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Life Aquatic Chemosynthetic in the Photic Zone -Up the Food Chain?

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Abstract

Life on Earth has proven highly adaptable, thriving across the most extreme environments, from the highest peaks to the deepest seas, where chemosynthetic microbes (chemoautotrophs) derive energy from inorganic chemical oxidation. In turn, chemoautotrophs are consumed by other organisms and/or have symbiotic associations with other organisms, allowing chemosynthetic energy to percolate up the food chain [1]. For deepwater seeps, this energy is known to ultimately support top predators - fish [2,3]. Here, we argue that chemosynthetic energy also plays a role in photic zone ecosystems, including potentially, an important role in fisheries.

The ecosystem importance of the flow of chemosynthetic energy likely would be enhanced, potentially critically, in nutrient limited environments, such as the deep sea, winter Arctic, or coastal waters when nutrients are for example, sequestered by phytoplankton blooms.

Keywords: Seep; Chemosynthetic; Tropic level; Food chain; Fisheries; Microbes; Bubbles

Introduction

Natural seepage of fluids from geological sources is widespread on land and offshore, the most common fluids being hydrocarbons, particularly methane (CH_4) both from petroleum sources and from the microbial degradation of organic matter. Onshore examples include the La Brea tar pits in California [4] and eternal flames [5] at places like Chimera, Turkey and Yanar Dag, Azerbaijan. Offshore examples are reported for water depths ranging from inter-tidal (e.g. San Simón Bay, Galícia, Spain; [6] to >4,000m in the Aleutian Trench [7]) in every sea and ocean [6]. Although CH_4 dominates, other compounds, including higher hydrocarbons, also may be present. Some compounds, such as higher alkanes and hydrogen sulfide (H_2S) are toxic.

Methane utilization at the seabed

The escape of CH_4 from seabed seep sites is limited by anaerobic oxidation of methane (AOM) that occurs close beneath the seabed; Reeburgh [8] suggests that the 'benthic filter' oxidizes as much as 80% of CH_4 migrating through seabed sediments. Moreover, the benthic filter is the first step by which chemosynthetic energy enters the food chain, albeit in the seabed in the immediate vicinity of seepage. This microbially-mediated process produces two significant by-products: CH_4-derived authigenic carbonate (MDAC), a mineral precipitate that cements the local seabed sediments to form a concrete-like rock, and H_2S. MDAC provides a hard substrate that attracts many species, which might otherwise not be found on the 'normal' (non-seep) seabed.

It is well known that deepwater chemosynthetic communities associated with marine hydrocarbon seepage include methanotrophs (which oxidize CH_4) and thiotrophs (which oxidize H_2S) that, like their hydrothermal equivalents, support localized ecosystems with a high biomass and biodiversity. Associated macrofauna may include species that host chemoautotrophic endosymbionts (siboglinid tube worms, bivalves, sponges, etc.) and predatory and opportunistic feeders such as shrimp, crabs, and fish. The vast majority (to 100% in lower tropic levels) of the energy in such ecosystems derives from non-photic sources. In shallower (<400m) water; however, seep-specialist organisms tend to be out-competed by 'normal' benthic organisms reliant on energy derived from the photic zone i.e., from phototrophs [9], although typical seep species are found for strong shallow seeps [10]. For infaunal species, these oases are density rich relative to the surrounding seabed, although species diversity tends to be relatively reduced [11-13]. Species spatial distributions and community composition are correlated closely with chemosynthetic flows [14] and seep-associated substrates [15,16]. Isotopic analysis has identified chemosynthetic energy transfer from chemoautotrophs to nematodes, polychaetes, and other infaunal organisms [17].

Within the immediate vicinity of seeps sediment toxicity impoverishes benthic communities relative to 'normal' seabed [18,19]. However, seep specialists, such as the bivalve *Thyasira sarsi* and the nematode *Astonomena southwardorum* (both with endosymbionts) live at North Sea seeps [19]. At the Coal Oil Point seep field, offshore California (and far from a major urban outflow) isotopic studies identifying petroleum energy transfer from chemoautotrophic sulfide oxidizers (Beggiatoa spp.) to nematodes, polychaetes, and other infaunal organisms [17].

Certain polychaete families (Siboglinidae, Capitellidae, and Ampharetidae) and oligochaetes are characteristic of seep sites, some of which benefit from reducing conditions [12]. Sibuet [1] identified five families of bivalves (Vesicomyidae, Mytilidae, Solemyidae, Thyasiridae, and Lucinidae) known to inhabit seep sites; some (at least) of them host methanotrophic and/or thiotrophic symbionts. Bacterial mats, most commonly ascribed to the thiotrophic genus Beggiatoa, are a common (maybe ubiquitous) feature of seep sites at any water depth.

Methane utilization in the water column

Marine seepage is most recognizable as rising bubbles. Bubble plumes are significant for several reasons. Firstly, CH_4 is transported up into the water column. Although bubbles at the seabed may be entirely CH_4, gases exchange across the bubble surface leading to CH_4 loss into the water, enhancing CH_4 in the water above seeps relative to 'ambient' seawater [20,21]. Once in the water column, CH_4 is subject to methanotrophic bacterial oxidation [22]. This provides another pathway by which chemosynthetic energy enters the food chain as these bacteria are themselves available for predation by higher organisms. CH_4 oxidation is not constrained to near the seeps but follows the plume of dissolved CH_4-rich water.

Secondly, rising bubbles provide a highly efficient transport mechanism for surface-active materials on the bubble interface ('hitch-hikers'). This transport process shuttles chemoautotrophic microbes up into the water column [23]. Upon bubble dissolution, any surface-attached microbes and other material (organic material, nutrients etc.) are deposited into the water where they become available and attractive to higher tropic level organisms and their predators. Leifer and Judd [24] hypothesized this mechanism as explaining a layer of jellyfish (predators) in an area of North Sea seepage.

Thirdly, bubble plumes entrain surrounding water, generating upwelling flows that transport bottom water and nutrients up into the water column [25]. Pohlman [26] reported that a consequence of this upwelling, and the consequent nutrient enrichment of the upper water column, is increased primary productivity; this seems similar to enhanced productivity associated with other areas of upwelling.

Seepage plumes therefore can be considered beneficial to marine biological productivity because of these features. It has been shown [27,28] that a strong thermocline presents a very real barrier to the upwelling flow, consequently – as also described by Leifer and Judd [24], there tends to be a significant increase in CH_4 concentration, and therefore CH_4 oxidation and nutrients at and immediately below the thermocline. This creates a layer that would be particularly attractive for higher-level organisms. Such nutrient aggregation could explain reports of significantly increased chlorophyll concentration at the thermocline above on-going seepage from a blow-out site in the North Sea [29].

3 Occurrence of seeps

Marine seepage is widespread, particularly associated with areas of rapid sediment accumulation such as deltas (e.g., the Mississippi, Nile, Niger, East Siberian Sea, etc.), and sedimentary basins, which host petroleum accumulations (the North Sea, Gulf of Mexico, South China Sea, etc.). As pointed out by Judd [30] many of these areas also have highly productive fisheries. We suggest that this is not a coincidence, but relates to the significant advantages provided by seepage, first and foremost by their upwards transport of bio-available chemosynthetic energy and nutrients. Secondly, bubble plumes obscure sonar and sight, protecting against predation. Seepage also is associated with hard seabed substrates that provides habitat.

Bioavailability

Seepage provides a non-seasonally varying source of energy – whereas nutrients and sunlight exhibit strong annual cycles in phytoplankton and zooplankton populations that support the marine food web. Thus, photic zone chemosynthetic energy can provide bridging nutrients for a range of conditions. Specifically, during food-limited time periods, in chronically nutrient-limited areas, on the continental slope below the photic zone (deep sea), during the Arctic winter (night), and for ice-covered waters that block solar insulation. Marine CH_4 seepage has been estimated at from 20Tg yr^{-1} [31] to ~ 50Tg CH_4. yr_{-1} [32] with oil contributing 0.6Gg yr_{-1} [33], of which a portion is bioavailable. This amounts to a significant contribution to the marine carbon cycle and potentially to the marine ecosystem, particularly for nutrient-limited habitats.

Where nutrient limitation is seasonal, chemosynthetic energy could provide critical bridging support during these seasons and thus support increased diversity. This would be similar to the role watering holes play during the African dry season.

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Predation Protection

Seep bubble plumes confuse sonar and sight, protecting against predation. Seep bubble plumes are highly dynamic zones of turbulent upwelling flows that could be highly distracting to predators- the survival strategy of dense fish schools - both visually and by blocking sonar. Seep bubbles also are a locally important noise source that could distract predators.

Interestingly, this very characteristic could make them attractive to cetaceans. The acoustic signature of seeps would be highly audible to cetaceans, serving as acoustic signposts along migration pathways particularly, in basins that support rich fisheries. Additionally, bubble motions could be of interest to intelligent and curious cetaceans, creatures that use bubbles for play and for fishing.

Seepage could explain an energy deficit in cetacean foraging in the Gulf of Mexico (GOM). Based on prey biomass [34], and whale body mass considerations [35] and a tropic level of 4.22 [36], net primary productivity per whale can be calculated. Combined with the conservative NOAA estimated stock [37] of deep-foraging whales (sperm, Gervais', Cuvier's and Kogia) in the Gulf of Mexico suggests ~4x10^4 metric tons of primary productivity is required (96% from Sperm whales). This is about double the entire GOM open sea (311,000km^2) daily phytoplankton primary productivity (2.1x10^4 metric tons). Chemosynthetic primary production could make up the deficit for these deep foragers.

Recommendation

Given the importance of fisheries to the economy and the need for sustainable management, the hypothesis that seepage supports higher fishery productivity merits investigation. Such research should map the flow of chemosynthetic energy up the food chain in the deep sea and in the photic zone to also better understand their contribution to middle tropic levels. Of interest to fisheries globally, the potential Arctic impacts merit special consideration. In the Arctic, destabilization of submerged permafrost [38] is releasing vast chemosynthetic energy stores – energy that persists through the long dark winter.

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