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New perspectives on the feeding ecology and trophic dynamics of fishes

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Feeding – the linked processes of finding, eating, and digesting food – is a complex interplay between behavior, morphology, physiology, population dynamics (of predators, prey and competitors), and predator-prey interactions. Feeding occurs in an ecological context, where it affects not only the energy transfer and subsequent growth and survival of individual predators and prey, but also their distribution, abundance, and demographics. Moreover, these processes can be dynamic, changing population productivity and trophic structure at ecological or evolutionary time scales. Thus, feeding ecology and trophic dynamics is a broad, interdisciplinary field that spans across organismal, population, community and ecosystem science.

In aquatic systems, predator-prey interactions are difficult to observe directly. Scientists have met such challenges by collecting individuals in the field and subsequently visually examining the stomach contents (Hyslop 1980; Gerking 1994). Technological innovations have expanded the toolbox in recent decades, particularly with molecular methods such as analysis of fatty acids, stable isotopes, or the genetic code. A suite of holistic ecosystem modeling tools, such as ECOPATH, ATLANTIS and their derivatives, have allowed more robust analysis of such data (Pauly et al. 2000; Gaichas et al. 2009; Fulton 2010). Policy shifts have also affected the study and purpose of feeding ecology and trophic dynamics, as fisheries managers have adopted ecosystem-based fisheries management (EBFM) as a guiding principle toward a more holistic approach to resource management (Pikitch et al. 2004; Link 2010). However, given the complexity of many ecosystems, we often lack basic knowledge on the trophic interactions critical to understanding system productivity or applying such knowledge in a management context, leading to potential bias and poor management decisions. Given this need and in this increasingly broader context, broad evaluations of fish feeding ecology and trophic dynamics have appeared and are warranted.

A history of scientific progress in fish feeding ecology and trophic dynamics has been captured in an irregular series of symposia and subsequent publications titled '*GUTSHOPS*.' The first of these, "*GUTSHOP '76: Fish Food Habits Studies*," was a small volume (193 pp.) that highlighted a full range of best practices in the field, in the laboratory, and in terms of statistical analysis and interpretation (Simenstad and Lipovsky 1977). Each subsequent GUTSHOP documented, and in their own way spurred, a transformation of this increasingly transdisciplinary field of study. They occurred fairly frequently, published in a variety of

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formats, up until the late 1990s (e.g., Simenstad and Cailliet 1986; MacKinlay and Shearer 1996). In 2014, a modest revival of the GUTSHOP concept occurred in Quebec City, Canada, with a symposium titled "Community Ecology and Trophic Interactions of Fishes," at the 144th Annual Meeting of the American Fisheries Society. Although no symposium volume was planned, the enthusiastic response of presenters clearly suggested that the GUTSHOP concept should be revived and continued into the future.

This special volume in '*Environmental Biology of Fishes*' represents a compendium of selected papers presented at the subsequent "*GUTSHOP 2015: New perspectives on the feeding ecology and trophic dynamics of freshwater and marine fishes,*" which was held at the 145th Annual Meeting of the American Fisheries Society (AFS), Portland, Oregon. GUTSHOP 2015 included 53 talks over three days dealing with newer techniques and advances on a myriad of topics related to fish feeding. These included functional morphology, feeding physiology, bioenergetics, predator-prey behavior, consumption estimates and impacts, sampling design and statistics, as well as ways that feeding dynamics can be integrated into fisheries management. Presentations also examined alternative ways to examine diets beyond direct stomach analysis (e.g., genetic, stable isotopes, fatty acid signatures, scanning techniques).

The keynote address was appropriately led by Charles Simenstad and Gregor Cailliet, both originators of the GUTSHOP series. In their overview paper, Simenstad and Cailliet (2016) summarize the history of the GUTSHOPS. These were mostly small independent workshops held on the west coast of the US. Simenstad and Cailliet provide an overview of the evolution of the field through these workshops, highlighting four research foci that they feel have specifically benefitted from these GUTSHOPS, including 1) methods of prey identification, 2) analysis of sample size requirements, 3) trophic indices of relative prey importance, and 4) the use of bioenergetic modeling to estimate food consumption or growth.

In a novel approach to prey recognition and feeding behavior, Collins and Motta (2016) observed wild Goliath grouper (*Epinephelus itajara*) in the field consuming both mobile and non-mobile prey on an artificial reef in the Gulf of Mexico. The kinematics of feeding were monitored by video cameras positioned at various perspectives relative to the predator and prey. They found that mobile food elicited different feeding modes (ram feeding) compared to immobile food (suction feeding) and most of the metrics involved with feeding (striking distance, mouth gape, capture times) also varied by food type. The finding that this heavily-exploited species utilizes different functional feeding strategies depending on prey activity levels has important implications for sport fishing management in this region. This work also highlights the ability to study fish feeding via technological advancements such as affordable underwater video systems that were not available until recently.

Aguilar et al. (2016) evaluated DNA barcoding as a method for piscine prey identification of three catfish species (one native and two invasive) of Chesapeake Bay, USA. Visual prey identification has limitations due to material being highly digested and unrecognizable. Here, DNA barcoding was 90% successful with identifying piscine prey in catfish stomach contents. Of these prey, 92% were successfully identified to species and included Alosa spp. (under restoration), and commercially important fishes (e.g. striped bass *Morone saxatilis*, white perch *Morone americana*, American eel *Anguilla rostrata*, and menhaden *Brevoortia tyrannus*). Overall, DNA barcoding was highly successful at identifying all but heavily degraded prey. It can be an effective method for obtaining high resolution trophic information. This work represents an example of molecular tools that the field has been utilizing much more frequently given the advent of widely available DNA sequencing.

The paper by Litz et al. (2016) integrates fatty acid and isotopic analysis to understand foraging ecology of Chinook salmon in the California Current and demonstrates the value of combining these analyses for resolving foraging ecology. They reported a shift in carbon from terrestrial sources in the fish tissues to marine sources that coincided with an increase in fatty acids indicative of marine phytoplankton. As the fish grew, fatty acid markers for piscivory increased in their tissues as did their trophic position. The timing of these events depended on growing conditions in the marine environment. The two methods were clearly able to resolve ontogenetic shifts in the energy sources consumed by Chinook salmon in the California Current and place those shifts into a context that relates to their survival. The use of these methods has broad applicability to our understanding how environment influences trophic interactions between species. This study demonstrates the utility of tying together two different analytical approaches and we expect future approaches to provide an even greater understanding of foraging ecology in marine ecosystems.

In the Bering Sea, there is interest in developing a commercial fishery for giant Pacific octopus (*Enteroctopus dofleini*), yet there is insufficient catch history data, absence of fundamental life history information, and lack of directed sampling on this species to conduct a stock assessment. To address this issue, Rohan and Buckley (2016) used Pacific cod (*Gadus macrocephalus*) diet data as a basis for estimating octopus complex natural mortality and minimum biomass. The data for this analysis come from long-term collections of Pacific cod stomach contents from stock assessment surveys conducted on the eastern Bering Sea shelf. They found that the consumption-based stock assessment method may underestimate total octopus complex biomass because the stomach contents of Pacific cod tend to be biased toward smaller octopus in the region. Regardless, this approach emphasizes the novel use of fish food habits data that can inform data-poor situations, serving as an alternative and creative means to inform fisheries management decisions.

Bizzarro et al. (2016) conducted a meta-analysis of the diets of 18 commercially-important groundfishes and their life stages from the U.S. Pacific Coast. By developing a Major Prey Index, unidentified fishes, euphausiids, and brachyuran crabs were determined to be important prey. Considering the variables: predator species, life stage (e.g. juvenile, adult), functional group (e.g. benthic, pelagic), and taxonomic group (e.g. elasmobranch, roundfish), the primary source of diet variability was between predator species. Significant feeding differences were found among functional groups, and two significantly distinct trophic guilds (1. consuming polychaetes and hard-shelled molluscs, and 2. consuming euphausiids) were identified. This work helps to fill an informational diet data gap in this region and will contribute to habitat-based management of commercially-important groundfishes. This work also represents an example of the advances in multivariate statistics that have further elucidated fish feeding ecology.

Two studies in this volume investigated the trophic impact of the invasive zebra mussel (*Dreissena polymorpha*) in different aquatic systems. Working in the Hudson River estuary, Smircich et al. (2016) examined diets of early-stage striped bass (*Morone saxatilis*) in 14 years of a 25-year period. They predicted that indicators of bass feeding success (i.e., gut content volume and predator condition) would decrease, and that diet composition would shift, in relation to increased abundance of mussels. The abundance of mussels varied over the period and so did feeding success, however, a strong negative effect was noted only at upper estuarine locations. The effect of mussels as competitors was modified by both prey density and select environmental conditions, notably salinity and dissolved oxygen. Fluctuations in mussel abundance did not affect bass diet composition. Although the invasion of zebra mussels to the Hudson River system was a major perturbation, it is unlikely that a short-term study would have revealed these trophic effects as evident here, in altering the early-stage growth of striped bass.

In Lake Huron, Thompson et al. (2016) investigated the trophic impact of the zebra mussel, where its introduction had already been associated with a decline in *Diporeia*, a common benthic prey item, and this decline was evident in changes in native benthivore diets as well. Here, the diet of deepwater sculpin (*Myoxocephalus thompsonii*) was examined for the years 2010–2014 and compared to an earlier diet study (2003–2005), a period when *Diporeia*'s abundance and distribution declined. In the more recent period, *Diporeia* had become important in sculpin diets but only in deeper strata, and the weight of the sculpin increased but only among the largest size class. This study documented not only the resiliency by *Diporeia* in deeper habitats and its continued role as sculpin prey, but it also revealed broader dynamics of diet composition, specifically increased consumption of *Mysis* prey in the shallow depth strata. Both of these studies, in the Hudson River and Lake Huron, demonstrated the value of longer time series and relevant spatial coverage to evaluate the dynamics of trophic interactions in nature, thus emphasizing the need for and value of routine monitoring of fish food habits.

Buckley and Whitehouse (2016) examined the summer diet of Arctic cod (*Boreogadus saida*) across a latitudinal gradient extending from the southern limit of their distribution in the eastern Bering Sea to the northern margins of the eastern Chukchi Sea continental shelf. Regional variations in the diets of Arctic cod were found. For instance, the demersal Arctic cod diets in the northern latitudes were dominated by copepods, whereas their diets consisted of a variety of prey items in the southern latitudes. Within the Chukchi Sea, consumption of fishes and decapod crustaceans were positively correlated with Arctic cod length, while consumption of euphausiids and copepods had the opposite relationship. The authors note that Arctic cod diet variability highlights the need to monitor changes in trophic relationships especially for rapidly changing ecosystems. This again reinforces the need for routine monitoring of fish food habits, particularly in response to climate change effects that can have major implications for food webs.

Finally, Livingston et al. (2017) provide an overview of the Alaska Fisheries Science Center's Groundfish Trophic Interactions Database as an aid for the interpretation and application of these diet data stemming from the eastern Bering Sea, Gulf of Alaksa, and Aleutian Islands large marine ecosystems in the North Pacific Ocean. The database (1981–2011; 233,541 fish stomachs) includes diet information for 159 total species, and focuses on four primary species: walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and arrowtooth flounder (*Atheresthes stomias*). These data permit the quantification of food web interactions, and are the building blocks to develop ecosystem indicators and support ecosystem-based fisheries management for this highly-productive Alaskan ecosystem.

In summary, although there certainly have been many advances in the discipline of fish feeding ecology, there are many traditional aspects of this field that continue to be refined by researchers working in both freshwater and marine ecosystems. We hope that the papers presented here will serve as a stimulus for more in-depth work to come that examines the complexity of food web linkages and their role in fisheries management (Hunsicker et al. 2011).

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