

# Oxygen, ecology, and the Cambrian radiation of animals

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**The Proterozoic-Cambrian transition records the appearance of essentially all animal body plans (phyla), yet to date no single hypothesis adequately explains both the timing of the event and the evident increase in diversity and disparity. Ecological triggers focused on escalatory predator–prey “arms races” can explain the evolutionary pattern but not its timing, whereas environmental triggers, particularly ocean/atmosphere oxygenation, do the reverse. Using modern oxygen minimum zones as an analog for Proterozoic oceans, we explore the effect of low oxygen levels on the feeding ecology of polychaetes, the dominant macrofaunal animals in deep-sea sediments. Here we show that low oxygen is clearly linked to low proportions of carnivores in a community and low diversity of carnivorous taxa, whereas higher oxygen levels support more complex food webs. The recognition of a physiological control on carnivory therefore links environmental triggers and ecological drivers, providing an integrated explanation for both the pattern and timing of Cambrian animal radiation.**

evolution | hypoxia | Ediacaran | Metazoa

Cambrian fossils chronicle the appearance of essentially all high-level animal body plans, as measured by cumulative first appearances of metazoan phyla and classes, in a geologically brief interval between ~540 and 500 million years ago (1, 2). Hypotheses to explain this event have commonly focused on either external controls, such as increasing oxygenation of the atmosphere–ocean system (1, 3–5), or internal controls based on an evolutionary, ecological, or genomic breakthrough (2, 6–11). Recently, hypotheses in the latter category have emphasized the importance of macropredation in facilitating observed increases in diversity and disparity across the Proterozoic-Cambrian transition (6–10).

External and internal controls have distinct attractions as triggers for Cambrian radiation. External controls relating to environmental oxygenation can explain the timing of the radiation—in other words, why animals radiated so dramatically beginning ~540 Ma, and not earlier or later. Indeed, the appearance of large, complex animals in the fossil record seems to follow directly on the heels of an Ediacaran increase and stabilization of marine oxygen levels as inferred from a number of different proxy records (12, 13). Such an environmental shift could remove a barrier to animal evolution, but aside from direct links to maximum permissible body size (14), it lacks an explicit mechanism to generate diversity (new species) and disparity (new body plans). There is no theoretical reason why ocean redox change should generate the evolutionary novelties—specifically the fundamentally new bauplans—seen in the Cambrian fossil record (15).

In contrast, ecological hypotheses focused on predation contain a clear driving mechanism for morphological innovation, namely selection pressures in evolving food webs. They can also explain the origin and maintenance of high-level body plan disparity through the principle of frustration: organisms optimally suited to one task will be less well suited for another, leading to a roughening of the fitness landscape and isolation of distinct fitness peaks (16). Consistent with this hypothesis, the origin of

carnivory itself appears to be temporally correlated with the Proterozoic-Cambrian transition (Fig. 1), a prerequisite if predator–prey “arms races” are to be viewed as the driving forces behind morphological innovation. In this discussion, we distinguish carnivory as mobile animal–animal interactions, as opposed to predation, which more broadly refers to one organism consuming another and may be as ancient as Eukarya (17). The oldest paleontological evidence for carnivory comes from circular perforations interpreted as drill holes in the lightly biomineralized metazoan fossil *Cloudina* from upper Ediacaran rocks in China (18). Strong evidence for carnivory can further be found in chaetognath fossils—voracious predators in the modern ocean—including the widespread early Cambrian skeletal fossil *Protohertzina*, interpreted as chaetognath grasping spines (19), and early Cambrian body fossils (20). Fossil aggregates and preserved gut contents in Cambrian Lagerstätten (e.g., hyolith shells in priapulid guts) provide additional fossil evidence for carnivory in early Cambrian oceans (21).

Support for the origin of carnivory near the Proterozoic-Cambrian boundary also comes from the qualitative mapping of feeding strategies onto a time-calibrated metazoan phylogeny (2). This suggests that the last common ancestor of bilaterians and the last common ancestors of the bilaterian superclades Deuterostomia, Ecdysozoa, and Lophotrochozoa were unlikely to have been carnivorous. Evolution of the carnivorous habit cannot be constrained with confidence on the tree until the origin of crown group Nemertea (Fig. 1). Priapulids are another clade that likely evolved carnivory around the Proterozoic-Cambrian transition, although the timing can only currently be constrained between their divergence from kinorhynchans and the appearance of early Cambrian predatory forms (21), as the Priapulida crown group is undated and it is unclear whether the small nonpredatory forms at the base of this clade in morphological cladistics trees (22) represent the primitive form or are derived from a larger, potentially carnivorous ancestor. Molecular clock ages for nodes constraining the evolution of carnivory (2, 23) clearly suggest that bilaterians originated long before carnivory evolved within the clade around the Proterozoic-Cambrian transition (Fig. 1). It is worth noting that the derived nature of carnivory and the logic of phylogenetic systematics requires such a conclusion at some level regardless of the accuracy of molecular clock ages. A carnivory-based ecological hypothesis, then, can explain the pattern of morphological diversification seen in the Cambrian fossil record but does not directly address its timing.

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chemosymbiosis. Third, their feeding biology is relatively well understood (31), and although the feeding of most deep-sea polychaetes has not been observed *in vivo*, it is possible to code feeding strategies with reference to shallow water relatives. Fourth, polychaetes are more tolerant of low-oxygen levels than most other bilaterians, including arthropods and vertebrates (26, 32) and so constitute a conservative choice for our study. Finally, the use of a single group ensures that all taxa will have broadly similar physiologies and body plans, and observed trends will not be the result of ecological replacement by a different taxon with a fundamentally different bauplan. Similar correlations between oxygen and feeding ecology were found for the entire fauna in a single basin investigation of the western Indian OMZ (33), suggesting that the results extend beyond polychaetes and are unlikely to be specific to this clade.

A total of 10 published studies were identified that met the oxygen, depth, and sieve size requirements outlined above, resulting in a full data set that includes 962 polychaete species occurrences from 68 stations worldwide (Table 1 and Dataset S1). In addition to the 10 studies analyzed quantitatively for the relationship between oxygen and carnivory, a new data set from the Bay of Bengal, which contains additional very low-oxygen sites, was analyzed qualitatively for the presence–absence of carnivores. All species occurrences were coded for their likely feeding mode based on the literature, incorporating both classical observations and gut content analyses, as well as new insights from tracer studies, stable isotopes, and fatty acid analysis (see *SI Materials and Methods* for full coding details). In some cases, there was uncertainty in coding due to either contradictory information in the literature or low taxonomic resolution in faunal lists for higher taxa that are known to feed heterogeneously. In these cases, as well as for omnivorous taxa, we followed the logic of ref. 34 in counting these taxa as one-half carnivore for the purposes of calculating the number of carnivorous individuals in a fauna and the number of carnivorous taxa. To test the effect of this coding strategy, sensitivity analyses were conducted wherein all uncertain and omnivorous taxa were coded as either entirely carnivorous or noncarnivorous.

The percentage of carnivorous individuals in an assemblage and number of carnivorous taxa in an assemblage were binned for four different oxygen levels: suboxia (0–0.2 mL/L O<sub>2</sub>, or 0–9 μM; 26 stations), severe hypoxia (0.2–0.5 mL/L O<sub>2</sub>, or 9–22 μM; 13 stations), moderate hypoxia (0.5–1.0 mL/L O<sub>2</sub>, or 22–45 μM; 9 stations), and mild hypoxia (1.0–2.0 mL/L O<sub>2</sub>, or 45–89 μM; 20 stations). Binning of stations was guided by table 1 of ref. 35, which describes various O<sub>2</sub> thresholds currently used in the low-O<sub>2</sub> literature. We acknowledge that there are several different definitions for these thresholds, and, in particular, any definition

of suboxia based on dissolved O<sub>2</sub> concentration will encompass a variety of biogeochemical environments including many dominated by purely aerobic metabolisms (36) (see *SI Materials and Methods* for binning details).

Presence–absence data for carnivores across the data set illustrate a clear relationship to oxygen. Some carnivores can survive at low oxygen levels—but carnivores are only absent from an assemblage when oxygen is <0.34 mL/L (~15 μM; Fig. 2A). A similar pattern was seen in the Bay of Bengal (Table S1). The other investigated metrics for carnivory also show a relationship with oxygen level (Fig. 2B and C). To test for significant differences in percent of carnivorous individuals and number of carnivorous taxa among oxygen levels, the data were log-transformed and compared using ANOVA. Post hoc Tukey-Kramer tests ( $\alpha = 0.05$ ) were used to further explore significant differences among oxygen levels. Percent carnivorous individuals (Fig. 2B) increased dramatically between suboxic and hypoxic environments ( $F_{3,64} = 14.25$ ;  $P < 0.0001$ ). Indeed, half the suboxic stations had no carnivores at all. The striking relationship between oxygen and feeding ecology is further shown by comparing the number of carnivorous taxa present, a measure of food web complexity, against oxygen (Fig. 2C). The number of carnivorous polychaete taxa in suboxic conditions was significantly lower than at higher oxygen settings ( $F_{3,64} = 20.4$ ;  $P < 0.0001$ ). These results are robust with respect to assumptions regarding feeding mode uncertainty (Tables S2 and S3). Although these analyses focus on oxygen, we recognize that other environmental parameters and physiological stressors may be important in shaping the biology of modern OMZs (26). Many potentially important variables, such as lower pH or high ammonium and sulfide levels in the sediment, can be ameliorated physiologically, although this typically requires an energetic expenditure (37). Because aerobic respiration is the means by which animals regenerate the majority of their ATP, the ability to cope with these stressors thus largely remains linked to oxygen availability.

The global analysis of feeding strategies demonstrates a strong relationship between oxygen and the presence–absence of carnivores, the percentage of carnivores in an assemblage, and food web complexity as measured by species diversity of carnivores. The precise reasons why carnivores are excluded from low-oxygen environments are not fully understood, but several (non-exclusive) possibilities can be considered. The ability to be a successful carnivore will relate fundamentally to the energy expended while catching and digesting prey vs. the total energy gained. In general, macrofaunal abundances remain steady, or even increase (28), with respect to declining oxygen until it reaches very low levels, below which organismal densities drop precipitously (26). The lack of predators at the very lowest

**Table 1. Analyzed studies**

Study	Reference	Margin	Number of stations	Oxygen range (mL/L)
Díaz-Casteñada and Harris, 2004	49	Baja California, Mexico	6	1.0–1.4
Vetter and Dayton, 1998	50	Southern California	5	0.45–1.39
Levin et al., 2010; this study	51	California and Oregon	9	0.22–0.66
Levin et al., 2000	52	Oman	5	0.13–0.52
Hughes et al., 2009	53	Pakistan	8	0.1–1.78
Gallardo et al., 2004	54	Central Chile	2	0.13–0.52
Palma et al., 2005	55	Chile	11	0.06–1.93
Levin et al., 2009	56	Pakistan	16	0.117–0.2
Levin et al., 1991	57	Volcano 7, off Mexico	3	0.09–0.81
Ingole et al., 2010	27	Western Indian	3	0.08–1.35
A. Raman, this study		Bay of Bengal	38	0.01–1.19

Number of stations refers to the stations within the specified depth and O<sub>2</sub> range investigated here and not the total number of stations in a given study. Oxygen concentrations reported as in the published studies (mL/L O<sub>2</sub>); for reference, 0.2 mL/L ~ 9 μmol/kg ~ 0.29 mg/L ~ 9 matm (also see ref. 35).



to carnivores with the fluctuating oxygen demands described above. Escalatory arms races driven by these newly evolved carnivores could then explain the relatively rapid expansion of metazoan diversity and disparity near the beginning of the Cambrian Period.

An Ediacaran transition in the availability of oxygen, allowing widespread carnivory, can thus explain both the timing and recorded biological pattern of Cambrian animal diversification. Specifically, the key physiological threshold in regard to the Cambrian radiation was likely not one of body size alone but rather ecological feeding strategy. Given evolving physiologies through time, the specific oxygen levels at which ecological effects are seen in the modern may not directly relate to Proterozoic oceans. However, because carnivory in polychaetes is limited at low oxygen levels despite their being among the most low oxygen-tolerant taxa in the modern ocean (26, 32), with high-affinity respiratory pigments and good acid-base regulation—and 500 million years of natural selection doubtfully made carnivores less fit—it seems inescapable that low Proterozoic oxygen levels would have limited early animal food webs. Other factors besides carnivory and oxygen may have been important, but many of them are related to carnivore evolution itself (e.g., the evolution of sensory apparatus and vision) (11). This focus does not obviate a role for developmental genetics, but because most gene families that govern bilaterian development originated well before Cambrian body

plan diversification (2, 45), the prime role of development was in assembling these preexisting genes into coherent networks to build body plans suited to the evolving Cambrian fitness landscape. The primary question in this integrated causal hypothesis now remains the timing and absolute magnitude of hypothesized late Neoproterozoic oxygenation. Continued exploration of the causes, timing, and magnitude of oxygenation will provide further insight into the role of oceanographic change in the evolution of carnivory and this unique geobiological event. Further study of the relationship between feeding ecology and oxygen in modern OMZs, as well as the coevolutionary history of animals and ocean redox state in deep time, may also help us predict future changes associated with ocean deoxygenation and expanding oxygen minimum zones (46).

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# Supporting Information

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## SI Materials and Methods

**Station Binning.** The total number of stations investigated in this study was 106. Binning of stations was guided by table 1 of Hofmann et al. (1), which describes various  $O_2$  thresholds currently used in the low- $O_2$  literature. As the goal of this study was to investigate how an increase in oxygen might affect feeding ecology in a low-oxygen world, the upper limit for the study was set at 2.0 mL/L  $O_2$ , classified by ref. 2 as the onset of hypoxia for normal marine fauna. There are several definitions for the onset of hypoxia in the literature (1). We used the most inclusive definition, but the first bin here also encompasses other definitions for the onset of hypoxia, including the “classic” definition of hypoxia of 2.0 mg/L  $O_2$  (~1.42 mL/L  $O_2$ ) and the median lethal concentration in a comprehensive literature review (1.6 mL/L  $O_2$ ) (3). The first bin (mild hypoxia) ranged from the onset of hypoxia at 2.0 mL/L  $O_2$  to moderate hypoxia (1.0 mL/L  $O_2$ ), or the point at which many invertebrates exhibit sublethal responses such as arm tipping in ophiuroids or extension from the sediment in sea anemones (4). The second bin (moderate hypoxia) ranged from moderate hypoxia to severe hypoxia (0.5 mL/L  $O_2$ ), where mass mortality occurs in shallow marine faunas (2). The third bin (severe hypoxia) ranged from the onset of severe hypoxia to the onset of suboxia (0.2 mL/L  $O_2$ ) (5), or the point at which nonoxygenic heterotrophy (suboxic metabolisms) begins to dominate. The fourth bin (suboxia) ranges from the onset of suboxia to absolute anoxia at 0 mL/L  $O_2$ . As with the onset of hypoxia, there are several possible definitions in use for this suboxic or biogeochemical boundary. This boundary was delineated as 0.2 mL/L  $O_2$  by Tyson and Pearson (5). In recent years, it has generally shifted toward 0.1 mL/L  $O_2$  or 5  $\mu\text{M}$  (see table 1 of ref. 1). However, in either case, these values are arbitrary—see extended discussion by Canfield and Thamdrup (6). Specifically, anaerobic processes such as nitrate reduction are often essentially absent (as measured by the lack of a nitrite peak) well below 0.1 mL/L or 5  $\mu\text{M}$   $O_2$ , whereas in other cases, these processes occur at far higher oxygen levels; there is no direct relationship between oxygen levels and the onset or dominance of anaerobic microbial respiration. We have chosen the onset of our suboxia bin at the original 0.2 mL/L  $O_2$  level (5) and acknowledge that this will represent a variety of biogeochemical environments, including many dominated by purely aerobic metabolisms (6). Binning the low-oxygen data into two separate bins based on the alternate 5  $\mu\text{M}$   $O_2$  boundary (e.g., 0–0.114 and 0.114–0.2 mL/L  $O_2$  bins) did not produce significant differences in the means for either percent carnivorous taxa in a fauna (Student two-tailed  $t$  test,  $P = 0.14$ ) or number of carnivorous taxa present ( $P = 0.78$ ). As the combined suboxia bin is significantly different from the higher-oxygen bins (Fig. 2; Table S2), choice of bins based on alternate definitions for suboxia does not appear to affect the results.

Despite sampling all known studies with available faunal lists that met our criteria, most of the very low oxygen (<0.2 mL/L  $O_2$ ) stations were located in the Indian Ocean, specifically the Pakistan margin, the Oman margin, and the Bay of Bengal (Dataset S1). As current sampling for the lowest-oxygen bin is restricted geographically, the possibility remains that some of the effects seen at the very lowest oxygen levels are related in part to geography. One very low oxygen site on the Chilean margin (295-m station of ref. 7; 0.06 mL/L  $O_2$ ) has no carnivores, suggesting that the relationship between carnivory and oxygen is not a purely geographical effect. Further testing the influence of

geography will require more detailed oceanographic sampling of very-low-oxygen regions outside the Indian Ocean.

**Feeding Mode Coding.** As discussed in the main text, polychaetes were chosen to examine the relationship between oxygen levels and metazoan feeding ecology for several reasons. In addition to these reasons, polychaetes have been shown to be a good exemplar group for the entire fauna (8).

Regarding taxon inclusion or exclusion in faunal lists examined, taxa identified only as Polychaeta were excluded as their feeding modes are not codable. Oligochaetes and siboglinids, which are phylogenetically “polychaetes,” (9, 10) were included. Other phyla such as echiurans and sipunculans that are often associated with annelids in molecular phylogenies and may in fact be included within Polychaeta (9), but which have fundamentally different bauplans, were not included. In reality, the inclusion or exclusion of these four higher taxa will not affect the results, as they are all relatively rare in these data sets and all non-carnivorous.

Coding polychaete feeding strategies is facilitated by the compilation of Fauchald and Jumars (11), which has been highly cited and used both by polychaete workers and in general ecology studies. The key insight of this compilation is that feeding ecology in polychaetes is generally conservative at the family level. Thus, given even a rough taxonomic assignment, an organism’s likely feeding strategy can be determined. Although this compilation is more than three decades old, the general pattern has, notwithstanding some new insights, stood the test of new observations and new methods, including light stable isotope analysis (12–17), fatty acid analysis (18), isotopically labeled tracer studies (19), gut architecture studies (20), and new gut content analyses (21) (but see ref. 22 for syllids, which suggests the possibility of a more omnivorous lifestyle for the Eusyllinae).

Many studies simply adopt the coding in table XXXI of Fauchald and Jumars (11), likely with high accuracy considering how well the classification scheme has held up to further research. However, some carnivorous groups (see below) can be heterogeneous in their feeding strategies, and thus the finer taxonomic resolution in published faunal lists can better help guide coding. Here, for each species occurrence, a Google search was conducted at the lowest taxonomic resolution possible (genus or species) using the searches “*Genus species*” + feeding and “*Genus species*” + diet. In cases where no information could be found for a specific species, or the faunal list identified the organism to the generic level only, data for other species within that genus were used. In these cases, preference was generally given to geographically closer congeners. In some cases, conflicting information was found for a given genus, leading to uncertainty in coding (see below).

Although we attempted to extend beyond Fauchald and Jumars (11) and incorporate local and more recently published data at a lower taxonomic level into our coding, it should be noted that there may be some circularity. Specifically, many studies discuss or code the feeding strategies of polychaetes with reference to Fauchald and Jumars (11). Nonetheless, scientists working in a specific geographical locale can be expected to have a strong understanding of the natural history of the fauna, and although Fauchald and Jumars (11) will remain a starting point, new insights into the local fauna will be incorporated through time into more recent publications. As knowledge of the feeding strategies of polychaetes grows (especially for deep-sea polychaetes), it is likely that the codings for some of these taxa will change.

However, as with any large synthesis, errors are expected to be randomly distributed (23), and it is unlikely that the overall pattern will change with additional observations (also see sensitivity analyses with respect to coding uncertainty in Table S3).

In addition to the references listed above (11, 12–22) and information in the studies themselves (Table 1), refs. 24–92 were additionally used to guide coding (Dataset S1).

Complete environmental data and faunal lists for each station, with references justifying each coding decision and annotations regarding the references and any uncertainty in coding, are contained in Dataset S1. Faunal lists and their codings for each study are contained in individual tabs within the excel file. The raw count data are presented in the same format as provided by the authors of each study to retain their original structure.

**Uncertainty in Coding Feeding Modes.** Several sources of uncertainty exist in coding feeding modes. First, many organisms are simply omnivorous, or opportunistic, and do not fit easily into defined feeding categories (93, 94). Some polychaete families show a tendency toward omnivory, for instance the Onuphidae (11). These taxa are coded as omnivores, and as described in the main text, we followed the logic of Jumars and Fauchald (95). Each taxon was counted as one-half carnivore for the purposes of calculating the number of carnivorous individuals in a fauna and the number of carnivorous taxa. For other taxa, contradictory information was found in the literature. This was most common when the taxonomic resolution in faunal lists extended only to the generic level, and our coding was based on other species in the genus. It is possible that heterogeneity of feeding modes exists within the genus, but also possible that many of these species exhibit a degree of omnivory. When faced with contradictory information from the literature, these taxa were coded as Carnivore(?). Taxa coded as Carnivore(?) were also counted as one-half carnivore in Fig. 2. Thus, taxa coded as either Omnivore or Carnivore(?) are functionally the same in the statistical analysis, but represent true evidence for omnivory in the former and uncertainty in coding in the latter. As an example, amphinomids are generally considered carnivores (11), but there is stable isotope evidence (12) (*Paramphinome*) and tracer studies (96) (*Linopherus*), sometimes combined with lipid evidence (97), indicating that some deep-sea amphinomids are deposit feeders or detritivores. Therefore, species identified in faunal lists simply as Amphinomidae sp. were coded as Carnivore(?). On the other hand, studies of gut contents in the amphinomid *Chloeia pinnata* from the Southern California borderland (48) demonstrated that this species feeds on both animals and detritus, and the diet varies based on the time of year. As there is species-level information available for this taxon, this species in the Del Mar margin and La Jolla Canyon data sets of Vetter and Dayton (98) was coded as an omnivore. Species that are primarily scavengers were not coded as carnivores, although it is recognized that some may feed opportunistically as carnivores.

A second source of uncertainty, as hinted above, is low taxonomic resolution in faunal lists. Most polychaete families are conservative in their feeding strategies and can be coded according to table XXXI of Fauchald and Jumars (11). This is particularly true for many of the filter feeding families (such as the Serpulidae and the Sabellariidae) and the deposit feeding families (e.g., the Ampharetidae, Capitellidae and Cossuridae as three examples). Others exhibit heterogeneity in feeding mode but remain noncarnivorous (e.g., the Spionidae, some of which can switch between surface deposit feeding and suspension feeding) (37, 38). Many of the carnivorous families are entirely carnivorous, although in some, like the hesionids, the meiofaunal members and members at vents and seeps are not and feed on bacteria or diatoms (11). In a few groups, however, specifically the Amphinomidae, Dorvilleidae, Eunicidae, Lumbrineridae,

Nereidae, Phyllodocidae, and Syllidae, there is strong evidence for noncarnivorous feeding habits in some but not all species (11–92, 96, 97). Consequently, taxa identified, for instance, only as Nereidae sp. or unidentified Syllidae in faunal lists cannot be coded with confidence. Such taxa were also coded as Carnivore(?).

As a final point, this coding strategy results in conservative coding for polychaetes at the very lowest oxygen levels. Specifically, there is evidence that many of the typically carnivorous polychaete groups switch to omnivorous or noncarnivorous habits at very low oxygen levels. For instance, the amphinomid *Linopherus* on the Pakistan oxygen minimum zones (OMZs) can feed as a carnivore or scavenger, but feeds in large part on phyto-detritus at very low  $O_2$  (96, 97). Isotopic studies have recently demonstrated that jawed dorvilleid polychaetes from Costa Rican methane seeps feed primarily on prokaryotes, specifically archaea/bacteria anaerobic oxidation of methane consortia (86). It is likely that dorvilleids (and also the jawed hesionids) at very low oxygen levels are feeding on microbes, especially in settings where large, filamentous, sulfide-oxidizing mats occur. Thus, although such taxa are conservatively coded as Carnivore or Carnivore(?) if the taxonomy is not well resolved, in reality this coding is potentially incorrect and they are noncarnivorous. In other words, given current knowledge, Fig. 2 likely overestimates the number of carnivorous taxa and percent carnivorous individuals present in a fauna in the suboxia bin. As there is no such bias affecting the higher-oxygen bins, the difference between low- and high-oxygen stations is probably even greater than our coding suggests. Future stable isotopic and fatty acid analysis, pulse-chase labeling experiments, and gut content analyses of putative carnivores living at very low oxygen levels will be instrumental in providing more concrete constraints on the diets of these organisms.

## SI Analyses

**Bay of Bengal Data Set.** In addition to the 10 published studies analyzed quantitatively for the statistical relationship between oxygen levels and carnivory (Fig. 2; Table S2), we coded and investigated a macrofaunal data set from the Bay of Bengal (Dataset S1). This data set has previously been discussed in ref. 99 and has led to important inferences about the relationship between environmental parameters and ecological responses in this region. However, this data set was investigated qualitatively here for carnivore presence-absence rather than being included in the quantitative synthesis for several reasons. First, the study was conducted using a Smith-McIntyre grab instead of a coring device as in the other studies. For a number of reasons from possible loss of mud to unequal sampling with depth due to the bite of the grab (100), the results are less quantitative (or rather, it is more difficult to monitor the quality of each sample) than multicores. Finally, the size of the data set (orders of magnitude more than many of the other studies) is problematic from a statistical point of view; inclusion of this study would dwarf the others and lead to strong geographical biases.

The Bay of Bengal data set is valuable to consider in the context of oxygen and carnivory, however, because it includes many sites at the very lowest end of the oxygen spectrum (suboxia bin of Fig. 2). Importantly, it includes five stations below 0.10 mL/L  $O_2$ —an alternate threshold for suboxia (1)—compared with only three stations below this level in the remainder of the data set. As the observation that carnivores are rare or absent in suboxia is based on a relatively small sampling of the seafloor compared with the total area bathed by low- $O_2$  waters, this data set provides an opportunity to examine other stations in this bin.

Examination of these data demonstrates that stations in the suboxia bin from the Bay of Bengal exhibit the same pattern seen in other very low- $O_2$  stations, with low percentages of carnivores relative to the entire fauna, and low (0–2) numbers of carnivorous

taxa present. Stations 66 DP S1 202 (0.20 mL/L O<sub>2</sub>) and 78 CLK S2 202 (0.23 mL/L O<sub>2</sub>) also have no carnivores present. Therefore, the Bay of Bengal data set provides additional support for the hypothesis that low-O<sub>2</sub> sites are characterized by low percentage of carnivores and low species diversity of carnivorous taxa.

**Testing the Effect of Uncertainty in Feeding Mode Coding.** To test whether omnivory, contradictory information in the literature, or low taxonomic resolution in faunal lists was affecting the results, two sets of sensitivity analyses were conducted. In the first, all taxa coded as Omnivore or Carnivore(?) were coded as Carnivore. In the second, all taxa coded as Omnivore or Carnivore(?) were coded as Non-Carnivore. As described in the main text, to test for

significant differences in percent of carnivorous individuals and number of carnivorous taxa among oxygen levels, the data were log-transformed and compared using ANOVA. Post hoc Tukey HSD tests ( $\alpha = 0.05$ ) were used to further explore significant differences among oxygen levels.

The analyses demonstrate that the results are robust with respect to the strategy for coding uncertainty as implemented here. Specifically, under all coding schemes, the percent carnivorous individuals in a fauna and number carnivorous taxa for the suboxia bin (or suboxia + severe hypoxia) are significantly lower than the remaining higher-oxygen bins. The different coding strategies do have some effect on which specific bins are significantly different.

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**Table S1. Stations in the suboxia bin (<0.20 mL/L O<sub>2</sub>) from the Bay of Bengal data set**

Station	Depth	Dissolved oxygen	Polychaete density (individuals/m <sup>2</sup> )	Carnivorous individuals/m <sup>2</sup>	Percent carnivores	Number and identity of carnivorous taxa
190 DP 203	203	0.01	270	0	0.00	0
604 BRU 150	150	0.01	70	10	14.29	1 ( <i>Ancistrosyllis parva</i> )
191 DP 152	152	0.03	710	0	0.00	0
198 KKD 150	150	0.03	70	0	0.00	0
206 BRU 201	201	0.03	50	10	20.00	1 (Aphroditidae sp. 1)
72 VSKP S1 207	207	0.12	9,635	20	0.21	2 (Polynoinae UI and Pilargidae SI)
75 BRU S1228	228	0.13	1390	10	0.72	1 (Pilargidae SI)
81 PDP S1 254	254	0.15	8955	10	0.11	1 (Pilargidae SI)
79 CLK S3 537	537	0.18	518	4	0.72	0.5 ( <i>Leptonereis</i> sp.)
69 KKD S1 202	202	0.19	511	6	1.08	2 (Polynoinae UI and <i>Hermonia hystrix</i> )

**Table S2. Results of ANOVA and post hoc Tukey HSD tests: Data in Fig. 2 (uncertain taxa coded as one-half carnivore following ref. 95)**

Source	df	Sum of squares	Mean of squares	F ratio	P	Post hoc Tukey HSD
Percent carnivores (log-transformed)						
Oxygen	3	9.18	3.06	14.25	<0.0001	a, b, b, b
Error	64	13.75	0.21			suboxia, severe, moderate, mild
Total	67	22.93				
Number of carnivorous taxa (log-transformed)						
Oxygen	3	4.73	1.58	20.4	<0.0001	a, b, c, bc
Error	64	4.95	0.08			suboxia, severe, moderate, mild
Total	67	9.68				

**Table S3. Results of ANOVA and post hoc Tukey HSD tests: Sensitivity analyses coding either all omnivorous or uncertain taxa as carnivores or all omnivores and uncertain taxa as noncarnivores**

Source	df	Sum of squares	Mean of squares	F ratio	P	Post hoc Tukey HSD
Percent carnivores (log-transformed); coding uncertainty as carnivorous						
Oxygen	3	9.78	3.26	13.36	<0.0001	a, b, b, b
Error	64	15.61	0.24			suboxia, severe, moderate, mild
Total	67	25.4				
Number of carnivorous taxa (log-transformed); coding uncertainty as carnivorous						
Oxygen	3	5.26	1.75	20.03	<0.0001	a, b, b, b
Error	64	5.61	0.09			suboxia, severe, moderate, mild
Total	67	10.87				
Percent carnivores (log-transformed); coding uncertainty as noncarnivorous						
Oxygen	3	9.4	3.13	13.32	<0.0001	a, ab, c, bc
Error	64	15.05	0.24			suboxia, severe, moderate, mild
Total	67	24.44				
Number of carnivorous taxa (log-transformed); coding uncertainty as noncarnivorous						
Oxygen	3	4.22	1.41	18.02	<0.0001	a, a, b, b
Error	64	4.99	0.08			suboxia, severe, moderate, mild
Total	67	9.21				

## Other Supporting Information Files

[Dataset S1 \(XLSX\)](#)