RESOURCE PARTITIONING AMONG DORIDACEAN NUDIBRANCH MOLLUSCS OF THE SAN JUAN ARCHIPELAGO, WASHINGTON—A GUILD HYPOTHESIS

BLOOM, Stephen A., Ph.D.
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Chairman: Professor Alan J. Kohn

Six sponge-eating dorid nudibranchs common to the San Juan Archipelago, Archidoris montereyensis, Archidoris odhneri, Cadlina luteomarginata, Diaulula sandiegensis, Anisodoris nobilis and Discodoris heathi belong to two exploitive guilds. Members of the guild to which the first three species belong are characterized by having a caecum (a spicule-compacting organ of the stomach); a thin-walled, narrow intestine; and a radula with many fine, moderately hooked teeth. These nudibranchs preferentially consume sponges with an unorganized relationship of spicules and spongin and feed intermittently on available food, a reflection of their cyclic digestive physiology. This digestive cycle is composed of sequential steps of ingestion, extracellular and intracellular digestion, and elimination of organic and inorganic wastes and results in a slow passage of material through the gut and a relatively high efficiency of extraction of digestible organic material from the food. The ceacate dorids belong to the Doridinae, Kentodoridinae, Archidoridinae, Halgerdinae and Chromodoridinae of the Dorididae and to the Hexabranchidae. Members of these taxa usually prey on sponges of the orders Halichondrida and Hadromerida. Specifically in nature, 74% of the diet of Archidoris montereyensis was Halichondria panicea. H. panicea (37%) and Terpios sp. (26.5%) together composed the majority of the diet of Archidoris odhneri. The diet of Cadlina luteomarginata was primarily composed of Higginsia sp. (35%) and Myxilla incrustans (18%).

The other three species belong to the acaecate dorid guild. These nudibranchs do not possess caeca. They have robust intestines and radulas with strongly hooked teeth. These dorids preferentially feed on sponges with highly organized skeletons (strongly reticulated meshes of spicules and spongin). They feed steadily when food is available, a reflection of their non-cyclic digestive phsiology. Non-cyclic feeding proceeds by constant ingestion, extracellular digestion and continual elimination of organic and inorganic wastes resulting in the pattern of constant feeding and in a rapid passage of material through the gut and a relatively low efficiency of extraction of digestible organic material from the food. These dorids belong to the Discodoridinae, Diaululinae and Aldisinae of the Doridiidae. Their usual prey species are in the orders Haplosclerida and Poecilosclerida. Specifically in nature, Halichondria panicea (35%) and Haliclona permollis (33%) were the prime components in the diet of Diaulula sandiegensis. Biemma rhadia (27%) and Myxilla incrustans (25%) dominated the diet of Anisodoris nobilis. Discodoris heathi tended to be a generalist on poecilosclerida sponges; Myxilla incrustans (19%), Mycale adhaerens (19%) and Mycale lingua (24%) dominated the diet of this dorid species. An extensive review of dorid-sponge literature supports the general validity of the existence of these two distinct exploitive guilds.

Iteroparity appears to be normal for sponge-eating dorids i.e., they repeatedly undergo cycles of gamete production and spawning does not imply imminent death. An energy allocation scheme in which a reproductive quota is met before energy is channeled into growth is proposed. The selective advantage of this allocation scheme when the prey is patchy is discussed.

Selection to maximize net energy input by the minimization of utilization costs on morphologically diverse prey could account for the observed patterns of specializations of different dorids on different prey species. Laboratory food preference studies of caecate and acaecate dorids showed that the preferred food was of the type predicted from dorid morphological considerations.

Growth was greater on these foods relative to less preferred foods which have higher digestible organic contents than the more preferred foods. The total amount of material ingested, processed and excreted per unit time for both caecate and acaecate dorids was twice as much when the dorids fed on the less preferred foods than when they fed on the more preferred foods. Based on growth and processing rate differences, caecate and acaecate dorids appear to be able to extract significantly more energy from the more preferred foods even though the less preferred foods have higher digestible organic contents. Small dorids fed and processed food at twice the rates of large dorids feeding on the same sponge but grew at slower rates than did the large dorids.

These observations are consistent with the hypothesis that due to consumption of prey to which the dorid is only marginally adapted (less preferred versus more preferred foods) or due to being smaller than the most efficient size to process the food (small versus large dorids consuming the same prey), assimilation efficiency is decreased. The decrease in assimilation efficiency leads to increased ingestion to compensate for a lower net energy input. Further, the compensation appears to be incomplete leading to decreased growth rates.

In order to assess the ecological similarity of species utilizing discontinuous resource gradients (food, space, etc.), overlap indices and the concept of limiting similarity (species-packing) were briefly examined. The graphical model of species-packing along a continuous resource gradient was converted to a plot of values of overlap indices versus the distance between means of resource utilization functions along the gradient. The value of $\sqrt{2}\sigma$ approximates 0.65 overlap. Several empirical studies suggest that this value of overlap may be the critical minimal ecological distance in species-packing.

Utilizing the knowledge of dorid food preferences and sponge distributions gained from the above research, a sponge-

scallop association was examined. The association of sponges and scallops was shown to be a mutualism. Dorid predation on the sponges and starfish predation on the scallops were shown to be minimized by the mutualism.

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