not preclude a role of selection but sets up an alternative null hypothesis for contextualizing the effects of habitat affinity on patterns of genome evolution within mussels and tubeworms.

In addition to the inherently ephemeral nature of organic falls, accelerated substitution rates in organic fall consumers could also result from anthropogenic effects on whale populations. Commercial whaling in the 20th century dramatically reduced whale population sizes and the average size of individuals within populations (Roman & Palumbi, 2003; Smith et al., 2019). This may have reduced the availability of whale fall substrate, which may have led to population bottlenecks in whale fall consumers (Figure 5B). However, an examination of several *Osedax* species failed to detect signs of recent bottlenecks (Amon et al., 2014). Amon et al. (2014) emphasized that their results stem from a limited analysis of a few species but also pointed out that whalers stripped whale blubber to extract its oil and left behind the carcasses. The discarded bones may have sunk to the seafloor and continued to provide habitat for whale fall specialists despite shrinking whale populations. Thus, while we cannot exclude the possibility that elevated substitution rates among organic fall mussels and tubeworms stem from whaling-induced bottlenecks, we are not aware of any genetic data supporting this hypothesis.

Conclusions

Understanding how an organism's environment affects patterns of evolution is a fundamental theme in ecology and evolutionary biology. Here, we identify evidence of a link between rates of molecular evolution and habitat association in two clades of deep-sea invertebrates: mussels and tubeworms. Within both phyla, species from organic falls—an ephemeral habitat—exhibit the fastest rates of CO1 substitution, while species from cold seeps—which are relatively stable—exhibit the slowest. In both groups, the smallest species occur at organic falls and the largest at vents and seeps. However, after considering phylogeny, animal size did not confound differences in substitution rates among habitat types. These results suggest a strong relationship between habitat association and mussel and tubeworm CO1 substitution rates.

Overall, our results are consistent with a resource longevity hypothesis, which, depending on environmental context, predicts an inverse relationship between resource longevity and rates of molecular evolution. Analysis of CO1 is especially relevant in deep-sea reducing environments due to CO1's susceptibility to sulfide toxicity (McMullin et al., 2007). However, since the resource longevity hypothesis describes a primarily neutral process, we predict similar trends in neutral

markers of other genes in these clades. Despite the limited availability of genetic data, deep-sea mussels and tubeworms provide a model for examining associations between environmental stability and life-history evolution. Broadly, the patterns reported herein may exemplify a general relationship between life-history evolution and environmental variability.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All data and software code generated for the present manuscript, including imputed data, are available at the GitHub repository: https://github.com/jakeberv/deep_sea_evolution and archived at Zenodo <https://doi.org/10.5281/zenodo.14927706>

Author contributions

A.K.W.: Conceptualization, Investigation, Resources, Data Curation, Methodology, Writing—Original Draft, Writing—Review & Editing, Visualization, Project Administration, Funding Acquisition. J.S.B.: Methodology, Software, Validation, Formal Analysis, Investigation, Writing—Review & Editing, Visualization, Funding Acquisition.

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