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# Commentary

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## Exploring Ecology's Attic: Overlooked Ideas On Intertidal Food Webs

*There is an operational uncertainty principle of sorts present when discussing the accomplishments and contributions of any particular area of ecology, for its current status is a product of past research and prevalent opinion, but its validity or utility rests on future developments, especially more rigorous testing.*

—Paine 1977

While the above statement could preface reviews on any subject in ecology, it lacks two additional, interrelated cautions. First, both the current status of a subject and prevalent opinion may not be products of all relevant past research, if ecologists do not seek out those valid and useful findings that were previously reported but are presently overlooked. Second, when research is overlooked, rigorous testing of past ideas is precluded and the potential for restating former findings is great. These concerns extend beyond ecology and were summarized by the psychologist Wolfgang Köhler in 1913:

*Each science has a sort of attic into which things are almost automatically pushed that cannot be used at the moment, that do not quite fit...We are constantly putting aside, unused, a wealth of valuable material [which leads to] the blocking of scientific progress. (as quoted by Sacks [2002])*

Therefore, as recent examples have established (Allee 1934, Allee et al. 1949, Dobzhansky 1959, Jackson 1981, Carothers 1986, Brown and Lomolino 1989, Young 1990, Oksanen 1991, Connell 1992, Lawton 1992, Cohen 1994, Owen 1997, Grant 2000, Dayton and Sala 2001, Egerton 2001, Wool 2001,

Graham and Dayton 2002), it is incumbent on all ecologists not only to explore in the field, but also to thoroughly explore ecology's attic.

Here I draw attention to the significance and details of one of the oldest food web diagrams from North America, and possibly the first intertidal marine food web ever illustrated. Harold Sellers Colton (1916) produced this depiction after his observations on rocky shores in the vicinity of Mount Desert Island, Maine—though it has remained largely overlooked by contemporary ecologists. Based on the lack of references to Colton's (1916) food web findings by succeeding researchers who similarly portrayed species interactions within comparable assemblages throughout New England (Dexter 1947, Menge and Sutherland 1976, 1987, Edwards et al. 1982, Leonard et al. 1998) and the United Kingdom (Lewis 1964, Little and Kitching 1996), I document parallels and contrasts between some of these relatively recent investigations and Colton's descriptions. This discussion may be of general interest to ecologists, as others involved in documenting and comparing food webs have also overlooked Colton's (1916) example (Elton 1927, 1953, Pimm 1982, Paine 1988: Table 2, Cohen et al. 1990). Like his other achievements (ESA 1972, Miller 1991), Colton's early contributions to food web ecology should be appreciated and shared.

While descriptions of feeding relationships and food chains extend back to antiquity (Egerton 1973), food web diagrams are thought to have made their initial appearance much later. Such illustrations potentially provide compelling representations of complex trophic relationships not immediately apparent from lists of interactions or predator gut contents. Food web diagrams are further used for comparisons among regions (e.g., Paine 1966, Menge and Sutherland 1976) and have been a focus of food web theory (Pimm 1982, Paine 1988, Cohen et al. 1990, Polis 1991). As noted by Pimm et al. (1991), the earliest terrestrial food web diagrams were thought to have

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been published in 1912 and 1913—though subsequent exploration of historic literature has uncovered at least one earlier example (Camerano [1880], its context and significance highlighted by Cohen [1994]). Colton's (1916) characterization of the Mount Desert Island "Rock Association" (Fig. 1) was among these earliest recognized food web diagrams and preceded Hardy's (1924) famous depiction of the North Sea herring *Clupea harengus* L. and its prey. However, the earliest published marine food web illustration may be Petersen's (1915) preliminary result from the Kattegat, following his years of research on the marine bottom fauna around Denmark and his analyses of fish stomach contents. Discussion of the Kattegat food web and additional food web diagrams were published in subsequent reports (Blegvad 1916, Petersen 1918).

Colton (1916) presented what can now be considered a simplified, static web of interactions (Fig. 1). It is remarkable that he produced this figure based on observations during the summer of 1915, while collecting over 12,000 dogwhelks *Nucella lapillus* (L.) (as *Thais lapillus* in Colton [1916]) from 67 locations.

He noted, however, that his simple web had additional complexities, and so Fig. 1 was characteristic only of certain locations and conditions on the shore. Colton provisionally classified the "Littoral Formation" into seven "associations" and then noted within the "Solid Rock Association" six additional "zones." Within this classification system, Colton presented clear depictions of local habitat types (associations), vertical zonation (zones) and noted that at most only three of the associations and three zones were suitable for *N. lapillus*. Such descriptions of zonation provided the physical foundation for his food web, and occurred at the same time that experiments on causes of zonation were attempted on the United States Pacific coast (Benson 1992, 2002), though following Pearse's (1913) thorough descriptions of southern New England intertidal zones.

Colton (1916) also asserted that wave stress limited *N. lapillus* distribution within suitable zones in the rock association.

*Accidents, such as a surf heavy enough to move the rocks on which the animals live, may destroy others. In such habitats few if any are found. The maximum size of these rocks may in exposed places be boulders two to three feet in diameter, while in very sheltered places Thais will be found on pebbles two inches in diameter. The limit is obviously determined by wave action.*

Colton 1916:444

Associations between site-specific wave action and *N. lapillus* abundance, and also individual *N. lapillus* feeding rates, were later investigated experimentally through studies at contrasting surf areas across New England (Menge 1976, 1978, Menge and Sutherland 1976). In addition to habitat type and wave stress, Colton provided a list of biotic and abiotic factors observed to limit local *N. lapillus* abundance. They included: cannibalism of young within the egg capsule; limited refuge areas in rock cracks; predation; parasitism; ice scour; and inherent low dispersal ability across sand beaches.

Colton acknowledged in his original figure caption that it illustrated only the principal relations among some species and ignored important feedbacks to other components such as microbe communities and detritivores.

*To be complete this diagram should show an entire cycle of the material. Each one of the organisms listed above gives off liquids to the sea water that may be again used. They also furnish solids either as waste products or by death, which, when acted on by bacteria, will give more soluble matter as well as a residual solid that will help contribute to the sea bottom in other localities. The dead animals will supply food for amphipods, the amphipods food for fishes like the sculpin, and so relations are established with other associations. This diagram shows that the biota of the Rock Associa-*

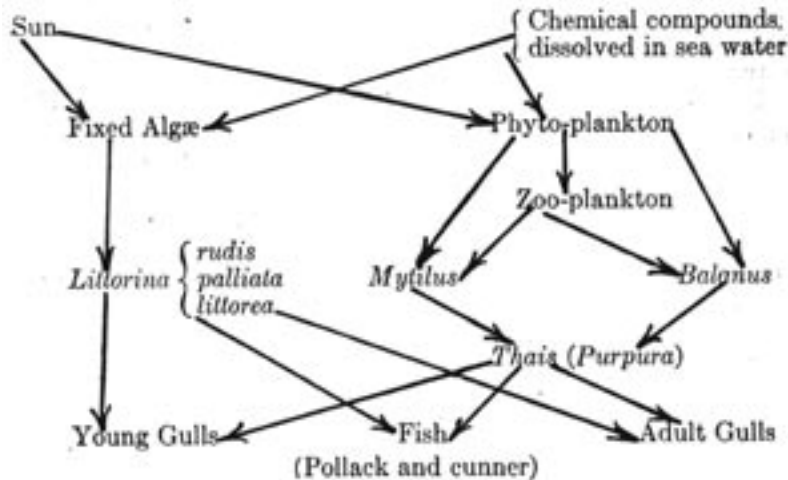


Fig. 1. H. S. Colton's (1916) food web diagram of the Mount Desert Island, Maine, rocky intertidal centered on the "principal relations" of his study species *Thais lapillus* (now *Nucella lapillus* (L.)): "... to its organic environment in the Rock Association." Reproduced with permission from the Academy of Natural Sciences of Philadelphia

tion is dependent alone on the pelagic formation. The relationships with other associations are destructive to it rather than constructive.

—Colton 1916:442

In subsequent depictions of New England intertidal food webs, little mention was made of details on the extensive potential interactions among assemblages as discussed by Colton (but see Dexter 1947, Menge and Sutherland 1987, Little and Kitching 1996). The opinion that contemporary food web simplifications left out important components was expressed decades later for food webs in general (Paine 1988, Polis 1991), Summerhayes and Elton's Bear Island terrestrial food web (Hodkinson and Coulson 2004), and for the New England intertidal specifically (Edwards et al. 1982).

Colton's (1916) food web illustration of "principal relations" (Fig. 1) could also now be considered a representation of only quasi "strong interactions" (MacArthur 1972, Paine 1980), given that though the strengths of interactions were not tested experimentally, presumed weak interactions were excluded.

*It [Nucella lapillus] feeds almost exclusively in this region on the mussel Mytilus edulis, and*

*the barnacle, Balanus balanoides [now Semibalanus balanoides (L.)]. . . . Not only do they [Nucella lapillus] sometimes attack the periwinkle, Littorina littorea, but will try to bore through the shell of one of their own kind. Although many shells show scars, there is no evidence, however, that many are destroyed in this way.*

—Colton 1916:440

Another parallel between Colton's food web portrayal and recent studies concerns the potential role of intertidal predators in addition to *N. lapillus*. As shown in Fig. 1, Colton envisioned two predatory fish species consuming *N. lapillus*, though he reported no direct evidence of this occurring.

*When the tide is high the cunner (Tautoglabrus adspersus) and the pollack (Pollachius virens) invade this formation to feed . . . [p. 441] A few Pollack that were caught at high water over a Thais habitat had their stomachs full of young Littorina palliata [now Littorina obtusata (L.)] which they had eaten from the same locality in which Thais lives. L. palliata cannot hide in the rock cracks, as their food is on the Fucus stems. If the fish could*

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*find young Thais, there is no reason why they should not be eaten as well as Littorina.* (p. 442)

Edwards et al. (1982) also argued that mobile predators including cunner are important in determining the structure of New England intertidal communities and similarly investigated the gut contents of some cunner that they caught. In parallel to Colton's (1916) inferences on the consumption of *N. lapillus* by pollock, Edwards et al. (1982) inferred a weak trophic link between cunner and *N. lapillus* in their revised diagram of the northern New England food web—though as Menge (1982) replied, no *N. lapillus* were reported consumed by cunner. However, in response to the feeding data presented by Edwards et al. (1982), Menge (1982) further implied that cunner were probably not feeding within the low or mid-intertidal zones because *N. lapillus* were not reported consumed by cunner despite high *N. lapillus* abundance throughout these areas. These recent inferences—that predatory fish could (Menge 1982) and do (Edwards et al. 1982) prey on *N. lapillus* when encountered—though separated by decades from Colton's (1916) publication, restated Colton's conclusions and illustrate how a relatively recent debate on food web structure was argued based on long overlooked assumptions.

The most striking characteristic of Colton's food web contribution is its definite resemblance to subsequent depictions, yet reference to his study in modern food web research is lacking. Remarkably similar diagrams of potential trophic linkages—with more and less detail on the direction of interactions—have been published repeatedly during the nearly nine decades since 1916 to illustrate North Atlantic rocky shore interactions, some using experimental methods (Dexter 1947, Lewis 1964, Menge and Sutherland 1976, 1987, Edwards et al. 1982, Little and Kitching 1996, Leonard et al. 1998). Notably, some recent illustrations highlighted contrasts in species' interactions between sites and were accompanied by multifactor hypotheses on physical and biological mechanisms underlying these differences (Menge and Sutherland 1976, 1987, Leonard et al. 1998); following Paine's (1966) influential experimental work on Pacific coast food web structure.

Despite its apparent relevance to these recent works, Colton's food web may have been overlooked due to any number of factors. Brown and Lomolino (1989) suggested four factors in their discussion of why MacArthur and Wilson's concepts of the equilibrium theory of island biogeography were widely acknowledged and accepted, while Munroe's earlier, nearly identical ideas were overlooked: (1) overlooked ideas were unpublished and/or presented in relatively obscure publications; (2) only later were ecologists more receptive to the successful idea; (3) immediate development of the successful idea into a more substantial published form; and (4) relatively elegant, simple, graphical form of presentation of the successful idea. In contrast to the greatest reason suggested for the triumph of MacArthur and Wilson's model (number 4 above, see Brown and Lomolino [1989]), it would be hard to support the notion that only later were food web diagrams more elegant, simple, or robust in comparison to Colton's earlier depiction, as Colton's food web had similar components and linkages, presented in very similar format as later depictions. Rather, I suspect that an interaction between factors 1, 2, and 3 (above) contributed to the neglect of Colton's findings.

Colton published the food web and its discussion as background information, under the section "Life history of *Thais*," in the first of his two papers devoted largely to the causes of morphological variation among *N. lapillus*, as his titles suggested. Though the second paper was published in a more specialized journal (Colton 1922), with requisite self-citation of the former paper, Colton's (1916) paper appeared prior to Elton's (1927) account of the importance of "food cycles" or food webs. Thus due to its publication in a natural history journal prior to the popularity of food web diagrams, it was overlooked by later generations of ecologists—including those who compiled an ever-lengthening list of food webs for tests of theory (e.g., Cohen et al. 1990). Some pairwise interactions between intertidal species have been reported based on Colton's (1916) interaction web (e.g., Fretter and Graham 1962, Largen 1967, Hughes and Dunkin 1984, Crothers 1985), but not his elegant diagram of interactions. Finally, Colton's two publications on *N.*

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*lapillus* represented the extent of his studies of communities on rocky shores. In 1926 Colton left marine biological research in the Northeast to study archeology in the deserts of the Southwest, distancing himself from any further studies on marine ecology (Miller 1991).

As his food web is seemingly among the first published, one additional question is raised: Did Colton's food web represent an origin of species interaction diagram independent from those developed by other terrestrial or marine researchers? It appears not. Shelford's (1913) illustrations of species interactions apparently influenced Colton's characterization of the relationships among Rock Association species. Though Colton did not directly mention Shelford's (1913) book in his paper, Colton did acknowledge Shelford (1913) within his "List of Literature" (Colton 1916:454).

In contrast to the reference by Colton to Shelford's previous food webs, contemporary researchers investigating intertidal assemblages have apparently not recognized Colton's early contributions to food web ecology. This is unfortunate, and again illustrates that while concepts, depictions, and theories generated by ecologists today may be supported or rejected by the rigorous tests of tomorrow, evaluating ideas based on present and future results is perilous without an appreciation of what has been previously reported (Lawton 1992, Graham and Dayton 2002). Without increased attention to ecology's past, contemporary researchers will continue to restate previous ideas—unknowingly substituting rediscovery for true discovery.

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### Literature Cited

Allee, W. C. 1934. Concerning the organization of marine coastal communities. *Ecological Mono-*

*graphs* 4:541–554.

- Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. *Principles of animal ecology*. W. B. Saunders, Philadelphia, Pennsylvania, USA.
- Benson, K. R. 1992. Experimental ecology on the Pacific coast: Victor Shelford and his search for appropriate methods. *History and Philosophy of the Life Sciences* 14:73–91.
- Benson, K. R. 2002. The study of vertical zonation on rocky intertidal shores—a historical perspective. *Integrative and Comparative Biology* 42:776–779.
- Blegvad, H. 1916. On the food of fish in the Danish waters within the Skaw. *Report of the Danish Biological Station* 24:17–75.
- Brown, J. H., and M. V. Lomolino. 1989. Independent discovery of the equilibrium theory of island biogeography. *Ecology* 70:1954–1957.
- Camerano, L. 1994. On the equilibrium of living beings by means of reciprocal destruction. [Dell'equilibrio dei viventi mercé la reciproca distruzione.] Translated by C. M. Jacobi, edited by J. E. Cohen. Pages 360–380 in S. A. Levin, editor. *Frontiers in mathematical biology*. Springer-Verlag, Berlin, Germany.
- Carothers, J. H. 1986. Homage to Huxley: on the conceptual origin of minimum size ratios among competing species. *American Naturalist* 128:440–442.
- Cohen, J. E. 1994. Lorenzo Camerano's contribution to early food web theory. Pages 351–359 in S. A. Levin, editor. *Frontiers in mathematical biology*. Springer-Verlag, Berlin, Germany.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community food webs: data and theory*. Springer-Verlag, New York, New York, USA.
- Colton, H. S. 1916. On some varieties of *Thais lapillus* in the Mount Desert region, a study of individual ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* 68:440–454.
- Colton, H. S. 1922. Variation in the dog whelk, *Thais* (*Purpura* auct.) *lapillus*. *Ecology* 3:146–157.
- Connell, J. H. 1992. The profound effect of a pioneer French ecologist—a Citation Classic commentary on: Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *ISI Current*

- 
- Contents (June 15) **24**:8. <<http://garfield.library.upenn.edu/classics.html>>
- Crothers, J. H. 1985. Dog-whelks: an introduction to the biology of *Nucella lapillus* (L.). *Field Studies* **6**:291–360.
- Dayton, P. K., and E. Sala. 2001. Natural history: the sense of wonder, creativity and progress in ecology. *Scientia Marina* **65** (Supplement 2):199–206.
- Dexter, R. W. 1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: a study in bio-ecology. *Ecological Monographs* **17**:261–294.
- Dobzhansky, T. 1959. Blyth, Darwin, and natural selection. *American Naturalist* **93**:204–206.
- Edwards, D. C., D. O. Conover, and F. Sutter III. 1982. Mobile predators and the structure of marine intertidal communities. *Ecology* **63**:1175–1180.
- Egerton, F. N. 1973. Changing concepts of the balance of nature. *Quarterly Review of Biology* **48**:322–350.
- Egerton, F. N. 2001. A history of the ecological sciences: early Greek origins. *ESA Bulletin* **82**:93–97.
- Elton, C. 1927. *Animal ecology*. Macmillan, New York, New York, USA.
- Elton, C. S. 1953. *The ecology of animals*. Third edition. Wiley, New York, New York, USA.
- ESA (Ecological Society of America). 1972. Resolution of respect. Harold Sellers Colton, 1881–1970. *ESA Bulletin* **53**:12–13.
- Fretter, V., and A. Graham. 1962. *British prosobranch molluscs: their functional anatomy and ecology*. Ray Society, London, UK.
- Graham, M. H., and P. K. Dayton. 2002. On the evolution of ecological ideas: paradigms and scientific progress. *Ecology* **83**:1481–1489.
- Grant, P. R. 2000. R. C. L. Perkins and evolutionary radiations on islands. *Oikos* **89**:194–201.
- Hardy, A. C. 1924. The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. *Fishery Investment Series II* **7**:1–53.
- Hodkinson, I. D., and S. J. Coulson. 2004. Are high Arctic terrestrial food chains really that simple?—the Bear Island food web revisited. *Oikos* **106**:427–431.
- Hughes, R. N., and S. de B. Dunkin. 1984. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. *Journal of Experimental Marine Biology and Ecology* **77**:45–68.
- Jackson, J. B. C. 1981. Interspecific competition and species' distributions: the ghosts of theories and data past. *American Zoologist* **21**:889–901.
- Köhler, W. 1913. Über unbemerkte Empfindungen und Urteilstäuschungen. *Zeitschrift für Psychologie* **66**:51–80.
- Largen, M. J. 1967. The diet of the dog-whelk, *Nucella lapillus* (Gastropoda Prosobranchia). *Journal of Zoology* **151**:123–127.
- Lawton, J. H. 1992. (Modest) advice for graduate students. *Oikos* **65**:361–362.
- Leonard, G. H., J. M. Levine, P. R. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* **79**:1395–1411.
- Lewis, J. R. 1964. *The ecology of rocky shores*. English University Press, London, UK.
- Little, C., and J. A. Kitching. 1996. *The biology of rocky shores*. Oxford University Press, New York, New York, USA.
- MacArthur, R. 1972. Strong, or weak, interactions? *Transactions of the Connecticut Academy of Arts and Sciences* **44**:179–188.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**:355–393.
- Menge, B. A. 1978. Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia* **34**:1–16.
- Menge, B. A. 1982. Reply to a comment by Edwards, Conover, and Sutter. *Ecology* **63**:1180–1184.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: syntheses of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110**:351–369.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**:
-

- 
- 730–757.
- Miller, J. H. 1991. The life of Harold Sellers Colton: a Philadelphia brahmin in Flagstaff. Navajo Community College Press, Tsaile, Arizona, USA.
- Oksanen, L. 1991. A century of community ecology: how much progress? *Trends in Ecology and Evolution* **6**:294–296.
- Owen, D. F. 1997. Natural selection and evolution in moths: homage to J. W. Tutt. *Oikos* **78**:177–181.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Pages 245–270 in C. E. Goulden, editor. *Changing scenes in natural sciences, 1776–1976*. Academy of Natural Sciences of Philadelphia Special Publication **12**, Philadelphia, Pennsylvania, USA.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development? *Ecology* **69**:1648–1654.
- Pearse, A. S. 1913–1914. Observations on the fauna of the rock beaches at Nahant, Massachusetts. *Bulletin of the Wisconsin Natural History Society* **11**: 8–34 (concluded in 1914, **12**:72–80).
- Petersen, C. G. J. 1915. A preliminary result of the investigations on the valuation of the sea. Report of the Danish Biological Station **23**:29–33.
- Petersen, C. G. J. 1918. The sea bottom and its production of fish-food. Report of the Danish Biological Station **25**:1–62.
- Pimm, S. L. 1982. *Food webs*. Chapman and Hall, New York, New York, USA.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature* **350**:669–674.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* **138**:123–155.
- Sacks, O. 2002. Scotoma: forgetting and neglect in science. Pages 70–83 in E. B. Hook, editor. *Prematurity in scientific discovery*. University of California Press, Berkeley, California, USA.
- Shelford, V. E. 1913. *Animal communities in temperate America*. University of Chicago Press, Chicago, Illinois, USA.
- Wool, D. 2001. Charles Lyell – “the father of geology” – as a forerunner of modern ecology. *Oikos* **94**:385–391.
- Young, C. M. 1990. Larval ecology of marine invertebrates: a sesquicentennial history. *Ophelia* **32**: 1–48.
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