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Individual diet variation in a marine fish assemblage: Optimal Foraging Theory, Niche Variation Hypothesis and functional identity

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ABSTRACT

Individual diet variation (i.e. diet variation among individuals) impacts intra- and inter-specific interactions. Investigating its sources and relationship with species trophic niche organization is important for understanding community structure and dynamics. Individual diet variation may increase with intra-specific phenotypic (or "individual state") variation and habitat variability, according to Optimal Foraging Theory (OFT), and with species trophic niche width, according to the Niche Variation Hypothesis (NVH). OFT proposes "proximate sources" of individual diet variation such as variations in habitat or size whereas NVH relies on "ultimate sources" related to the competitive balance between intra- and inter-specific competitions. The latter implies as a corollary that species trophic niche overlap, taken as inter-specific competition measure, decreases as species niche width and individual niche variation increase. We tested the complementary predictions of OFT and NVH in a marine fish assemblage using stomach content data and associated trophic niche metrics. The NVH predictions were tested between species of the assemblage and decomposed into a between- and a within-functional group component to assess the potential influence of species' ecological function. For most species, individual diet variation and niche overlap were consistently larger than expected. Individual diet variation increased with intra-specific variability in individual state and habitat, as expected from OFT. It also increased with species niche width but in compliance with the null expectation, thus not supporting the NVH. In contrast, species niche overlap increased significantly less than null expectation with both species niche width and individual diet variation, supporting NVH corollary. The between- and within-functional group components of the NVH relationships were consistent with those between species at the assemblage level. Changing the number of prey categories used to describe diet (from 16 to 41) did not change the results qualitatively. These results suggest that, besides proximate sources, intra-specific competition favors higher individual diet variation than expected while inter-specific competition limits the increase of individual diet variation and of species niche overlap with species niche expansion. This reveals partial trophic resource partitioning between species. Various niche metrics used in combination allow inferring competition effects on trophic niches' organization within communities.

1. Introduction

During the last decade, an increasing number of authors called for consideration of individual niche variation in community ecology (Albert et al., 2012; Bolnick et al., 2011; Pachepsky et al., 2007). In trophic ecology, individual diet variation (or individual trophic niche variation, i.e. diet variation among individuals) is known to be a relatively common phenomenon (Bolnick et al., 2003, 2007) that alters the average competitive pressure between conspecifics or with individuals from other species. Thus, individual diet variation may affect both prey and predator population dynamics that, together, may ultimately have important implications for trophic network structure and dynamics (Araùjo et al., 2011; Svanbäck and Bolnick, 2008).

Considering such ecological consequences, it is essential to document the patterns and to understand the causes of individual diet variation. Optimal Foraging Theory (OFT) suggests that individual diet variation depends on individuals' phenotype (or "individual state" such as size, sex or developmental stage) and prey availability (Schoener, 1971; Svanbäck and Bolnick, 2005; Werner and Hall, 1974). More precisely, although an individual is able to consume a wide diversity of prey items, it may adopt different diets and feed on specific organisms depending on energetic benefits relative to handling time costs. Such benefits will depend on the individual's state and on

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prey species available in its habitat. Consequently, individual state and habitat variation between conspecifics may be seen as "proximate sources" of individual diet variation (Araùjo et al., 2011).

Another source of individual diet variation is described by Van Valen's "Niche Variation Hypothesis" (NVH, Van Valen, 1965). It is related to the selective forces responsible for individual specialization and, thus, can be qualified as an "ultimate source" of individual diet variation that is complementary to the proximate sources proposed by the OFT. More specifically, the NVH indicates that a larger individual niche variation should be associated with a wider species ecological niche. In trophic terms, a species with a large trophic niche is expected to be composed of individuals that specialize on different diets. According to the NVH, individual diet variation and species trophic niche width can be interpreted as resulting from the interplay between intra- and inter-specific competition (Araùjo et al., 2011; Bolnick et al., 2003). Strong intra-specific competition for food resources is expected to promote species trophic niche expansion as individuals tend to diversify their diet so as to reduce competition between conspecifics (Bolnick et al., 2003, 2011; Svanbäck and Bolnick, 2007; Svanbäck and Persson, 2004; Tinker et al., 2012). In contrast, strong inter-specific competition may force individuals to forage on a few prey items in order to mitigate interactions with other species, thus inducing species niche contraction. Inter-specific competition also favors trophic niche diversification or resource partitioning across species according to the principles of competitive exclusion and character displacement (Schluter, 1996; Svanbäck et al., 2008). To summarize, species trophic niche width and individual diet variation may depend on the balance between intra- and inter-specific competitions (termed as "competitive balance" hereafter). Therefore, 3 different patterns may be expected under the NVH. First, a positive relationship between trophic niche width and individual diet variation is expected as the main prediction. Second, a negative (positive) relationship between inter-(intra-)specific competition and species trophic niche width is predicted as a corollary. Third, a negative (positive) relationship between inter-(intra-)specific competition and individual diet variation is also expected as a corollary. These 3 patterns should apply if, and only if, trophic resources are limiting.

The NVH was previously tested on color polymorphism maintenance in birds (Galeotti and Rubolini, 2004), on skull and canine shapes considered as surrogates for size and feeding niche, respectively, in terrestrial carnivores (Meiri et al., 2005), and on genetic variation used as an indicator of phenotypic variation in marine fishes (Somero and Soulé, 1974). Surprisingly, despite its obvious relevance for trophic ecology, only one study tested the NVH on trophic niche (Bolnick et al., 2007). These authors correlated species trophic niche width with individual diet variation across populations, but within taxa, of fishes, frogs, lizards and whelks. The NVH was successfully supported in all 4 taxa as trophic niche width increased with individual diet variation. However, this study did not provide the opportunity to test the implication of the competitive balance as it was based on comparing different populations of the same taxa belonging to distant ecosystems. A way to assess the involvement of the competitive balance in the NVH would be to compare the trophic niches of different species from the same community that may be potentially competing for food resources.

Another unexplored aspect of the NVH is how it relates to a species' ecological function or role. It is generally admitted that intra- and inter-specific trait variation influences the ecological function of species and, hence, ecosystem functioning (Cianciaruso et al., 2009; Petchey and Gaston, 2006). Influential traits are generally referred to as functional effect traits. Species performing particular ecological functions are generally expected to be characterized by highly specialized functional effect traits. It may then be hypothesized that, as specialists, they have a narrow ecological niche and they exhibit little individual niche variation (Devictor et al., 2010). On the opposite, species performing diversified functions can be expected to have a broad niche potentially allowing for high individual niche variation. If this hypothesis holds, then the type of function performed by species should determine their location along the co-gradient of niche width and individual niche variation expected under the NVH at the community level (i.e., across species). Species performing specialized functions should be located on the left side of the co-gradient characterized by a narrow niche and weak individual niche variation. In contrast, species performing diversified functions should be located on the right side characterized by a wide niche and high individual niche variation. As a result, species belonging to the same functional group should be grouped around the same location along the co-gradient of niche width and individual niche variation. NVH is thus expected to be observed between functional groups. Beyond between-functional group considerations, co-variation of niche width and individual niche variation within-functional groups can also be questioned. Due to closer species packing within functional groups, the effects of the balance between intra- and inter-specific competitions may be exacerbated. It is therefore interesting to assess whether the NVH also holds within functional groups. A way to assess how the NVH is related to species ecological function would be to decompose the co-variation between niche width and individual niche variation at the community level into a between- and a within-functional group component (Fig. 1). Of course, the same holds for NVH corollary predictions involving inter- and intra-specific competitions.

The objective of this paper was to investigate the potential sources of among-individual diet variation and between-species niche width variation within a marine fish assemblage by testing the complementary predictions of OFT and NVH. More precisely, the aims were to (i) assess the influence of individual state and habitat on individual diet variation and (ii) test whether NVH occurs between species within the assemblage as well as (iii) between- and within-functional species groups. An assemblage of 16 marine fish species, belonging to the community of the eastern English Channel, was taken as a case study. Characteristics of species trophic niches, namely species trophic niche width, species diet overlap, taken as an indicator of potential inter-specific competition, and individual diet variation were estimated. Firstly, following OFT, 4 potential "proximate" sources of individual diet variation related to individual state and habitat were investigated. These sources include individual length, sex, sexual maturity and community of origin taken as a proxy of habitat and prey availability. Secondly, the 3 relationships expected from the NVH – (1) a positive relationship between species trophic niche width and individual diet variation, (2) a negative relationship between species trophic niche width and species diet overlap (inter-specific competition), and (3) a negative relationship between individual diet variation and species diet overlap – were tested. Thirdly, species were assigned to functional groups according to 3 alternative classifications based on species habitat and life history, diet, and phylogeny, respectively. The 3 relationships expected from the NVH were then tested between- and within-functional groups for these 3 classifications.

2. Materials and methods

2.1. Sample collection

Sixteen fish species (Table 1), representing a wide range of trophic diversity, were collected in the eastern English Channel during the Channel Ground Fish Survey (CGFS) operated by IFREMER in October 2009 (Fig. 2). Fishes were caught on board RV "Gwen Drez" by towing a high opening demersal trawl (GOV) with a cod-end of 20 mm stretched mesh for 30 min at a speed of approximately 3.5 knots. A spatially stratified sampling scheme was used where the area, subdivided into $15' \times 15'$ rectangles in which the GOV trawl, was fished at least once (Fig. 2). Following their capture, focal fish species were identified and individually labeled, frozen on board with liquid nitrogen to stop digestion and then kept frozen until further use. In the laboratory, sampled fishes were defrosted, measured for their total length (L, cm), and dissected. Sex (S) and maturity status (M) were determined by