On the methodology of feeding ecology in fish

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ABSTRACT

Feeding ecology explains predator's preference to some preys over others in their habitat and their competitions thereof. The subject, as a functional and applied biology, is highly neglected, and in case of fish, a uniform and consistent methodology is absent. The currently practiced methods are largely centred on mathematical indices and highly erroneous because of non-uniform outcomes. Therefore, it requires a relook into the subject to elucidate functional contributions and to make it more comparable and comprehensive science. In this article, approachable methodological strategies have been forwarded in three hierarchical steps, namely, food occurrence, feeding biology and interpretative ecology. All these steps involve wide ranges of techniques, within the scope of ecology but not limited to, and traverse from narrative to functional evolutionary ecology. The first step is an assumption-observation practice to assess food of fish, followed by feeding biology that links morphological, histological, cytological, bacteriological or enzymological correlations to preferred food in the environment. Interpretative ecology is the higher level of analysis in which the outcomes are tested and discussed against evolutionary theories. A description of possible pedagogics on the methods of feeding ecological studies has also been forwarded.

INTRODUCTION

Irrespective of their way of feeding, say it be 'passive' or 'active', fishes are ultimate predator of phytoplankton (after Begon et al. 2006), zooplankton or small fishes. In all groups of fishes, the mode of predation (e.g. 'hang and wait' or 'move and hunt') has great contribution to successful feeding, mostly in preference and selection of specific food items from a diverse group of resources. Such 'preferential feeding' has rare possibility to be a linear ecological function, rather, it is a kind of non-linear behaviour, across many gradients scaled on time (e.g. ontogenic shifting of fish), space (e.g. across depth or temperature), morphology (e.g. prey morphology or predator size) or other biological attributes.

Feeding ecology, in animal science, defines a relationship where the animal adopts a strategy for optimum foraging of or predation on its preferred food. As a result of their complex life history, food preferences or trophic selection by fishes play crucial role in their development, growth and survival, which often shifts from one type of food or trophic level to other during ontogeny. Three most generalised ontogenic stages of fishes are larval, juvenile and adult. For migratory fishes, parr and smolt are additional morpho-physiological ontogenic stages. These ontogenic forms compete in water for feeding within the population itself and also with co-habiting species. Under such situation, similar to other vertebrates, fishes tend to fit through niche apportionment with minimum diet overlap to avoid unruly competitive outcomes. Therefore, how fishes 'optimally manage' to eat their preferred prey during ontogenic shifting as well as under high competitive pressure and remain cohesive to an ecologically sustainable model is the key criterion of their feeding ecology, and coincidently, sparks micro-evolution.

Feeding ecology in fishes questions how fish selectively ingest some food organisms over others in the aquatic

habitat (Wotton 1998) and analyses diverse modes of feeding adaptations complying their morphological (Cailliet et al. 1996; Wotton 1998), physiological and sensoneural responses to food types and food abundance in the habitat. This vertebrate group exhibits high variability from richness [approximately 33,200 species (Froese & Pauly 2016)] to distribution across all types of aquatic habitats. In addition, their habitat, body forms and growth patterns are also highly variable. In view of such high variability and diversity in structures and organisations, food preference of this group cannot be explained only through few selective methods but better interpretation can be presented encompassing different descriptive, numerical, biological and functional attributes that favour food preference in a particular environment.

Addressing ecological interactions of a species in terms of food is not a new practice (e.g. Northcote 1954), but feeding ecology as a concept was emerged probably in early 1980s (Cummis & Klug 1979). In fish, Gerking (1994) refined this concept on the background of optimal foraging theory, in relation to physiological adaptation of the fish. He solely emphasised to framework the concept and did not intend to elaborate a 'must do' kind of methodological approach to decipher it as biological phenomenon. Literally, voluminous methodological approaches on feeding ecology of fishes were emerged during the past few years, and the only basis of these methods included gut content analysis along with the computation of some randomly selected mathematical indices. To date, at least 15 of such indices are randomly and frequently used to report feeding ecology of fish (Table 1, A–D). These indices submit a mathematical count of the types of food being selected and eaten by a fish species in an environment but fail to justify 'why' these foods are selected or eaten over others? The fact is that feeding is more of biological activity than some mathematical interpretations. Extensive reliance on mathematical-model-based approaches without a justified bio-math consortium results blurred and inconsistent outcomes on foraging behaviour of a fish species. Optimal foraging, the core hypothesis of feeding ecology, in true sense explains 'why' animals make certain choices of food in their diet rather than evaluating how much it eats. The available diet-based observations are, therefore, needed to be critically evaluated and analysed under the preview of other major biological dimensions such as chemical, physiological, cytological, enzymological and sensory biology of fish. On a random survey with the key word 'feeding ecology and fish' in Google search (www.google.com) for a period from 2006 to 2015, studies were found to be largely dealing with one or other mathematical indices listed in Table 1. Both in fish related and ecology-related journals, more emphasis was given to mathematical indices over others (Fig 1). Of course, a few of which extended their studies up to stable isotope analysis of gut content and video recording of feeding. One of the great inconsistencies in these studies is the non-uniform selection of methods without any a priori justification. Except gut con-
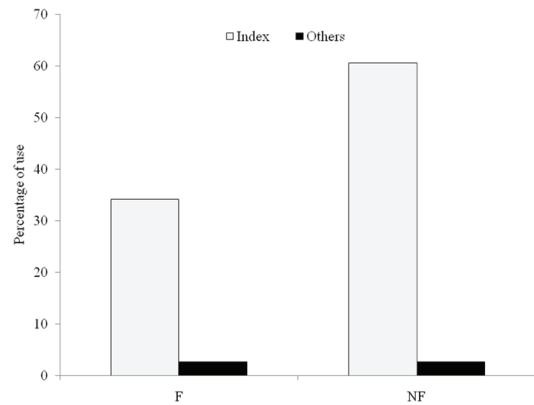

Figure 1. Survey on methods used to study feeding ecology of fish in fish-related (F) and ecological (NF) journals from 2006 to 2015 (N = 38). All data are collected from www.google.com on 01/05/2015. 'Index' are methods dealing with mathematical computations (e.g. indices in Table 1) and 'Others' includes all feeding ecological methods other than 'index'.

Table 1. Indices used to measure food occurrence (A), diet breadth (B), food selection (C) and diet preference and overlap (D) in the environment of fish. E lists indices used to determine mouth gape of fish.

A	B	C	D	E
Occurrence Index (Smyly 1952)	Levin's index (after Hulbert 1978)	Mac Arthur and Levins Index (1967)	Ivlev's selectivity index (1961)	MA (Erzini et al. (1997)
Index of Relative Importance (IRI) (Pinkas et al. 1971; Windell 1971)				GS 90° (Ponton & Müller 1990)
Frequency of Occurrence (Hyslop 1980)	Shannon-Wiener Index (Colwell & Futuyma 1971)	Index C (Pearre Jr 1982)	Schoener's index (1968, 1970)	
	Manly's α (Manly et al. 1972; Chesson 1978)	Percentage overlap (Renkonen 1938)		
	Smith index (1982)			

tent analysis as frequency of occurrence in majority of these studies, the core ecological indices were selected following a kind of 'pick and choose' pattern implying biases to the subject. To make it clear, 11 of such studies in high impact journals from fish biological as well as aquatic research were shown in Table 2. What is more, to such index-based feeding ecological reports, no single study incorporated two major biological dimensions of feeding, that is, morphology and physiology, that largely regulate their food selectivity. In the absence of any uniformity in methods and ignorance of associated biological dimensions of feeding in these studies, the outcomes are instantaneous, inconclusive and non-comparable. This otherwise illustrates the classical problem of not having a uniform and subjective methodological strategy to study feeding ecology of fish. A common and systematic strategy must be adopted to decipher maximum scientific information on the behavioural, anatomical and physiological flexibility of fish for feeding. Unfortunately, such an applied and holistic strategy is greatly lacking in fish biology and ecological research. The present review, therefore, is a maiden attempt to link available scattered methods and thereby to propose a line of systematic methodological approach with justifications that may help to best describe and configure more realistic accounts of feeding ecology in fish.

1. FOOD, FISH AND ECOLOGY OF FEEDING

Unlike all other animals, fish follows one of the three distinct options for feeding, as herbivorous or carnivorous or both. In relation to its feeding, the body of the fish adapts changes morphologically, anatomically and physiologically (Cortés et al. 2008; Wainwright 1988, 1996; Yashpal 2009). Conventionally,

body forms are considered as strong attributors to successful feeding in fish. There are direct feeding relationships to changes in several morphometric characters of fish in their environment (Bohórquez-Herrera et al. 2015). Further, food in the environment in combination with other physiological factors (e.g. temperature) could influence the overall feeding performance in fishes (Behrens & Lafferty 2007). Recent studies also showed functional relationship of gut microbial diversity in fish to generalise or specialists feeding habits (Bolnick et al. 2014). Similarly, their sensory organs as well as digestive functions adjust in concert to optimise the feeding mechanism (Wilkens et al. 2001; Scharnweber et al. 2013). A generalised outline of these attributors and their context-dependent role are explained in Fig. 2.
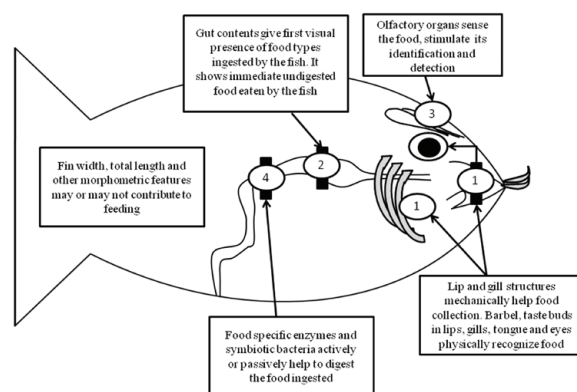

Figure 2. Different attributors that directly influence feeding ecology of fish. (1) Mouth morphometry, (2) gut characteristics, (3) olfaction and (4) Microbial diversity.

Table 2. Ten cases (2006-2015) showing variable methods of feeding ecological studies in leading fisheries and aquatic ecological journals.

Pothoven & Nalepa (2006)	Journal of Great Lakes Research	Percentage occurrence of diet, Prey specific abundance (Amundsen 1996)
Pelicice & Agostinho (2006)	Ecology of Freshwater Fish	Feeding Index (Kawakami & Vazzoler 1980), Overlap Index (Pianka 1973), Mean Stomach Fullness (Pelicice et al. 2005)
Northcote & Hammar (2006)	Boreal Environment Research	Overlap Index (Schoener 1970)
Navia et al. (2007)	BMC Ecology	Frequency of occurrence of diet, Index of Relative Importance, Levins diet breadth, Diet overlap (Pianka 1973)
Wells & Rooker (2009) and Albo-Puigserver et al. (2015)	Journal of Fish Biology Marine Ecology Progressive Series	Naturally occurring stable isotopes
Voss et al. (2009)	Oceanologia	Frequency of occurrence, Schoener's index (Schoener 1968), Index C (Pearre Jr 1982)
Anastasopoulou et al. (2013)	Mediterranean Marine Science	Vacuity Index, Stomach Fullness, Frequency of Occurrence Alimentary Co-efficient, Index of Relative Importance (Pinkas et al. 1971), Prey-Specific Abundance (Amundsen et al. 1996)
Saikia et al. (2013)	Zoology and Ecology	Levins and Smith diet breadth, Db (χ^2) (Saikia 2012)
Arai et al. (2015)	Oceanological and Hydrobiological Studies	Fatty acid composition
Dantas et al. (2015)	Journal of Fish Biology	Index of Relative Importance (Pinkas et al. 1971) Schoener's Index (Schoener 1970)

2. THE DOGMA OF THE METHODOLOGICAL APPROACH

In view of possible attributors of feeding in fish, which is outlined in Fig. 2, three successive and wide steps of methods could be proposed to enumerate their interactive roles on feeding. These are (1) diet occurrence (2) feeding biology and (3) interpretative feeding ecology (IFE) (Fig 3). In the first step, diets consumed by fish are identified, and in the second step, biological arrangements in the body of fish in relation to maximum selection and consumption of diets are justified. The essence of studying the first two steps and linking up them at the end bears immense significance because the former two steps are intricately interdependent and diet occurrence may offer hints for feeding biology, the second step. The final step, IFE is a holistic approach, in which the consequences of the development of feeding mechanism are discussed on an evolutionary aspect. All these steps are described in detail as follows.

2.1. Diet Occurrence

The foremost requirement that must be fulfilled to investigate feeding ecology is the diet of fish. At least three approaches are necessary for this purpose: (i) analysis of stomach or gut content (ii) prey availability in the immediate environment and (iii) analysis of preference/rejection of prey. Different measures are used (Table 1A) to obtain information on recently consumed prey items that remain undigested or poorly digested in the stomach or gut at the time of sampling (see the review of Hyslop 1980). Although statistical viability of many of these measures is in question (Carss 1995), they are easy to compute and more or less homogeneous in outcomes whilst evaluating common prey items of the fish species. However, Baker et al. (2014) expressed limitations to many of these indices and suggested percentage of food contents as robust measure to
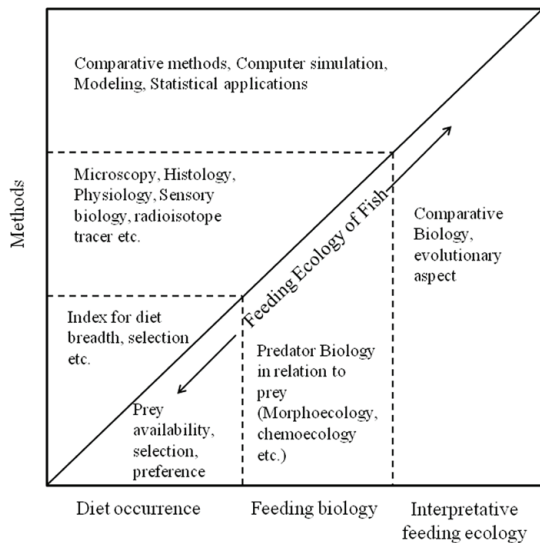

Figure 3. Three steps (Diet occurrence, Feeding biology and Interpretative feeding ecology) of feeding ecology in fish are shown on a two-dimensional plan, that is, subjects to discuss feeding ecology against methods needed to follow under each steps.

produce good results. To minimise statistical error in all such studies, analysis of large numbers of samples (or high statistical power) is always suggested. Whatsoever, the preliminary need of feeding ecological studies, that is, information on diet or prey of the fish can be easily gathered by using one or more of these indices.

A proportional relationship of prey items ingested by fish and their availability in the immediate environment can be explained by diet breadth of the fish. In spite of serious biasness associated with gut content analysis, there exist a large numbers of diet breadth indices (Table 1B) computed on gut contents to measure feeding ecology on a normalised scale (e.g. 0 to 1). A few of them, for example, Hurlbert index (1978), described the magnitude of utilisation of prey in comparison to its availability in the environment. Some of the diet-based indices indicate diet overlap of two species or two populations of single species inhabiting in the same habitat at a time (Table 1C), and some others measure diet selectivity as a function of feeding ecology (Table 1D). Based on the diet breadth, fishes were grouped as stenophagous with limited range and euryphagous with diverse ranges of prey (Oscoz et al. 2005). On selectivity, Costello's (1990) graphical plot for predator feeding strategy and prey importance and its modification by Amundsen et al. (1996) added visual dimension to feeding patterns computed on gut content data. Several classifications of feeding patterns were forwarded from these graphical plots. These were specialist and generalist (Costello 1990, Amundsen et al. 1996) and specialist, generalist homogeneous and generalist heterogeneous (Tokeshi 1991) (Fig. 4a, b and c). Although such classifications are based on rigid localisation of co-ordinates (such as frequency occurrence versus proportional abundance of prey), they could describe feeding behaviour of fish on a wider scale. Such information may be considered only prematurely conclusive because, in all the cases above, results are strongly biased by sampling time and frequency, sample size and numbers of resources considered (Ricklefs & Lau 1980; Smith & Zaret 1982; Ferry & Cailliet 1996). Hence, outcomes from these indices cannot be considered final, but best to fix modalities for further studies on resource utilisation by fish.

Horn (1966) and Hurlbert (1978) suggested repeated measurement of diet overlaps and computation of confidence interval and test of significance of the result to strengthen the feeding ecological indices. Ferry and Cailliet (1996) proposed construction of cumulative prey curves by plotting the cumulative number of prey types (i.e. unique items) against the cumulative number of guts analysed to adjust the problem of statistical power in diet analysis. More convincing approach is to consult multiple indices on considerably large numbers of gut samples to explain a single function (e.g. diet breadth). Sánchez-Hernández & Cobo (2011) used at least five different indices and feeding strategy plots of Amundsen et al. (1996) and Tokeshi (1991) to explain food resource partitioning of four sympatric fish species of River Thomes. Saikia et al. (2013) attempted to outline diet breadth of Labeo rohita Hamilton 1822 using three diet breadth indices in a periphytic environment.

They found that it is possible to describe variable features of diet breadth of *L. rohita* using more than one diet breadth indices. Another direct method of studying feeding ecology in fish is through the analysis of stable isotope in the body of fish as well as in food content. This technique can be performed under laboratory as well as field condition and is advantageous to avoid biased gut content sampling and statistical inconsistencies aroused from direct observation of food. Stable isotopes, primarily, the nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) are often used to determine trophic status and other food-related relationship of fish (Peterson & Fry 1987; Wells & Rooker 2009). Use of stable isotopes is advantageous in obtaining long-term feeding records over other methods estimating short-term food sources (e.g. gut content analysis). For this reason, the studies of stable isotope signatures in the stomach content as well as muscle tissue have been gaining popularity from ecologists in recent times (Rybczynski et al. 2008; Cresson et al. 2014; Shiffman et al. 2014). The feeding ecological information that can reliably be filled up through stable isotope analysis is the resource partitioning through fixing trophic positions of fishes following isotope discrimination factor. For example, the trophic level of fish can be assessed using one of the several available algorithms incorporating stable isotope standards (e.g. Cabana & Rasmussen 1994; Vander Zanden & Rasmussen 2001). Recent studies on stable isotope analysis delineating trophic positions in fishes have also consulted trophic positions based on the stomach content data of the fish for better interpretation of the outcome (Rybczynski et al. 2008; Albo-Puigserver et al. 2015).

Whatsoever, there are more flexibility to evaluate the diet preferences and feeding behaviour through feeding ecological indices over stable isotope analysis. Graphical plots of feeding strategy further add perceptibility to feeding nature. The feeding ecological indices, therefore, provide beginner's guide to overall feeding ecological studies in fish. As extensive reliance on these indices may oversimplify the explanation of food-environment interactions, supplementing these results with stable isotope analysis would be a better practice.

2.2. Feeding Biology

A substantial number of reports on feeding ecology in fish relied on mathematical indices as described earlier. However, in the absence of biologically sound interpretation, the realistic picture of feeding strategy of fish could still remain inconclusive. To establish desired ecological hypothesis on more scientific terms in the subject, integration of biological evidences on rejection and selection of food items or their categories at some appropriate levels of organisation is needed. Feeding ecology of fish shares its most descriptive and interactive part with the biology of the fish. The successful feeding of fish in general depends on three basic aspects of fish biology: (a) morphological (b) anatomical and (c) physiological adjustments and responses to accelerate and stimulate feeding activity (Boglione et al. 2003; Yúfera & Darias 2007a, b). Once the preferred food of the fish is known, the next step is to confirm the functional correlation between preferred food and the biology of the fish through observation and experimentation.

One of such methods with high functional attribute is the analysis of mouth morphometry of the fish, which is often discussed as morphoecology of mouth (Wainwright &
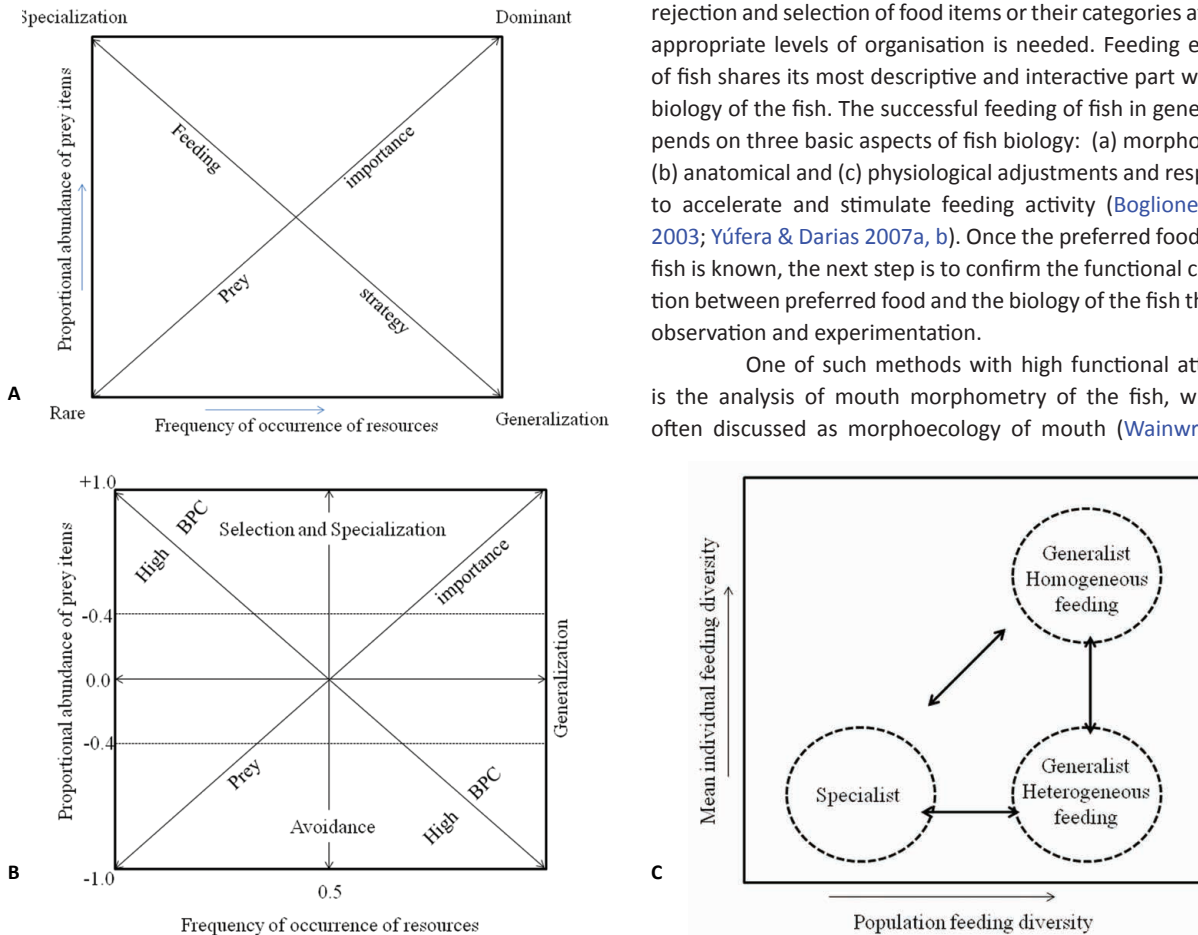

Figure 4 (A) Costello's (1990) graphical plot for predator feeding strategy.
(B) Costello's (1990) graphical plot of feeding strategy modified by Amundsen et al. (1996).
(C) Modified Tokeshi's (1991) graphical plot of feeding strategy.

Richard 1995; Wainwright 1996). This is known that changes in mouth morphometry and its apparatus significantly define feeding habit of fish during their ontogeny (Luczkovich et al. 1995). With the changes in life stages and the surrounding environment, fish responds differently to different food resources. For example, Indian major carp rohu (*L. rohita* Hamilton 1822) is carnivorous at fry stage and herbivorous on attaining the adulthood (Kamal 1967). Similarly, the fish Common carp (*Cyprinus carpio* Linnaeus, 1758) exhibits planktivorous nature in pond but shifts to periphytophagous in rice field (Saikia & Das 2009). The plasticity of mouth morphometry could greatly support such shifting of food habit, extending the functional diet breadth of fish. The most deterministic variables orienting mouth morphology in relation to feeding in fish can be both external and internal to the body.

Externally, mouth gape functions as the 'entry limiting point' at ingestion level in fish. In fish, it can be defined as the three-dimensional open area resulted from maximum vertical expansion of upper and lower jaw. There are growing interests to explain the relationship between mouth gape and prey size consumed by fish at their different life stages (Knutsen & Tilseth 1985; Mittelbach & Persson 1998; Lukoschek & McCormick 2001; Keppler et al. 2015). In carnivorous fish, such size-selective feeding is largely gape limited (Trauemper & Lauer 2005). A recent study of freshwater herbivorous fish *Amblypharyngodon mola* Hamilton 1822 showed that smaller gape size is related to small-sized prey and larger gape size to both small- and big-sized prey (Nandi & Saikia 2015). Gape size can also indicate feeding pattern (e.g. suction or ram) of fish (Wainwright & Richard 1995), which is often overlooked in feeding ecology. Morphologically, length of upper jaw and lower jaw or vertical and horizontal width of mouth and shape of the head region could be considered to explain why the fish categorically feeds on some sizes of food and not others. Gill pores can be added as additional feature in describing 'escape limiting point' of particulate food from mouth cavity (Nandi & Saikia 2015). There is a series of mathematical measures that give an estimation of gape size in fish (Table 1E). More frequently, the ratio of prey size to mouth gape in fish is mentioned as the indicator of performance on accessibility to food. Estimation of pore size in gills can be done using scanning electron microscope (SEM). The ratio of mouth area (or gape) to pore size in gills may help in understanding the filtering ability of particulate food items of specific size in filter feeding fishes.

Internally, the remarkable biological feature to define feeding ecology of fish is the taste bud, a common neurophysiological structure densely located on palatine as well as on tongue region. Taste buds may be seen on external surfaces too, especially on barbells. Occasionally, taste buds in gills are also considered important to feeding. However, fish with and without barbells possesses abundant taste buds in the oral cavity. Fine structure of taste buds can be obtained using sophisticated microscopy such as SEM. After obtaining the initial microphotographic information of taste bud, their histology could be a better option to correlate tissue and cellular adjustments to feeding. The three types of taste buds in fish (Type I, Type II and Type III) play different roles in the feeding mechanism (Reutter et al. 1974). They act as gustatory mechanoreceptor or chemoreceptor and are localised in the mouth, upper and lower palatine, tongue, branchial cavity, gills and other parts of the body (Whitear 1971; Reutter 1986; Finger 1997). These architectures may vary in different fishes depending on the function they execute through mechanoreception or chemoreception. Fish taste receptors have been reported to be responsive to wide ranges of substrates, especially amino acids with a well-orchestrated taste-dependent system for diet selection (Oike et al. 2007). Advanced immunohistochemical details could primarily establish their function in relation to food selection and rejection. For further details to ascertain such relationship, ligand-specific induction using fluorescent dye may be applied followed by histomicrography of samples (Døving et al. 2009).

Next to buccal cavity, the important organ that involves food selection and feeding is the stomach/gut region of the fish. The stomach of fish accommodates recently ingested foods, and this information is used to characterise food habits of the fish at first place. In stomachless fish, the first one or two coils of the alimentary canal are used to generate such reports. The presence and absence of stomach and length of the alimentary canal are traditionally described as rough estimator of feeding habit in fish. An estimate of the ratio of gut length to total length (or relative gut length, RGL) or body weight is often used as standard method for the classification of fish into herbivorous, carnivorous or omnivorous in nature. However, measures such as RGL are purely descriptive and statistically poor. A direct observation through microsection of gut across its length supported with enzymatic and bacterial assay can provide more accurate explanation and a better understanding on the feeding habit of fish. Guts of herbivorous fish may have different histological orientation and bacterial occupants than carnivorous fish. Existence of a particular group of bacteria may enhance the digestion of specific food ingested [e.g. phytase in *L. rohita* (Roy et al. 2009)] and can be used to characterise the feeding habits in fish. Many a times, misleading interpretation could arise when 'ingested food in the mouth cavity' and 'probable food in the stomach or gut' records conflict. For example, gut of filter feeding herbivorous fish mostly accommodates phytoplankton, not zooplankton. However, few zooplankton may find their way to stomach or gut along with phytoplankton during filter feeding. Such observations if encountered frequently may mislead as concocted feeding habit of the fish. Therefore, enzyme assay from fish gut could be more convincing method to explain qualitative selection of foods in the environment. After Bolnick et al. (2014), it is clear that gut-associated microbial diversity regulates food-specific nutritional functions in fish gut and, therefore, reliably confirm feeding nature of fish. Specific molecular approach to identify and quantify gut microbial diversity with further incorporation to bioinformatics are more advance scopes recently applied (e.g. Bolnick et al. 2014) in outlining feeding ecology of fish. In addition, diversified absorptive structures in the intestine of fish demonstrate a kind of food

selection (Horn et al. 2006) and, hence, more reliably explain on the selectivity towards a particular group of food organism.

With the development of global genetic databases and molecular techniques, remnant DNA in faecal or stomach samples have been emerging as a new source of study of food contents in the gut of animals (King et al. 2008; Corse et al. 2009; Murray et al. 2011). Few recent studies in fish that used stomach and faecal samples for DNA analysis revealed their confirmatory preys, especially of largemouth bass *Micropterus salmonids,* bluegill *Lepomis macrochirus* (Jo et al. 2014, Taguchi et al. 2014), *Sulmo trutto* (Jo et al. 2015) and Ocean sunfish *Mola mola* (Sousa et al. 2016). Carreon-Martinez et al. (2011) tested this method on piscivorous fishes (and also under variable temperatures) and suggested that DNA barcoding provides more precise information on the highly digested preys that have lost all physical characteristics. The gut content from stomach, rectum or colon region of fish is used for DNA extraction and amplified using Cytochrome Oxidase subunit I (COI) as metabarcoding marker. Use of bioinformatics is inherent to finalise the outcome. The DNA barcoding is useful when direct observation of diet is difficult or consumed items become indistinguishable. It also helps to confirm the taxonomic abundance of diet in the gut. This approach is most useful to identify nonnative preys in the gut of fish. Whilst studying feeding ecology of fish, such DNA-based analysis could be supplementary in nature if discussed with the information obtained through physical observation of gut content and, from case to case, may play principle role to provide more insight into the food habit of fish.

Another development is the advancement of chemosensory biology laying the foundation of Chemoecology, a new discipline demonstrating interactions of organisms with the environment through organic chemicals that explains evolutionary mechanisms based on chemical responses. It is known that some fishes often respond to different chemical stimulants that constitute their food (Adams et al. 1988; Xue & Cui 2001). Parts of the microscopic organisms often composed of molecules (e.g. amino acids) that may guide the fish towards the food through strong chemosensory ability. Studies showed that small or larval fish primarily ingest food by swallowing, probably through chemoreception, rather than preying upon it (Rønnestad et al. 2013). Common carp exhibited high chemosensitivity against Cysteine (Chervova & Lapshin 2005). Similarly, in addition to visual detection, *Trematomus newnesi* Boulenger 1902 also feeds on live feeds through chemoreception (Meyer & Fanta 1998). Migratory fishes are highly chemoreceptive to their feeding or breeding grounds. Such chemoreception in fishes is a kind of interactive biological phenomenon to their environments that needs to be explained in their feeding ecological studies. Detailed study on the chemoattractants in the natural diets of fish and receptive sensory structures such as olfactory rosette, sensory and non-sensory membranes and sensory receptor cells lying on the body surfaces are new and essential biological windows to draw a conclusive outline of chemoecology in fish. Further, in spite of its wide scope of application, molecular biological studies as extension of chemoecology have yet to draw attention of ecologists as well as fish biologists in delineating feeding ecology of fish.

2.3. Interpretative feeding ecology (IFE)

The two broad goals that feeding ecology fulfils are (i) revealing basic and accurate ecological interactions between food and the organism and application of such information to design and engineer culture technology as well as in their conservation, restoration and management. (ii) However, the most intelligent part of feeding ecology is its exhibition for evolutionary ecology of animal. One of the principal evolutionary factors determining ecological interaction in fish community is the 'feeding success' in natural habitat amongst the fish populations with common feeding habits. It is, in more general term, a subset of feeding ecology where the fish can competitively explore its food in the presence of several populations of fish species when their diet breadths are overlapped. Further, Darwinian competition for food within and between populations leads to resource partitioning and character displacement. The key evolutionary forces resulting character displacement directly influence morphological features, especially those directly involve in feeding mechanism, ensuring their survivability. These features would become prominent when trophic levels are assigned to congeneric or sympatric species in an ecosystem.

As a hallmark of advanced techno-driven integrated science with statistical analysis, morphoecology is now an established field in evolutionary ecology (Park et al. 2013). Morphometric variations amongst stocks of fishes often provide a basis for stock characterisation, explaining environmentally induced variations. In addition, development of taste buds, jaw modification and sensory (gustatory, olfactory) reception are the key characters to describe evolution (Kirino et al. 2014) on chemoecological perspectives that supply reliable inputs to justify diversification of feeding in fish. The micro-techniques (SEM, fluorescence) can be incorporated with molecular details to draw evolutionary comments through appropriate tools such as cluster analysis. Such interpretations can be supplemented by phylogenetic analysis of gut microbial diversity adapted on similar diet amongst different populations of fish (e.g. Franchini et al. 2014) and other organisms (Sullam et al. 2012). This field of feeding ecology is yet to be recognised in fish and needs immediate attention for standardisation.

3. PEDAGOGICS IN FEEDING ECOLOGY

All the methods of feeding ecology cited in the preceding discussions and justifications enlisted thereafter clearly advocate the need of orientation of methods to establish meaningful relation between food, feeding and the environment of the fish. It is advisable that researcher may adopt maximum of these methods that are functionally informative as well as reliably descriptive to decipher the complete feeding ecology of fish. Figure 5 presents possible pedagogy of methods for drawing and interpreting feeding ecology in fish in a holistic manner. Summarily, *first*, gut/stomach content data must be generated

through best possible identification procedure and quantitative analysis of such data may be carried out on error-free basis. *Second*, evaluating feeding ecological indices (e.g. diet breadth, diet overlap), especially Hulbert index (1978) or similar kind that accounts food resources along with gut content for computation of the index, is the essential step for conceiving the idea of the spread of the diet recorded in the gut. Subsequently, Ivlev's selectivity index (1961) or Tokeshi's (1991) individual feeding diversity and population feeding diversity index help describing dietary pattern of the fish. The graphical explanation of these indices confers feeding pattern (specific or generalistic) to the fish. However, all such interpretations should be based on randomness of the sample and valid statistical principles. Ferry and Cailliet (1996) proposed 'cumulative prey curves' to determine whether enough samples have been processed for diet analysis or not. A 'cumulative prey curve' is based on the relationship between sample size and species richness of gut content and it reaches the asymptote when no new prey types are being found in the diet. It indirectly ensures high statistical power to the analysis. *Third*, trophic levels of fish supplement the outcome of the methods described in the previous step. Both stable isotopes and gut/stomach invariably contribute in determining trophic level to studied fish species or populations. Prey categorisation for determining trophic levels can be prepared from available literature sources. *Fourth*, the attributed feeding pattern is now correlated to biological features of the fish. It could be assumed that evolutionary distances would be more between two different fish groups with different feeding pattern. The distances between the groups would be more if their feeding patterns hardly overlap. Tokeshi's (1991) graphical plot for feeding pattern has been modified and the explanation of 'feeding ecological distances' has been incorporated to explain such distances (Fig. 6). With this assumption, feeding

ecological hypothesis can be justified on an evolutionary scale where biological attributes contribute to the 'feeding ecological distances'. The major biological features contributing 'feeding ecological distances' are the mouth morphometry, microscopic structures on mouth region, gut histology, enzyme specificity and microbial diversity. All possible advanced techniques (e.g. molecular ecology, Bioinformatics) may also be consulted to generate more reliable information on feeding adjustments and modifications of these features and thereby justifying the corresponding feeding pattern and trophic level of the fish. Habitat specific adjustments, if any, may be incorporated at this stage. *Fifth*, such features and modifications should be linked to feeding strategy and ecological phenomena such as resource
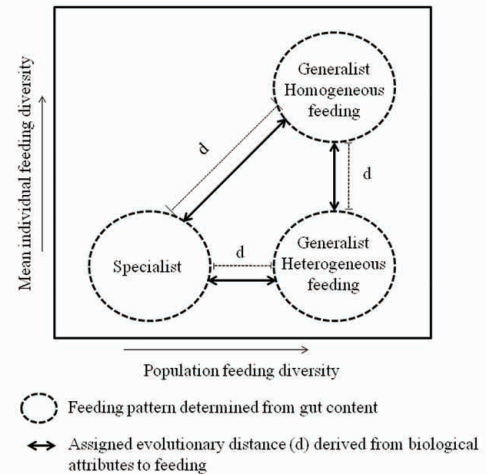

Figure 6. Tokeshi's (1991) graphical plot modified and biological attributes are added as to differentiate amongst feeding patterns. This differential distance may be hypothesised as evolutionary distance between two fish groups with differential feeding pattern.
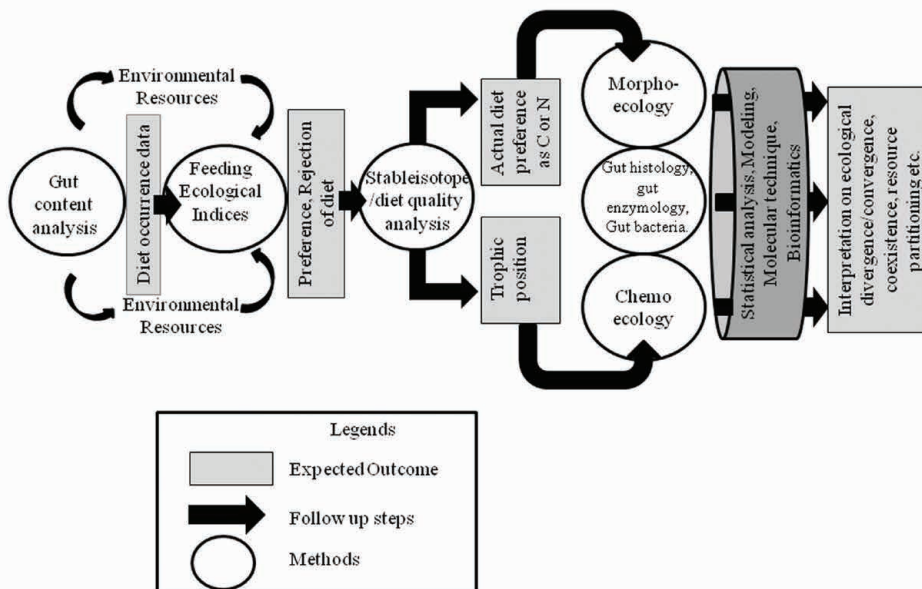

Figure 5. Proposed pedagogic of methods for the study of feeding ecology of fish.

partitioning, character displacements, co-existence and trophic divergences. The modified distance plot of Tokeshi's (1991) feeding groups proposed in this review may be adopted as early indicator to explain such ecological phenomena.

4. CONCLUSION

The above discussion deciphers the utility of feeding ecology as a more functional science over and above it to be merely a descriptive note. Rather describing what are the food fish ingests, feeding ecology is more accountable to explain organisational adaptation, resource partitioning, habitat utilisation, prey selection, Darwinian competition and, finally, their evolution. However, linking all these functional attributes and arriving at a realistic conclusion at once may not be possible, but appropriate methodological approach described here may do so on a cumulative basis. Adopting a kind of comprehensive strategy on the feeding ecology of fish could be more appropriate for the sake of science rather than accepting dubious conclusions gingering with conjecture from the currently practiced irreconcilable methods.

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