CONDENSATION

As noted previously, heat energy imparted to water as it evaporates is returned to liquid water as vapor condenses. During low tide, the rate of evaporation typically exceeds the rate of condensation, and it is this net rate of evaporation that we notice. At times, however, the rate of condensation exceeds that of evaporation. This is most commonly seen when the temperature of an object is lowered. For example, water condenses on a glass of iced tea or a can of cold beer. Similarly, if the surface of an intertidal organism is below the dew point (defined subsequently), water condenses on it, and the organism is warmed.

How cold must a surface be to accumulate condensation? This question can be answered through the use of Fig. 5. Consider the following example. The afternoon air temperature at an intertidal site is 30 °C and the relative humidity is 0.6. We can use Fig. 5 to tell us what the vapor concentration is under these conditions by following arrow 1 up from 30 °C to the line for 0.6 relative humidity. We then desire to know how much we must lower the temperature before this vapor concentration becomes saturating. We follow arrow 2 horizontally left until it contacts the line of saturation (relative humidity = 1.0) and then arrow 3 down to find the corresponding temperature. In this case, the temperature required to have net condensation is 21 °C. This is the dew point for these conditions. Different conditions have different dew points. The lower the relative humidity, the greater the drop in temperature required to reach the dew point.

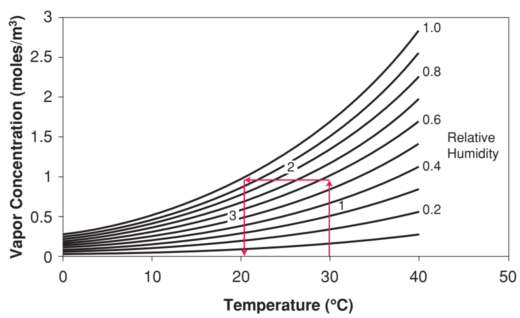

FIGURE 5 The information of Fig. 3 allows one to estimate the dew point corresponding to a given current air temperature and relative humidity (see text).

Condensation may be important in helping intertidal organisms to avoid freezing. Just as evaporation cools organisms, condensation warms them, and the condensation forming on an organism as air temperature approaches 0 °C can help to maintain the organism's body temperature several degrees above that of the air. Given the high relative humidity typical of intertidal environments, this mechanism may be particularly effective.

When water condenses onto a surface that is below 0 °C, it condenses as frost. The latent heat released under these conditions (approximately 2,830,000 joules per kilogram) is 16% larger than that released by vapor condensing into liquid water, augmenting the warming effect.

The biological role of condensation has been extensively studied for terrestrial plants (in particular for crop plants, for which frost damage has monetary consequences), but the effect has not been studied in detail for intertidal organisms.

SEE ALSO THE FOLLOWING ARTICLES

Desiccation Stress / Heat Stress / Seawater

FURTHER READING

Campbell, G. S., and J. M. Norman. 1998. *An introduction to environmental physics*, 2nd ed. New York: Springer-Verlag.

de Podesta, M. 2002. *Understanding the properties of matter*, 2nd ed. New York: Taylor and Francis.

Denny, M. W. 1993. *Air and water: the biology and physics of life's media*. Princeton, NJ: Princeton University Press.

Nobel, P. S. 1991. *Physicochemical and environmental plant physiology.* New York: Academic Press.

EXCRETION

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All animals produce nitrogen-containing compounds as byproducts of their metabolic processes. These compounds can be highly toxic and are actively excreted by intertidal invertebrates, usually in the form of ammonium ion (NH_4^+). In temperate marine ecosystems, the growth of seaweeds and phytoplankton is largely determined by nitrogen availability, and invertebrate-excreted ammonium can play an important role in ameliorating this nitrogen limitation and thereby influencing the recruitment, growth, and diversity of seaweeds on rocky shores.

NITROGEN EXCRETION BY INTERTIDAL INVERTEBRATES

Nitrogen is an essential component of many biological molecules, including amino acids, proteins, and nucleic acids. Nitrogen is therefore a somewhat unusual element, as it is both produced by and toxic to animals. Like all animals, invertebrates on rocky shores must consume proteins and other nitrogen-containing compounds, and the digestion and metabolism of these nitrogenous compounds produces waste nitrogen that must be excreted. In marine invertebrates, the primary excretory product is ammonium (NH_4^+), though small amounts of urea and organic nitrogen (amino acids) are also excreted by some species. Because ammonium is soluble in water, most excreted ammonium readily diffuses across the body surface (often gills) and into the surrounding water. In coelomate invertebrates, excretion of other compounds, including nonammonium nitrogenous wastes (urea, amino acids), salts, and byproducts of metabolism, occurs *via* ultrafiltration and reabsorption in specialized structures called filtration nephridia.

Nitrogen excretion rates vary over tidal and seasonal cycles as a result of changes in invertebrates' food supply (quantity and quality) and the status and use of their internal nitrogen reserves. Because nitrogen excretion is linked to protein metabolism, increases in protein in the diet (e.g., consumption of bacteria instead of phytoplankton) or the use of protein reserves as a substrate for respiration during starvation typically lead to increases in ammonium excretion. Site-specific differences in the quality and quantity of particulate organic material (phytoplankton and detritus) available to filter feeders can result in large differences in the biomass-specific ammonium excretion rates of filter-feeding invertebrates at different sites. Within a site, temporal variation in food availability and quality (e.g., summer versus winter or upwelling versus relaxation) can lead to similarly large differences in ammonium excretion rates. Other factors that influence excretion rates include tide height (which influences immersion time and thereby food availability), temperature (which affects physiological rates, including ammonium excretion), and salinity.

INVERTEBRATE-EXCRETED AMMONIUM AS A NITROGEN SOURCE FOR INTERTIDAL SEAWEEDS

Nitrogen is typically the most important growth-limiting nutrient for autotrophs in temperate coastal ecosystems, so the productivity of these systems is closely tied to nitrogen availability. In the near-shore waters of the northeastern Pacific Ocean, the amount of particulate organic nitrogen (associated with phytoplankton and detritus) can equal or exceed the amount of inorganic nitrogen (nitrate or ammonium). However, seaweeds and other marine primary producers cannot utilize particulate nitrogen, and they rely largely on nitrate and ammonium, which they assimilate into amino acids. By consuming particulate nitrogen, which is unavailable to seaweeds as a nitrogen source, and excreting inorganic nitrogen (ammonium), which is readily taken up and assimilated by seaweeds, invertebrates play an important role in the nitrogen dynamics of intertidal ecosystems.

For decades, biological oceanographers have differentiated between new production, or primary production associated with upwelled nitrate, and regenerated production, which is fueled by local-scale ammonium excretion by animals. However, it is only comparatively recently that benthic marine ecologists have begun to consider the potential role of nitrogen regeneration in fueling primary production in near-shore and intertidal ecosystems. Measurements of ammonium excretion and uptake by amphipods and seaweeds suggest that benthic macroalgae can potentially obtain approximately 50% of the nitrogen needed for growth from associated epifaunal invertebrates in subtidal seaweed beds. Excreted nitrogen has also been shown to influence seaweed growth, recruitment, and tissue carbon-to-nitrogen ratios (an indication of nitrogen limitation) in intertidal seaweeds.

Tidepools are a convenient system for quantifying the effects of invertebrate-excreted ammonium on seaweed growth and diversity. Intertidal pools, especially those high on the shore, are isolated from the ocean for substantial periods of time, and the seaweeds living in those pools (which rapidly deplete available nitrogen from the water) are therefore subjected to long periods without any external nitrogen. Adding controlled-release fertilizer pellets (inorganic nitrogen and phosphorus) to tidepools enhances seaweed growth and diversity, suggesting that seaweeds in mid- and high-zone pools are nutrient limited.

Can invertebrate-excreted ammonium ameliorate this limitation? Sessile invertebrates, especially mussels and sea anemones, excrete substantial amounts of ammonium into tidepools, so that inorganic nitrogen concentrations in invertebrate-dominated pools can equal or exceed those in the adjacent ocean, even during upwelling events. Seaweeds take up and assimilate this excreted ammonium; the rate of nitrogen incorporation into seaweed tissues increases with the rate of nitrogen loading by invertebrates into tidepools.

The excretion of ammonium by tidepool invertebrates and its uptake by seaweeds is associated with increased seaweed growth and diversity. For example, in Oregon-coast tidepools, a fourfold increase in the rate of ammonium loading by invertebrates into tidepools resulted in a doubling of the number of seaweed species present in

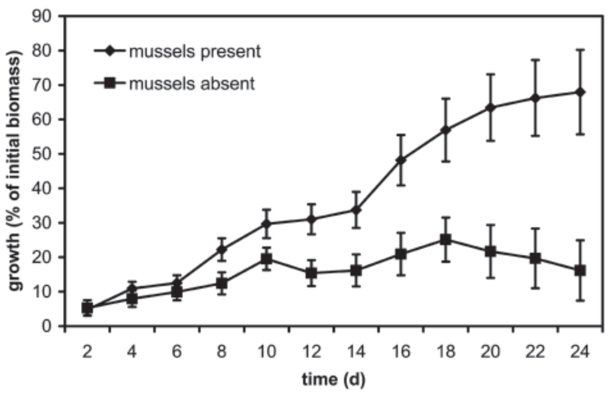

FIGURE 1 Growth of intertidal seaweeds in the presence and absence of mussels. When mussels are present in tidepools, seaweeds grow >40% more than when mussels are absent, because ammonium excreted by mussels enhances seaweed growth. From Bracken (2004), with permission of Blackwell Publishing.

those pools. Growth of the red alga *Odonthalia floccosa*, a common seaweed in high intertidal pools, is more than 40% higher when mussels are present (Fig. 1). Positive interactions such as this one tend to occur when conditions are stressful. Nitrogen limitation in tidepools is ameliorated by local-scale ammonium excretion, which promotes algal diversity and growth in an otherwise inhospitable environment.

SEE ALSO THE FOLLOWING ARTICLES

Algae / Facilitation / Nutrients / Water Chemistry

FURTHER READING

Bayne, B. L. 1976. *Marine mussels: their ecology and physiology*. Cambridge, UK: Cambridge University Press.

Bracken, M. E. S. 2004. Invertebrate-mediated nutrient loading increases growth of an intertidal macroalga. *Journal of Phycology* 40: 1032–1041.

Campbell, J. W., ed. 1970. *Comparative biochemistry of nitrogen metabolism*: 1. *The invertebrates*. New York: Academic Press.

Carpenter, E. J., and D. G. Capone, eds. 1983. *Nitrogen in the marine environment*. New York: Academic Press.

Dame, R. F. 1996. *Ecology of marine bivalves: an ecosystem approach*. Boca Raton, FL: CRC Press.