

DIGESTION IN MARINE HERBIVOROUS FISHES:

IS SOME FIBRE NEEDED IN THE DIET?

Kendall D. Clements
School of Biological Sciences, University of Auckland
Private Bag 92019, Auckland, New Zealand
phone: (64 9) 373 7599 fax: (64 9) 373 7417
E-mail: k.clements@auckland.ac.nz

EXTENDED ABSTRACT ONLY – DO NOT CITE

At present we lack a framework that allows us to understand the relationships between different diets and the diversity of digestive systems seen in marine herbivorous fishes. Such a framework would allow us to interpret diet composition, e.g. secondary metabolites, in the context of nutrition. An appropriate context does exist in the terrestrial literature (e.g. Van Soest 1994), where the fate of plant production is modeled with respect to the digestive processes of herbivores. I will review five inter-related areas (digestive mechanisms, plant composition, the concept of fibre, ingestion and throughput rates, and microbial processes) where I believe our progress is hampered by lack of knowledge and erroneous assumptions.

Digestive mechanisms

An examination of the literature suggests digestion in marine herbivorous fishes is largely understood in the context of the mechanisms for lysis of algal cells first proposed by Lobel in 1981 and developed by Horn (e.g. Horn 1989). These mechanisms are acid lysis in the stomach, trituration in a gizzard-like stomach, trituration in a pharyngeal mill, and microbial fermentation in the hindgut. While these were originally (and sensibly) proposed as mechanisms for cell lysis, they seem to be understood by many workers as digestive mechanisms, i.e. mechanisms that enable fishes to digest algal nutrients. Perhaps as a result, we know very little about the digestive enzymes of these fishes, a problem that has been identified previously (Horn 1989).

Plant composition

Marine algae contain a higher proportion of protein and a smaller proportion of structural components than terrestrial plants (Choat and Clements 1998). On this superficial basis the algal diet of marine herbivorous fishes may seem less refractory than the diet of terrestrial herbivores. However, the diversity of marine algae, and their disparity in terms of constituent polysaccharides, may constrain digestive specialization in herbivorous fishes. This may be especially marked in grazing fishes, which ingest a broad range of dietary substrates. It is widely acknowledged that algal cell wall polysaccharides are unlikely to be hydrolysed by endogenous digestive enzymes, yet even chlorophyte and rhodophyte starches vary in their susceptibility to fish amylases (Zemke White and Clements 1999). We need a better understanding of algal carbohydrates, so the relationships between diet choice (e.g. secondary metabolite deterrence) and digestive systems can be determined.

The concept of fibre

The diets of terrestrial vertebrate herbivores are generally explained in terms of fibre content. Animals with high fibre diets typically rely on gastrointestinal symbioses with microorganisms to extract sufficient energy from their food. We have no concept of fibre for marine herbivorous fishes. In other words, we are unable to predict how different algal components are degraded by endogenous (i.e. host fish) and exogenous (i.e. microbial) enzymes. As a result, we have no framework within which to characterise diets in relation to different digestive systems, i.e. predict diet quality. Given the disparity of algal carbohydrates, it seems likely that much of the material ingested by herbivorous fishes will be refractory to endogenous enzymes, i.e. fibrous.

Ingestion and throughput rates

Fish could respond to fibrous algal diets in at least three ways: (a) by employing high ingestion rates and rapid turnover of gut contents, (b) supplement their algal diet with animal material (or detritus) if they are incapable of properly digesting the plant component, and (c) salvage energy via the use of digestive symbioses with gut microorganisms. We have an extremely poor understanding of throughput rates in fishes, as illustrated by comparison with terrestrial studies. A model for quantifying relationships between diet quality, digestive processes and body weight in ungulates (Illius and Gordon 1992) contains 9 rate variables.

We do not have estimates for any of these variables in marine herbivorous fishes.

Microbial processes

It is becoming increasingly apparent that microorganisms play a role in digestion in some marine herbivorous fishes, as they do in most terrestrial vertebrate herbivores. However, work in this area is in its infancy. To date no published data exist on fermentation rates in these fishes. We have very little idea of the substrate utilisation (for an exception see Seeto et al. 1996) or species composition of these microbial communities. No published information exists on the stoichiometry of fermentation in these systems, i.e. the energetics of fermentation and the loss of short-chain fatty acids (SCFA) to microbial processes. We do not know whether the metabolic physiology of host fishes is geared towards a metabolic diet of SCFA. One current problem seems to be a reliance upon *in vitro* studies of isolated microorganisms, as these studies tell us little about processes taking place in microbial communities *in vivo*.

Acknowledgments

I am grateful to the following colleagues for helpful discussions on the topics of herbivory, plant digestion and microbial processes: Dave Bellwood, Howard Choat, Garth Cooper, David Crossman, Phillip Harris, Linn Montgomery, Doug Mountfort, Tony Roberton, Michael Slaytor, Sue Turner, and Lindsey Zemke-White.

References

- Choat, J.H. and Clements, K.D. 1998. Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. *Annu. Rev. Ecol. Syst.* 29: 375-403
- Horn, M.H. 1989. Biology of marine herbivorous fishes. *Oceanogr. Mar. Biol. Annu. Rev.* 27: 167-272
- Illius, A.W., and I.J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* 89: 428-434

- Seeto, G.S., P.C. Veivers, K.D. Clements and M. Slaytor. 1996. Carbohydrate utilisation by microbial symbionts in the marine herbivorous fishes *Odax cyanomelas* and *Crinodus lophodon*. J. Comp. Physiol. B 165: 571-579
- Van Soest, P. J. 1994. Nutritional ecology of the ruminant. 2nd Ed. Cornell University Press, Ithaca, New York
- Zemke-White, W.L., and K.D. Clements. 1999. Chlorophyte and rhodophyte starches as factors in diet choice by marine herbivorous fish. J. Exp. Mar. Biol. Ecol. 240: 137-149

