Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models

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ABSTRACT

Ontogenetic dietary shifts (ODSs), the changes in diet utilisation occurring over the life span of an individual consumer, are widespread in the animal kingdom. Understanding ODSs provides fundamental insights into the biological and ecological processes that function at the individual, population and community levels, and is critical for the development and testing of hypotheses around key concepts in trophic theory on model organisms. Here, we synthesise historic and contemporary research on ODSs in fishes, and identify where further research is required. Numerous biotic and abiotic factors can directly or indirectly influence ODSs, but the most influential of these may vary spatially, temporally and interspecifically. Within the constraints imposed by prey availability, we identified competition and predation risk as the major drivers of ODSs in fishes. These drivers do not directly affect the trophic ontogeny of fishes, but may have an indirect effect on diet trajectories through ontogenetic changes in habitat use and concomitant changes in prey availability. The synthesis provides compelling evidence that ODSs can have profound ecological consequences for fish by, for example, enhancing individual growth and lifetime reproductive output or reducing the risk of mortality. ODSs may also influence food-web dynamics and facilitate the coexistence of sympatric species through resource partitioning, but we currently lack a holistic understanding of the consequences of ODSs for population, community and ecosystem processes and functioning. Studies attempting to address these knowledge gaps have largely focused on theoretical approaches, but empirical research under natural conditions, including phylogenetic and evolutionary considerations, is required to test the concepts. Research focusing on inter-individual variation in ontogenetic trajectories has also been limited, with the complex relationships between individual

behaviour and environmental heterogeneity representing a particularly promising area for future research.

Key words: development-related dietary shifts, ecological dynamics, macroecology, predator–prey interactions, size-dependent mechanisms, trophic ontogeny.

CONTENTS

I. INTRODUCTION

Ontogenetic dietary shifts (ODSs), the changes in diet utilisation occurring over the life span of an individual consumer, are widespread in the animal kingdom. ODSs have been most extensively researched in insects, amphibians and fishes. The best-studied examples in insects and amphibians are associated with metamorphosis and the sometimes extreme shifts in habitat use, such as between freshwater and terrestrial environments [Nakazawa (2015) and references therein]. By contrast, fishes typically inhabit the same environments throughout their lives (except for diadromous fishes), allowing an examination of other factors influencing ODSs and whether or not conclusions can be generalised among contrasting aquatic ecosystems (e.g. freshwater, brackish and marine). Fish have been useful model species in both empirical and theoretical studies of trophic ontogeny (e.g. Schellekens, De Roos & Persson, 2010; Nakazawa, 2015; Sánchez-Hernández & Cobo, 2018), with a steep increase in the number of publications over the last decade (Fig. 1). Despite this growing interest, the majority of research has addressed changes in diet composition during development or differences between size classes (e.g. Lukoschek & McCormick, 2001; Davis *et al*., 2011; Sánchez-Hernández & Cobo, 2016). In the early stages of the life cycle, many fish species prey upon phytoplankton, zooplankton or small macroinvertebrates, but may switch to larger macroinvertebrates, fish, plants or detritus later in development (Nunn, Tewson & Cowx, 2012; Huss *et al*., 2013). Conversely, generalist species, such as most salmonids, often forage on a wide range of aquatic invertebrates when small, but may include terrestrial invertebrates, fish, amphibians or rodents at larger sizes (Eloranta, Kahilainen & Jones, 2010; Jensen, Kiljunen & Amundsen, 2012; Sánchez-Hernández *et al*., 2013). Pronounced dietary shifts sometimes coincide with specific events in development, such as the transition from 'finfold' to 'finformed' larvae or from larvae to juveniles (Nunn, Harvey & Cowx, 2007), but few studies have attempted to disentangle the potentially confounding influences of ontogeny (i.e. processes scaling with body size) on ODSs.

Although ODSs in fishes are well documented (e.g. Amundsen *et al*., 2003; Kolasinski *et al*., 2009; Nunn *et al*., 2012), the majority of research has focussed on a small number of economically important species, and our comprehension of the exact nature of ODSs, the driving mechanisms and their consequences is incomplete. Nunn *et al*. (2012) described the occurrence of ODSs in a review of the foraging ecology of larval and juvenile fishes, but adults and the causes and consequences of ODSs were not explored. In particular, attempts to separate the drivers and consequences of ODSs have been equivocal. For example, many researchers have concluded that ODSs are related to the specific habitat requirements of prey following ontogenetic changes in habitat use by fish (e.g. Lukoschek & McCormick, 2001; Choi & Suk, 2012), but habitat changes can be a consequence of other drivers, such as changing predation risk or prey availability (e.g. Werner & Hall, 1988; Wu & Culver, 1992). Theory predicts that ODSs are influential in community and food-web stability (Schellekens *et al*., 2010; Miller & Rudolf, 2011; Rudolf & Lafferty, 2011; de Roos & Persson, 2013; van Leeuwen *et al*., 2013, 2014; Nilsson, McCann & Caskenette, 2018), but we currently lack a holistic understanding based on empirical evidence of their consequences for populations, communities, food-web dynamics and ecosystem processes and functioning. Because morphological, behavioural, physiological and life-history traits play an important role in foraging specialisation and define intra-specific trophic polymorphisms where they exist [Smith & Skúlason (1996) and references therein], identification of the role of traits linked with foraging should help to disentangle the causes and consequences of

ODSs. However, little attention has been given to exploring specific events in fish ontogeny during which diets switch and during which rapid change in selection pressures could trigger evolutionary branching (Claessen & Dieckmann, 2002; ten Brink & de Roos, 2017). To overcome the challenges associated with this knowledge deficit and equivocal conclusions, we aim to synthesise: (*i*) the biological concepts (i.e. the causes and consequences of ODSs), setting them in a broad ecological and evolutionary framework, and (*ii*) enhance our current understanding of the drivers and consequences of ODSs in fishes, using pertinent examples from marine and freshwater ecosystems. Understanding ODSs provides fundamental insights into the biological and ecological processes that function at the individual, population and community levels, and is critical to the development and testing of hypotheses around key concepts in trophic theory on model organisms.

II. THE NATURE OF ODSs

ODSs are often linked to other ontogenetic niche shifts, in particular habitat choice, which influences the availability of different prey types to the consumer (e.g. Werner & Hall, 1988). For organisms with distinct life stages, such as aquatic insects and amphibians, these shifts are typically abrupt and consist of complete switches between separate niches following metamorphosis (Claessen & Dieckmann, 2002; Bassar, Travis & Coulson, 2017). Most organisms, however, exhibit less-abrupt shifts in niche utilisation, but ODSs may nonetheless manifest as relatively distinct changes in prey choice or diet composition associated with shifts in habitat use during ontogeny, as is often seen in fish (Fig. 2; Werner, 1986). Most ODSs are size-related (Werner & Gilliam, 1984) as, for many species, the body size of a consumer significantly affects its feeding ability and the size range of prey that is available for consumption (Werner, 1986; Mittelbach & Persson, 1998). Hence, ODSs are commonly observed in organisms that undergo large changes in body size (Werner & Gilliam, 1984; Werner, 1986). With the notable exceptions of birds and mammals, whose juveniles are typically approximately adult-sized when they commence independent foraging, individuals of most animal taxa vary greatly in body size over their lifetime (Werner, 1986). Accordingly, ODSs are a common feature of the life cycles of a diverse range of organisms (Kimirei *et al*., 2013), including most invertebrates, fishes, amphibians and reptiles (Werner & Gilliam, 1984). The relationship between body size and prey size is particularly strong in fish, which do not have any appendages to manipulate prey. Their ability to handle prey thus generally scales with mouth gape size, which, in turn, scales with body size (e.g. Dunic & Baum, 2017). Hence, unlike amphibians and aquatic insects, body size seems to play a critical role in ODSs in fishes, although there are a few exceptions (e.g. lampreys) in which ODS is linked to metamorphosis.

In fishes, the body mass of conspecifics may span several orders of magnitude from first-feeding larvae to the largest adults, and extensive ontogenetic niche shifts are a nearly universal phenomenon within size-structured fish populations (Werner & Gilliam, 1984; Werner, 1986). In many species, the size of consumed prey usually increases with fish size (Scharf, Juanes & Rountree, 2000; Cocheret de la Morinière *et al*., 2003; Sánchez-Hernández & Cobo, 2012*b*), and different size classes typically consume different prey types as a result of, for example, differences in foraging abilities or habitat use (Mittelbach & Persson, 1998; Lukoschek & McCormick, 2001; Nunn *et al*., 2012). The resulting diversity of ontogenetic diet trajectories followed by fish species may range, for example, from rapid dietary changes in the larval period to multiple broad-scale changes over the complete life cycle of the individual. Examples of the former are riverine cyprinids and salmonids, for which dietary shifts may occur in association with improvements in vision and swimming performance, and increases in gape size (e.g. Wanzenböck & Schiemer, 1989; Mittelbach & Persson, 1998; Ojanguren & Braña, 2003). Additionally, brown trout (*Salmo trutta* L.) often switch from aquatic to water-surface prey in their first summer, although not all individuals of this age group may exhibit such a switch [Sánchez-Hernández & Cobo (2018) and references therein]. This phenomenon needs to be examined in other stream-dwelling species to be recognised as a general principle.

Profound multiple ODSs occurring over the life cycle are frequently seen in piscivorous fish species (e.g. Mittelbach & Persson, 1998; Hjelm, Persson & Christensen, 2000; Amundsen *et al*., 2003; Hanson, 2011; Artero *et al*., 2015). Typically, such dietary switches involve distinct shifts in prey sizes from millimetre to centimetre and finally to decimetre orders of magnitude. The prey size increases with predator size following allometric scaling theory (Mittelbach & Persson, 1998; Dunic & Baum, 2017). For example, juvenile largemouth bass [*Micropterus salmoides* (Lacépede, 1802)] and European perch (*Perca fluviatilis* L.) primarily feed upon zooplankton before switching to benthic invertebrates, and later to small and, subsequently, large fish prey (e.g. Hjelm *et al*., 2000; García-Berthou, 2002; Amundsen *et al*., 2003). Moreover, studies focused on stage-structured models have concluded that an early ODS from zooplankton to macroinvertebrates is necessary for individuals to reach sizes large enough to enable subsequent exploitation of the ultimate piscivorous niche (Huss *et al*., 2013). Similar multiple ODSs from pelagic to benthic invertebrates and subsequently to increasingly larger fish prey are also seen in marine piscivorous fish, such as Atlantic cod (*Gadus morhua* L.) (Fig. 2; Link & Garrison, 2002), and benthic coastal marine fish, such as Atlantic John Dory (*Zeus faber* L.) (Stergiou & Fourtouni, 1991). Some cyprinids may, by contrast, follow a different dietary trajectory during their ontogeny (e.g. Penttinen &

Holopainen, 1992; Sánchez-Hernández & Cobo, 2012*a*; Dadebo *et al*., 2014). The first ODS in cyprinids is invariably from plankton to benthic invertebrates (Penttinen & Holopainen, 1992), but the contribution of detritus and plant material increases during ontogeny in some species, whereas others feed largely on insects (Sánchez-Hernández & Cobo, 2012*a*; Dadebo *et al*., 2014). A consequence of ODSs is that, whereas the diets of many fish species are frequently similar during the larval period, juveniles and adults often diverge into a broad spectrum of feeding strategies, such as herbivory, detritivory, omnivory and carnivory (see for example Davis *et al*., 2011).

The current literature indicates that ODSs are flexible in nature. Indeed, considerable variation in ODSs can be observed even among conspecifics at the same life stage (e.g. Post, 2003; Sánchez-Hernández & Cobo, 2018). In addition to individual ontogenetic trajectories, many fish species experience gradual ODSs at the population level (e.g. Stergiou & Fourtouni, 1991; Cocheret de la Morinière *et al*., 2003; Ramos-Jiliberto *et al*., 2011), whereas they occur abruptly in others. Abrupt ODSs are most apparent in diadromous or amphidromous species (e.g. many salmonids, lampreys and galaxiids), which inevitably shift their diets (both in terms of prey size and species composition) when migrating between freshwater and marine environments, leading to marked changes in the origin of utilised carbon and nitrogen sources and concomitant changes in the trophic level at which they feed (Keeley & Grant, 2001; Dixon *et al*., 2012; Hertz *et al*., 2016). ODSs are generally more distinct when the switch occurs following migration between marine and freshwater ecosystems than within freshwater ecosystems (e.g. riverine *versus* lacustrine). Many ODSs in freshwater species involve life stages feeding mainly on insects, a prey category that, with the exception of river mouths, is not generally present in marine ecosystems. Based on the reviewed literature, we conclude that the dietary role occupied by insects in fresh water chiefly is filled by crustaceans and/or cephalopods in marine ecosystems (Fig. 2). Ontogenetic diet trajectories thus depend upon the type of ecosystem inhabited (e.g. freshwater *versus* marine), although a switch to piscivory, when fish become top predators, seems to be a common feature of many ecosystems (e.g. Winemiller, 1989; Jensen *et al*., 2012; Artero *et al*., 2015). Species with highly specialised diets in the adult period invariably also experience abrupt ODSs. Many lampreys, for example, are filter feeders during the freshwater phase of their life cycle, but haematophagous (blood feeders) during the marine phase (Silva, Barca & Cobo, 2016). Some fish species, such as many Neotropical characids, undergo ODSs from terrestrial insects to fruits and leaves (Drewe *et al*., 2004), and fish-scale consumption by facultative scale feeders usually increases with fish size (Peterson & Winemiller, 1997; Hahn, Pavanelli & Okada, 2000).

In recent decades, there has been a strong interest in the period of ontogeny in which fish become piscivorous (Mittelbach & Persson, 1998; Hanson, 2011; Sánchez-Hernández *et al*., 2017). An early transition to piscivory may increase somatic growth, lead to early maturation or enhance lifetime fitness (Werner, 1986; Olson, 1996; Mittelbach & Persson, 1998; Post, 2003), but the size-related timing of the switch is highly variable among freshwater fishes (see Mittelbach & Persson, 1998). Brown trout is a widely distributed and extensively studied species that provides a good example of ODSs to piscivory (Fig. 2). Although it has been claimed that brown trout become piscivorous at a minimum body length of 200–300 mm, the switch may occur at smaller sizes [Sánchez-Hernández *et al*. (2017) and references therein]. Importantly, the size-related timing of the switch seems to be dependent upon the presence of small-sized prey fish and competition with other species (Sánchez-Hernández *et al*., 2017). Similarly, fish species typically become piscivorous above a threshold size in the marine environment (Hanson, 2011; Artero *et al*., 2015). For example, Hanson (2011) observed that white hake [*Urophycis tenuis* (Mitchill, 1814)] and Atlantic cod become piscivorous when they are greater than 350 and 450 mm in length, respectively. By contrast, other marine species can become piscivorous very early in ontogeny (e.g. Reglero *et al*., 2011; Llopiz, 2013). It is possible that an early switch to piscivory is connected to water temperature, as higher temperatures tend to promote a higher frequency of piscivory (Reglero *et al*., 2011). This was corroborated by Llopiz (2013), who found that piscivory in the early development of fish was most frequent at lower latitudes, but a mechanistic understanding of how water temperature influences the size-related timing of ontogenetic switches to piscivory is missing. Factors other than temperature, such as prey-encounter rates and size-selective predation, probably also influence piscivory and growth in the larval and early juvenile periods of species displaying ODSs (e.g. Huss, Byström & Persson, 2010). Thus, we conclude that the nature of ODSs can differ among ecosystem types as a consequence of differences in food availabilities and the inherent food preferences of particular species which is most likely linked to phylogenetic relatedness.

III. DRIVING MECHANISMS

The potential drivers of ODSs in coral reef fish have been thoroughly reviewed by Kimirei *et al*. (2013). Here, we attempt to identify the general mechanisms that drive ODSs in fish in riverine, lacustrine and marine systems, as well as the most directional drivers involved. It should be kept in mind that there are numerous biotic and abiotic factors, both known and unknown, that have the potential to influence directly or indirectly ontogenetic diet trajectories, and consequently affect the timing and nature of ODSs in fishes (Fig. 3). These include competitive interactions, prey availability, predation risk and internal mechanisms (Werner, 1986; Olson, 1996; Sherwood *et al*., 2002; Galarowicz, Adams & Wahl, 2006; Kimirei *et al*., 2013). With so many factors that directly or indirectly influence ODSs, separating the most important driving mechanisms is a complex task, especially as many factors seem inter-related (see Sánchez-Hernández & Cobo, 2018).

Using the work of Kimirei *et al*. (2013) as a starting point, and based on the reviewed literature, we grouped the drivers of ODSs into nine categories: (1) predation risk, (2) competition, (3) prey availability and suitability, (4) habitat use, (5) morphological constraints, (6) swimming ability, (7) gut length, (8) metabolism and enzymes, and (9) feeding behaviour and foraging modes. These categories covered broad drivers, including biological (1–3), environmental (4), intrinsic (5–8) and behavioural (9) factors. We used the following key word search in *Web of Science* in an attempt to identify the most important drivers of ODSs: TOPIC “fish” AND “ontogenetic shifts” AND “predation risk” OR “competition” OR “prey availability” OR “habitat use” OR “gape” OR “gill raker” OR “swimming ability” OR “gut length” OR “metabolism” OR “enzymes” OR “feeding behaviour” OR “foraging modes”. This allowed us to explore information across the nine categories in relation to ODSs. The original search identified 926 papers from *Web of Science* Core Collection (Fig. 3A). First, these articles (only title and abstract) were reviewed and selected to remove any irrelevant literature. To be included, a study had to focus on the causes of ODSs. A total of 64 studies were found to provide high-quality data about the causes of ODSs according to the eligibility criteria. Second, the selected literature was thoroughly reviewed in an attempt to disentangle the role of each driver of ODSs by applying a binary response set (yes/no). That is, each study was screened to provide a simple designation of the effect (yes = evidence supporting and no = evidence refuting) of ODSs for each of the nine categories. Thus, the conclusion of the literature was assigned to one or more of several categories (Table 1). For example, the work by Walters & Juanes (1993) provided evidence supporting predation risk but not for the remaining categories (Table 1). To disentangle the most important drivers of ODSs, we calculated the prevalence (percentage of reviewed articles) of positive effects (evidence supporting) for each of the nine potential drivers of ODSs. This enabled us to estimate the relative importance of the nine potential drivers on ODSs (Fig. 3B).

(1) Predation risk

Small fish are more vulnerable than larger fish to predation, and consequently ODSs can in part be driven by a release from predation pressure related to body size. For example, the classic work by Werner & Hall (1988) demonstrated that the ODS from benthic invertebrates (in the littoral zone) to zooplankton (in the pelagic zone) by the bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819) is chiefly driven by the abundance of its main predator, the largemouth bass, which usually prefers to inhabit the littoral zone. Similarly, Walters & Juanes (1993) suggested that ODSs where fish move into previously risky habitats become more likely as fish size increases. Thus, fishes have the potential to exploit an increasing variety of food resources as predation risk decreases during ontogeny (Reñones, Polunin & Goni, 2002). However, the importance of predation risk as a driver of ODSs may not be stable as, for example, Dahlgren & Eggleston (2000) observed that coral reef fish can adjust the length-related timing linked to habitat shifts in response to changes in perceived predation risk. Kimirei *et al*. (2013) concluded that predation risk, in combination with the opportunity to utilise more energetically profitable habitats, may be the primary mechanism driving ODSs. Predation risk appears to influence ODSs in fishes through changes in habitat use irrespective of ecosystem configurations (i.e. freshwater, brackish and marine ecosystems) (e.g. Werner & Gilliam, 1984; Werner & Hall, 1988; Dahlgren & Eggleston, 2000; Kimirei *et al*., 2013). Thus, predation risk may not impact directly on the trophic ontogeny of fishes, but it can have an indirect effect on diet trajectories through predation risk-driven changes in habitat use (e.g. previously risky habitats becoming available during ontogeny).

(2) Competition

Fish abundance, assumed to be a principal mediator of intra- and interspecific competition, can play a role in driving ODSs in fishes (e.g. Persson & Hansson, 1999; Kimirei *et al*., 2013; Sánchez-Hernández & Cobo, 2018). Theoretical approaches to the relationship between competition and diet trajectories posit that competition is a key variable that forces individuals to shift their foraging behaviour to alleviate intra- and interspecific competition (see Section IV). However, this mechanism is likely relevant only for consumers with overlapping trophic niche requirements (Persson & Hansson, 1999; Huss, Byström & Persson, 2008).

ODSs can be influenced by competition (e.g. Werner & Hall, 1988; Choi & Suk, 2012; Kimirei *et al*., 2013). In an illustrative example, Persson & Greenberg (1990) observed that the body length-related timing of an ODS from zooplankton to macroinvertebrate feeding in juvenile European perch changed (that is switched to earlier) in response to a competitor [roach *Rutilus rutilus* (L.)] with a superior efficiency when foraging on zooplankton. Similarly, Persson & Hansson (1999) showed that common bream [*Abramis brama* (L.)] shifted to benthic organisms earlier in ontogeny following a reduction in fish abundance, although it was not clear whether the change was associated with a reduction in intra- or interspecific competition. Huss *et al*. (2008)

provided experimental evidence that in the initial stages of fish ontogeny (juveniles), size-related morphological constraints prevented European perch from making an early shift from zooplankton to macroinvertebrates at high levels of intraspecific competition. Based on our literature review, we conclude that competition is a major driver of ODSs in fishes (Fig. 3B).

(3) Prey availability and suitability

There is considerable evidence that prey availability and suitability are important mechanisms driving ODSs in fishes (e.g. Hjelm *et al*., 2000; Choi & Suk, 2012; Kimirei *et al*., 2013; Sánchez-Hernández & Cobo, 2018). For example, the switch in summer by many juvenile cyprinids to aufwuchs (the periphyton and associated microfauna that grow on underwater surfaces), considered a poor food resource because of its low digestibility and nutritive value (e.g. Lemke & Bowen, 1998), is probably linked to a lack of suitable animal prey; the evidence for this is that the switch may not occur if sufficient invertebrates are available [Nunn *et al*. (2007) and references therein]. Similarly, Wu & Culver (1992) observed that juvenile yellow perch [*Perca flavescens* (Mitchill, 1814)] shift from zooplankton to benthic prey in response to a decline in the abundance of zooplankton in summer. In addition to species composition, García-Berthou (2002) observed that the ODS to piscivory by largemouth bass can be influenced by the size structure of the prey fish assemblage. Specifically, a dominance of centrarchids within the body length range 75–150 mm with anti-predator mechanisms (e.g. spiny rays in the dorsal and anal fins) can have a strong negative influence on the ontogenetic shift to piscivory, preventing the switch occurring (García-Berthou, 2002). Takimoto (2003) concluded that an early shift to the next ontogenetic niche can occur when the abundance of prey in the first niche is low. Thus, the evidence suggests that prey availability and suitability impose important limitations on the timing and extent of ODSs (Fig. 3B).

(4) Habitat use

Ontogenetic changes in habitat use is a clear example of where a process may be driving an ODS or where the ODS may be a consequence of other drivers, such as changing predation risk or prey availability (see Sections III.1 and III.3), and thus the ontogenetic habitat change may be a simple consequence of an ODS driven by other factors. Thus, in both marine and freshwater systems, many prey taxa frequently have specific habitat requirements (Chapman, 1999; Tachet *et al*., 2010) and, consequently, ontogenetic changes in habitat use by a predator may lead to unavoidable changes in diet. This is particularly evident in diadromous species (that migrate between freshwater and marine ecosystems; Dixon *et al*., 2012; Hertz *et al*., 2016) and lacustrine migrants (moving between littoral and pelagic or profundal habitats; Werner & Hall, 1988; Knudsen *et al*., 2006).

The habitat preferences of fishes commonly change during development (e.g. from nursery to adult habitats), and may provide new foraging opportunities (McCormick, 1998; Dahlgren & Eggleston, 2000; Choi & Suk, 2012). For example, Werner & Hall (1988) demonstrated that a switch of bluegill sunfish from littoral prey to zooplankton coincided with a shift from the littoral to the pelagic zone during ontogeny. Cocheret de la Morinière *et al*. (2003) postulated that ODSs may crucially influence changes in habitat use and promote nursery-to-coral-reef migrations. Notwithstanding, for some fish species, such as the striped mullet (*Mugil cephalus* Linnaeus, 1758), changes in habitat use during ontogeny do not necessarily lead to changes in diets (Eggold & Motta, 1992). This may underline the difficulty in identifying the role of habitat use as a driving mechanism of ODSs. It is possible that ontogenetic changes in habitat use are drivers of ODSs in some species, but a consequence of ODSs in others. The relatively sparse literature on this topic suggests that this would be a fruitful area for future research.

In addition to horizontal habitat shifts (e.g. between the littoral and pelagial of lentic systems), which are common in both marine and freshwater fish species (Werner & Hall, 1988; Polte *et al*., 2017), changes in diet composition can occur in response to vertical habitat shifts (i.e. through the water column). Although such patterns do not apply to all species, there are some common themes from both marine and freshwater systems that are informative. It seems that vertical and resource-driven ontogenetic habitat shifts are frequently driven by differential predation risk in differing water depths regardless of ecosystem type. For example, Choi & Suk (2012) concluded that ontogenetic shifts from the upper to the lower water column often occur in marine species, with the common pattern being that large individuals feed closest to the benthic zone. In lacustrine ecosystems, this type of vertical habitat shift during ontogeny has been identified in smelt [*Osmerus eperlanus* (L.)], with this species undergoing a habitat shift towards deeper water as individuals grow (Hammar *et al*., 2018). However, the common ontogenetic theme of shifting through the water column may change across ecosystem type and fish species. Regarding differences among fish species inhabiting the same ecosystem, Hammar *et al*. (2018) observed that Arctic charr [*Salvelinus alpinus* (Linnaeus, 1758)] have the opposite vertical ontogenetic habitat shift than that of its prey (smelt). Similarly, the pattern in marine ecosystems is not always replicated in freshwater as small Arctic charr frequently make ontogenetic habitat shifts to the profundal zone in the ice-free season (Knudsen *et al*., 2006; Hammar *et al*., 2018), contrasting with the behaviour observed in the serpentine goby [*Pterogobius elapoides*

(Gunther, 1872)] (Choi & Suk, 2012). Rather than these habitat shifts being driven by differences in predation risk *per se*, it is likely that differences in water-column use between marine and freshwater fishes and among fish species might be explained by a trade-off between predation risk and prey availability. Our reasoning is that predation risk is usually lower near the bottom or in the profundal zone than at the surface in freshwater systems (Knudsen *et al*., 2006; Sánchez-Hernández & Cobo, 2018), whereas the water column, a potentially risky habitat in marine systems, seems to be optimal for small marine individuals to catch abundant small pelagic organisms (Choi & Suk, 2012). It is possible that predation risk is highest in the water column in marine ecosystems but near the water surface in fresh waters. However, species undergoing vertical habitat shifts during ontogeny with zooplankton as the first prey type, such as for example in smelt (Hammar *et al*., 2018), are forced simply to contend with this higher predation risk. Thus, a decision by small fish to utilise the water column as a habitat may be driven by prey availability regardless of, or in combination with, predation risk. This corroborates our earlier conclusion that prey availability and predation risk are key drivers of ODSs.

Dahlgren & Eggleston (2000) provided another example of ontogenetic habitat segregation where a foraging–predation trade-off is evident. These authors observed ontogenetic habitat shifts from the interstices of macroalgal clumps (a safe habitat) to outside of the algal habitat in the Nassau grouper [*Epinephelus striatus* (Bloch, 1792)], with small fish showing higher foraging rates (number of prey items ingested per 72 h) than larger fish in the macroalgal habitat. Additionally, Lukoschek & McCormick (2001) observed that large individuals of a marine benthic carnivorous fish preferred to forage at the reef edge and base, whereas small individuals tended to feed on the reef flat and slope. It is worth noting that habitat variation among species and individuals provides an indication to understand the causes of variations in ODSs in fishes, but the true role of habitat as a driver of ODSs is not yet clearly resolved.

Despite the fact that pronounced dietary shifts sometimes coincide with changes in habitat use, the theory behind switches in niche use needs to be set in a broad ecological and evolutionary framework (see for example ten Brink & de Roos, 2017). Knowledge of what is, and what is not, an evolutionary adaptation has in this respect become pivotal to understanding colonisation of new habitats by fishes. This is particularly relevant where sympatric trophic polymorphisms manifest (i.e. 'morphs' specialising on different food resources) and where ecologically distinct sub-populations evolve due to habitat specialisation (Gross, 1987; Knudsen *et al*., 2006, 2010). In such cases, ODSs may give rise to evolutionary branching resulting in resource polymorphism and potentially speciation (see Claessen & Dieckmann, 2002 and Section IV). Based on a review of the literature, we conclude that ODSs can be influenced by trade-offs between the habitat-driven requirements to forage and to avoid predation (greater amongst smaller individuals), causing variation in ODSs within and among species. Thus, we believe that habitat use represents an unlikely direct driver of ODSs and ontogenetic shifts in habitat use are more likely to result as a consequence of other drivers (Fig. 3C).

(5) Morphological constraints

Body size determines a suite of morphological traits that can affect the transition among prey types across the lifetime of fish. Indeed, changes in body morphology, such as mouth gape and gill raker size or density, during ontogeny can be a determinant of ODSs in fishes. Mouth gape certainly imposes limitations on ODSs in fishes through its effect on prey-handling ability. Thus, gape is closely correlated with body size-related changes in diet during ontogeny (Magalhães, 1993; Scharf *et al*., 2000; Linde *et al*., 2004; Sánchez-Hernández *et al*., 2013). In fish species that consume whole prey, increasing mouth dimensions are generally closely and positively related to mean and maximum prey size (Scharf *et al*., 2000; Sánchez-Hernández *et al*., 2013). This effect is most easily observed in the switch to piscivory, with fish species with larger mouth gapes typically becoming piscivorous at smaller body sizes (Mittelbach & Persson, 1998). This pattern is repeated within species as ontogenetic changes in mouth dimensions account for diet shifts such as, for example, the switch to cephalopods or fish prey at larger individual size (Scharf *et al*., 2000; Linde *et al*., 2004; Belinda, Ward-Campbell & Beamish, 2005). Additionally, changes in mouth dimensions with body size may drive changes from generalist to more specialised feeding in some species (Linde *et al*., 2004). Thus, prey-handling characteristics impose important limitations on the timing and extent of ODSs.

In many filter-feeding fish species, gill raker length and inter-raker spacing increase with body size, and prey particle size increases concomitantly (Eggold & Motta, 1992; Gerking, 1994). The number of gill rakers can also increase with fish size (Hjelm *et al*., 2000). Therefore, any variation in the size and structure of the gill rakers during ontogeny can have direct consequences for ontogenetic dietary trajectories and, thereby, on the timing of ODSs (Eggold & Motta, 1992; Hjelm *et al*., 2000). It has been widely accepted that individuals with a large number of gill rakers are better adapted to zooplankton feeding because dense gill raker spacing is assumed to be most efficient for retaining small prey in the mouth cavity [Kahilainen *et al*. (2011) and references therein]. Ontogenetically, one consequence of having a large number of gill rakers is an increase in the size at which a shift from zooplankton to other prey may occur, presumably because of the relatively higher foraging efficiency on zooplankton of individuals with a higher density of gill rakers (Hjelm *et al*., 2000). This conclusion was based on a freshwater model organism, the European perch, and may not apply to all fish species. In addition, some marine species seem to change feeding strategies with increasing fish size, which may be related to gill raker length and inter-raker spacing (Gerking, 1994; Hirota, Uehara & Honda, 2004). It is possible that small individuals are often more selective in their feeding strategy (showing selective browsing) than larger conspecifics, which frequently rely more on grazing feeding strategies (Eggold & Motta, 1992).

In territorial species, body size can modify foraging behaviours through size-structured dominance hierarchies, where dominant and often large individuals gain access to the best patches for feeding and, as a consequence, grow faster than subordinates (e.g. Nakano, Fausch & Kitano, 1999). Thus, individual differences in feeding behaviour in species exhibiting dominance hierarchies linked to fish length can influence ODSs in fishes. Indeed, individual variation in feeding behaviour has recently been demonstrated as more important than prey availability, habitat characteristics and competition in the switch from autochthonous (aquatic) to allochthonous (surface) prey during ontogeny in stream-dwelling salmonids (Sánchez-Hernández & Cobo, 2018). Thus, it is reasonable to posit that the behavioural dominance status of an individual, which may be linked to body size, could have a strong influence on ODSs, and may be a promising avenue for future research. In this regard, we support the view of Belinda *et al*. (2005), that ontogenetic changes in body morphology are of secondary importance to ODSs in fish. Our reasoning is that, according to allometric theory, changes in morphological traits (e.g. mouth gape and gill rakers) and dominance status have the potential to affect ODSs, but body size *per se* may not be a primary driver of ODSs (Fig. 3C). In particular, body size is unlikely to have a direct effect on ODSs in species with no gape limitations from early ontogeny. Additionally, any effects of body size on ODSs could be masked by the influence of site-specific prey community composition (see Section III.3), as well as other drivers, such as predation risk and competition (Fig. 3C).

(6) Swimming ability

Improvements in swimming ability during ontogeny have the potential to lead ODSs, thereby poor swimming ability may be a constraint on ODSs in some cases. Although more pronounced during early ontogeny, the swimming ability of fishes tends to increase with fish length through the development of fins, body shape and muscle anatomy (e.g. Ojanguren & Braña, 2003; Koumoundouros *et al*., 2009; Butler *et al*., 2012). Based on the principle that prey species have specific habitat requirements and behaviours (Chapman, 1999; Tachet *et al*., 2010), increased swimming ability enables access to additional habitat types and/or new foraging opportunities (Hasegawa *et al*., 2012; Sánchez-Hernández & Cobo, 2018). For example, many salmonid species are able to exploit higher velocity and deeper water as they develop and grow (e.g. Hasegawa *et al*., 2012). Additionally, improvements in swimming ability during ontogeny can lead to ODSs because (*i*) the capture success of mobile prey may increase (e.g. Juanes & Conover, 1994*a*), and (*ii*) improved escape swimming performance may release individuals from former constraints of predation (Gibb *et al*., 2006). Thus, swimming performance usually improves during ontogeny, which, in turn, indirectly impacts on the diets of fishes.

(7) Gut length

Generally, gut length in fishes increases as a consequence of increasing body size during ontogeny, although there is some evidence that ontogenetic changes in relative gut length (i.e. gut length independent of body size) generally differ between herbivorous and carnivorous species (German & Horn, 2006; Davis *et al*., 2013). There is considerable evidence that gut length changes in response to exposure to different prey (Belinda *et al*., 2005; German & Horn, 2006; Davis *et al*., 2013; German, Gawlicka & Horn, 2014), but little support for the hypothesis that gut length may drive ODSs. Belinda *et al*. (2005), for example, could find no evidence for gut length being a driver of ODSs in snakehead [*Channa limbata* (Cuvier, 1831)], but showed that mouth dimensions were influential.

(8) Metabolism and enzymes

Some studies have supported the idea that ODSs could be driven by internal physiological mechanisms such as metabolic rate, digestive enzymes and muscle enzymatic activity (e.g. Sherwood *et al*., 2002; Drewe *et al*., 2004; Jackson *et al*., 2004). A recent laboratory-based study demonstrated that the main digestive enzymes (except pepsin) are present before the onset of exogenous feeding in butter catfish [*Ompok bimaculatus* (Bloch, 1794)] (Pradhan *et al*., 2013). Thus, it is theoretically possible for enzymes to drive ODSs such as during the transition from endogenous to exogenous feeding. However, it is reasonable to posit that, at least for some species, changes in digestive enzyme activity are a consequence of a changing diet (e.g. German, Horn & Gawlicka, 2004; German *et al*., 2014). A typical example is that of Neotropical characid fish species, which switch from feeding upon terrestrial insects to fruits and leaves during their life history. With this switch comes a concomitant increase in α-amylase activity but a decrease in pepsin and trypsin activity (Drewe *et al*., 2004). The limited literature generally supports the conclusion that digestive enzyme activity is a consequence, not a driver, of ODSs (Fig. 3B). However, given the potential complexity of physiological interactions and the paucity of the literature on the subject, this is likely to be a fruitful area for future research. In particular, future studies might consider the ontogenetic development of digestive enzymes from the pancreas, stomach and intestine of fishes (e.g. German *et al*., 2004; Pradhan *et al*., 2013).

Size-scaling metabolic theory predicts allometric relationships between metabolic rate and body mass in fishes [Yagi & Oikawa (2014) and references therein], and such ontogenetic changes in metabolic rate may improve swimming ability and lead to ODSs. Indeed, Jackson *et al*. (2004) concluded that changes in metabolic rate may determine the size at which diet shifts occur, playing a key role, alongside handling time, in determining prey choice. Other factors, such as muscle enzymatic activity, also appear to change during ontogeny. For instance, it has been observed that wild fish show changes in muscle enzymatic activity, such as lactate dehydrogenase activity, with diet switches to planktivory, benthivory, and piscivory (Sherwood *et al*., 2002). This enzyme has an important role in glycolysis, and concentrations seem to be higher in fishes exhibiting dietary shifts (Sherwood *et al*., 2002). Enzymes that enhance glycolysis in the white muscle during exercise can have a positive impact on swimming ability, and thus theoretically may affect prey capture ability (see Section III.6). Notwithstanding, it is doubtful that either metabolic rate or enzyme activity (either digestive or muscle physiology) are direct drivers of ODSs.

(9) Feeding behaviour and foraging modes

The feeding behaviour strategies (e.g. planktivory, benthivory and piscivory) and foraging modes, i.e. the type of prey-search behaviour [‘ambush’ (sit-and-wait) or ‘cruise’ (active) *sensu lato*], of fishes can change during ontogeny (e.g. Werner & Hall, 1988; Browman & O’Brien, 1992; Sánchez-Hernández & Cobo, 2018). A number of laboratory and field studies have identified size-dependent effects on the foraging modes of fishes and, ultimately, on ODSs (e.g. Nakano *et al*., 1999; Persson & Brönmark, 2002*a*,*b*; Gustafsson, Bergman & Greenberg, 2010; Sánchez-Hernández & Cobo, 2018). Gustafsson *et al*. (2010) noted that large brown trout used the upper water column to forage on surface-drifting prey (drift foraging) more often than did smaller individuals, which remained closer to the bottom and fed on aquatic prey. In another example, Sánchez-Hernández & Cobo (2018) demonstrated size-related changes in foraging modes, namely an increasing probability of switching to drift foraging with increasing fish size. Although it is possible that these foraging shifts (i.e. from the benthos to the water surface) may be triggered by intrinsic features linked to body size, they seem to be influenced by a number of inter-related factors in addition to intrinsic features, such as environmental variation (mainly benthic invertebrate density and water current velocity) and competition (Sánchez-Hernández & Cobo, 2018). Similarly, there are several examples from lacustrine and marine ecosystems supporting the view that feeding behaviour and foraging modes change during ontogeny through ontogenetic habitat shifts (see Section III.4). A common ontogenetic pattern amongst lacustrine fish is a switch in foraging along the littoral–pelagic axis (i.e. from littoral to pelagic foraging or *vice-versa*) (e.g. Werner & Hall, 1988; Wu & Culver, 1992). From marine ecosystems, it has been observed that the foraging behaviour of many species changes from planktivory to benthivory (Choi & Suk, 2012) or browsing to grazing (Eggold & Motta, 1992). In addition, Linde *et al*. (2004) observed ontogenetic changes from a passive (preying on sedentary taxa) to an active (preying on nekton) behaviour in the foraging strategy of the dusky grouper [*Epinephelus marginatus* (Lowe, 1834)]. Because foraging specialisation and fish ontogeny are closely linked, we tentatively conclude that changes in foraging strategy related to ontogenetic shifts in specialisation can be a mechanism driving ODSs, but that such changes are likely ultimately driven by predation risk, competition and/or prey availability.

To summarise, the *Web of Science* core collection indicated that habitat use emerged as the most recurrent topic in explaining ODSs (Fig. 3A), but that competition, prey availability, feeding behaviour, foraging modes and predation risk also seem to be influential. It is doubtful that some putative drivers (gut length, metabolism and enzymes) are direct drivers of ODSs (Fig. 3B), but their true roles are not yet clearly resolved and represent fruitful areas of future research. Based on the reviewed literature, we posit that habitat use, feeding behaviour and foraging mode are a consequence of other drivers, such as changes in predation risk, competition and prey availability (Fig. 3C). Although prey-handling constraints can play a significant role in the timing of ODSs (see Section III.5), we conclude that any impacts may be masked by inter- or intraspecific competition through density-dependent effects on developmental processes and, in particular, the body size of fishes. Similarly, we suggest that morphological constraints, swimming ability, gut length, metabolism and enzymes are consequences of body size and not drivers of ODSs *per se* (Fig. 3C). Prey availability, predation risk and competition emerged as the most important drivers of ODSs in fishes, with prey availability providing the potential for other factors to influence ODSs. Thus, it is reasonable to posit that the transition among prey types across the lifetime of fishes is closely related to their availability, but that other drivers may be responsible for the size-related timing and/or magnitude (i.e. some or all individuals of a population) of the ontogenetic switches. Consistent with this view, predation risk and competition do not impact directly on the trophic ontogeny of fishes, but can have indirect effects on diet trajectories through ontogenetic changes in habitat use and concomitant changes in prey availability (Fig. 3C). Notwithstanding this, we still lack a clear understanding of the true drivers of ODSs and require new and integrative approaches to identify possible false-positive drivers.

IV. CONSEQUENCES

(1) Individuals, populations and communities

ODSs in fishes often coincide with increases in individual growth rates (Fig. 3C), and many studies have suggested that the relationship is causal (e.g. Olson, 1996; McCormick, 1998; Mittelbach & Persson, 1998; Jensen *et al*., 2012). A key challenge, however, is to disentangle the true relationship between ODSs and fish growth, as ODSs can be a consequence of, as well as a contributor to, growth (Fig. 3C). Most studies indicate that increases in growth rates can be caused by switches to more profitable food resources. For example, growth rates can increase substantially after switching from invertebrates to fish in many marine (e.g. Juanes & Conover, 1994*b*; Bromley, Watson & Hislop, 1997; Tanaka *et al*., 2014) and freshwater (e.g. Olson, 1996; Mittelbach & Persson, 1998; Pazzia *et al*., 2002; Persson & Brönmark, 2002*b*) fish species. Indeed, the growth rates of individuals that become piscivorous early in development can be almost double those of conspecifics that switch later (Post, 2003; Tanaka *et al*., 2014). Other ODSs, such as from zooplankton to macroinvertebrates, may also have consequences, as growth is often faster in zoobenthivorous than zooplanktivorous individuals (Persson & Brönmark, 2002*a*; Svanbäck & Eklöv, 2002). ODSs can have a positive influence on growth, when prey-handling efficiency conforms with allometric scaling theories, otherwise ODSs can be a consequence of growth (e.g. when prey is outside of the optimal predator–prey size ratio) as we outlined in Section III.5. Alternatively, ODSs may be overridden by lifestyle in species whose feeding-behaviour strategies does not change much but which show growth. This is exemplified by many species undergoing discrete ODSs; with no ontogenetic shifts in prey-type consumption but shifts in maximum prey-width consumption (e.g. Egan *et al*., 2017). In addition, herbivorous species; for example, grass carp [*Ctenopharyngodon idella* (Valenciennes, 1844)] can absorb plant-derived nutrients and undergo rapid growth during ontogeny (Wang *et al*., 2015). Using the behavioural traits and life histories of fish to examine the consequences (and causes) of ODSs (see Hin *et al*., 2011) is a promising area for future research.

The survival and recruitment of many fish species is positively associated with growth and successful dietary shifts in the first year of life (Myers, 1995; Houde, 1997; Nunn *et al*., 2010). ODSs therefore have the potential to influence the lifetime fitness of individual fish and population dynamics, and other size-dependent processes, *via* their impacts on growth (Olson, 1996; Post, 2003; Huss *et al*., 2013; Tanaka *et al*., 2014). Depending upon resource availability, individuals that undertake ODSs can accrue an advantage over competitors that do not (Pazzia *et al*., 2002; Post, 2003; Schellekens *et al*., 2010). Alternatively, and on the basis of resource partitioning theory (Schoener, 1974), ODSs may allow individuals to avoid potential recruitment bottlenecks caused by competition for food resources (e.g. Polis, 1984; Olson, 1996; Cowan, Rose & DeVries, 2000; King, 2005) and facilitate the coexistence of consumers (e.g. Amundsen *et al*., 2003; Sánchez-Hernández & Cobo, 2012*b*; Wollrab, de Roos & Diehl, 2013; Pereira *et al*., 2015). Reductions in the intensity of competition could lead to increases in growth rates and, consequently, in survival and recruitment (Post, 2003). ODSs, especially early transitions to profitable food sources (e.g. fish), could also have implications for the lifetime fecundity of individual fish (Post, 2003), because several important maternal traits (e.g. egg quality and quantity) frequently increase with body size (Mittelbach & Persson, 1998; Venturelli *et al*., 2010). Size differences among individuals produced by ontogenetic variation in the transition to piscivory are commonly maintained at later ages (Pazzia *et al*., 2002; Post, 2003), so fish that grow large relative to their conspecifics may have a disproportionately strong influence on population dynamics through enhanced recruitment success.

As demonstrated by previous studies, ODSs are a key factor in determining how ecological communities are structured (e.g. de Roos & Persson, 2013; van Leeuwen *et al*., 2013, 2014). These theoretical studies focussed on stage-structured models and did not address evolutionary dynamics, but nonetheless provided the basis for empirical work to increase ecological realism and identified promising evolutionary research directions to explore the consequences of ODSs in population and community ecology. Indeed, ten Brink & de Roos (2017) recently demonstrated that ODSs are evolutionary advantageous when switches to alternative food sources involve higher intake rates for consumers. Thus, a strategy to understand ODSs better in an evolutionary framework would be to take foraging specialisation and trophic polymorphisms into account (Fig. 3C). Our reasoning is that previous studies have assumed that switching niches during ontogeny can lead to trophic polymorphisms (e.g. Adams & Huntingford, 2002; Knudsen *et al*., 2006, 2010) and/or evolutionary branching (see Claessen & Dieckmann, 2002) in population ecology. Based on the premise that niche shifts and trophic polymorphisms are genetically determined (Adams & Huntingford, 2002; Claessen & Dieckmann, 2002), ODSs may constitute an early phase in the evolution of trophic polymorphisms leading to ecologically distinct sub-populations due to foraging specialisation. Indeed, several studies have highlighted the evolutionary implications of the combination of ODSs and the environment (Claessen & Dieckmann, 2002; Whiteley, 2007; ten Brink & de Roos, 2017). Especially relevant are the theoretical considerations of Claessen & Dieckmann (2002) that foraging differences determine the type of feeding trajectory (i.e. monomorphic, ontogenetic generalist or polymorphism) adopted in fish populations. Whiteley (2007) observed that eco-evolutionary traits responsible for stage-specific developmental switches in feeding in the mountain whitefish [*Prosopium williamsoni* (Girard, 1856)] can occur late in ontogeny. This was supported by ten Brink & de Roos (2017), who highlighted that individuals usually display a dietary shift late in ontogeny to maximise food intake. Thus, it is reasonable to assume that ODSs are a strong candidate for a mechanism of divergence within fish populations, but the trade-off between early and late foraging success can impede the evolution of an ODS (ten Brink & de Roos, 2017). We suggest that the eco-evolutionary consequences of ODSs on fish populations are a promising area for further investigation and should not be neglected.

(2) Food webs and ecosystem processes

It has long been recognised that fishes can have a major influence on the abundance and species and size composition of prey assemblages through top-down mechanisms (e.g. Mehner & Thiel, 1999; Rosenfeld, 2000; Baum & Worm, 2009; van Leeuwen *et al*., 2013). Knowledge of ODSs is therefore vital to understand how they influence food webs and ecosystem processes (e.g. respiration and primary productivity). Network-based approaches have demonstrated that the functional role of fish is developmental-stage specific (Ramos-Jiliberto *et al*., 2011; Sánchez-Hernández, 2016). ODSs, therefore, have the potential to have important effects on energy pathways and food-web structure and dynamics (Woodward *et al*., 2005; Miller & Rudolf, 2011; Nakazawa, 2015).

ODSs usually result in individuals feeding higher up food chains, which increases food-web complexity (e.g. the number of feeding linkages) as different functional groups occupy alternative positions (i.e. alternative stable states) in the food web (Amundsen *et al*., 2003; Takimoto, 2003; Nakazawa, 2011*a*, 2015; van Leeuwen *et al*., 2014; Sánchez-Hernández, 2016). However, it may not be possible to identify alternative positions in food webs clearly when predators undergo multiple ODSs (i.e. feeding on additional resources before switching to piscivory) (van Leeuwen *et al*., 2013). Thus, there may be interspecific differences in the influence of ODSs, with generalist species expected to increase food-web complexity in comparison to specialist species. Indeed, niche breadth and diet modularity (the subgroup of predators and prey interacting in a network) can decrease following ODSs in some fishes [e.g. Spanish toothcarp (*Aphanius iberu*s Valenciennes, 1846)] (Ramos-Jiliberto *et al*., 2011), especially in species that switch from animal resources to plants or detritus, such as grass carp, fathead minnow (*Pimephales promelas* Rafinesque, 1820) and thin-lipped grey mullet [*Liza ramada* (Risso, 1810)]. As ODSs can involve littoral, pelagic and profundal resources in lentic ecosystems (e.g. Knudsen *et al*., 2006; Kolasinski *et al*., 2009; Eloranta *et al*., 2010), there can be direct and indirect consequences for energy pathways and the dynamics of food webs and ecosystem processes through cascading (both top-down and bottom-up) effects (Nakazawa, 2011*b*, 2015).

Understanding stability in stage-structured food webs is an emerging field in ecology, and much attention is being paid to identify and disentangle the contributing factors (de Roos & Persson, 2013; Caskenette & McCann, 2017; Nilsson *et al*., 2018). Theory predicts that ODSs and stage-structured populations are key determinants of food-web stability (de Roos & Persson, 2013; Nilsson *et al*., 2018). Indeed, in accordance with biomass reallocation theory (see de Roos & Persson, 2013), Caskenette & McCann (2017) recently demonstrated that stage-structured predators increase the stability of food webs. Size-structured predator–prey models have demonstrated that predatory size effects are species specific and that food webs can be dynamically stable (Emmerson & Raffaelli, 2004). Importantly, there are stabilising and destabilising aspects of stage structure that need to be taken into consideration (see Nilsson *et al*., 2018). For example, predators feeding on the same food resource can strongly destabilise a system, whereas size- or stage-specific feeding can have a stabilising effect when predators feed selectively on one consumer stage or at high interaction strength (Nilsson *et al*., 2018). However, exactly how ODSs affect food-web stability in nature is still unclear and under debate. It seems reasonable to posit that ODSs can have a stabilising or destabilising effect depending upon what is studied (population, community or food web). More precisely, whereas ODSs generally seem to stabilise consumer–resource dynamics and, through resource partitioning, can increase population and community stability by reducing inter- or intraspecific competition (Amundsen *et al*., 2003; Schellekens *et al*., 2010; Sánchez-Hernández & Cobo, 2012*b*), the effect at the food-web level is variable. For example, ODSs commonly reduce the stability of complex trophic networks (Miller & Rudolf, 2011; Rudolf & Lafferty, 2011), but can increase food-web stability when the resources used by adults are less abundant than those used by juveniles (Schellekens *et al*., 2010). The influence (positive or negative) of ODSs can be complex and reversible, however, as fish that appear to be generalists at the species level can sometimes function as sequential specialists (see Rudolf & Lafferty, 2011). Models applied to developmental-stage-structured communities have demonstrated that ODSs may also affect community resilience and disturbance responses (Nakazawa, 2015), but this has yet to be tested in natural ecosystems.

V. CONCLUSIONS

(1) Although ODSs in fishes are well documented, our comprehension of their exact nature and driving mechanisms is incomplete because the knowledge is biased towards economically important species, and we currently lack a holistic understanding of their consequences for population, community, consumer–resource and food-web dynamics, and ecosystem processes and functioning. Studies attempting to address these knowledge gaps (e.g. Takimoto, 2003; Schellekens *et al*., 2010; Nakazawa, 2011*b*; Wollrab *et al*., 2013; Nilsson *et al*., 2018) have largely focused on theoretical approaches. Although some empirical attempts have been made to explore the implications of ODSs on consumer–resource and food-web dynamics (e.g. Persson & Greenberg, 1990; Persson & Hansson, 1999; Persson & Brönmark, 2002*a*), it is recommended that empirical research under natural conditions is instigated to corroborate the theory-based concepts behind the consequences of ODSs on the dynamics, processes and functioning at the population, community and ecosystem levels. It is also recommended that large-scale patterns in ODSs and common drivers in the animal kingdom are examined, so that novel ecological theories can be formulated and tested.

(2) Because body size tends to dominate the transition of ODSs, it is important to model the likelihood of size-related variations in ODSs. This can easily be accomplished through logistic regression models based on presence/absence information (e.g. Kahilainen & Lehtonen, 2003; Sánchez-Hernández *et al*., 2017), but such studies have usually only explored the probability of ontogenetic shifts to piscivory as a function of body size. More attention needs to be paid in the future to understanding whether the variation in ODSs is more likely to be among populations, seasons, cohorts or evolutionary time.

(3) Numerous biotic and abiotic factors can directly or indirectly influence ODSs, but the most influential likely vary spatially, temporally and interspecifically. We confirm that the major drivers of ODSs in fishes are prey availability, predation risk and competition. This review provides novel insights into trophic ontogeny theory, highlighting that some of the most influential drivers (predation risk and competition) do not impact directly on the trophic ontogeny of fishes, but can have an indirect effect on diet trajectories through ontogenetic changes in habitat use and concomitant changes in prey availability.

(4) Phylogenetic and evolutionary considerations on ontogenetic trajectories represent novel research lines and emerging frameworks (Claessen & Dieckmann, 2002; German & Horn, 2006; German *et al*., 2014; ten Brink & de Roos, 2017) that should receive further attention. Predation and competition are likely to promote the evolution of ontogenetic trajectories (Claessen & Dieckmann, 2002; ten Brink & de Roos, 2017), but we are not able to specify the importance (i.e. relative likelihood) of these factors as a mechanistic understanding of evolution in ODSs. Thus, the identification and quantification of these drivers represents an excellent opportunity to explore the evolutionary ontogenetic diet trajectories of fishes.

(5) ODSs can have profound ecological consequences for fishes, in particular by enhancing individual growth and lifetime reproductive output or reducing the risk of mortality (Fig. 3C). ODSs also have the potential to promote ecological release, facilitating the coexistence of sympatric species. It should be kept in mind that this conclusion may be context dependent as environmental conditions can change temporally or spatially. For example, factors impacting on prey-encounter rate, such as vegetation and turbidity, can influence ontogenetic trajectories (see Vejříková *et al*., 2017) and consequently ecological release.

(6) Research focusing on inter-individual variation in ontogenetic diet trajectories (Olson, 1996; Post, 2003; Svanbäck *et al*., 2015; Sánchez-Hernández & Cobo, 2018) has been limited, and it is recommended that the complex relationships between individual behaviour and environmental heterogeneity, including the relative importance of environmental factors and heritable traits (see Shedd *et al*., 2015), should be prioritised in future research. Such research may benefit from the use of a combination of methodical approaches, such as traditional diet, stable isotope, DNA metabarcoding, RNA–DNA ratio and tissue stoichiometry analyses (e.g. Boros, Saly & Vanni, 2015; Nielsen *et al*., 2018).

(7) Further studies that include the concept of ODSs within a broader ecological and evolutionary framework are required, possibly with dietary shifts analysed in relation to the phylogenetic relatedness of species, rather than their exploration using single model species, to identify the basis of global patterns in ODSs. The exploration of temperature and latitudinal gradients in ODSs could be a promising avenue for future research. This was highlighted by Llopiz (2013), who found that the likelihood of ODSs in marine fish larvae decreases with decreasing latitude, but these findings need be extended to the whole life cycle and ecosystem (freshwater and marine species) dimension to be accepted as a general theory. Future studies will likely reveal whether ODSs vary geographically along latitudinal or broad climatic domains (e.g. tropical, temperate and polar), and produce novel insights into the implications of ODSs for populations, communities and ecosystem processes and functioning.

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Table 1. The potential drivers of ontogenetic dietary shifts (ODSs) in fishes.

Driving mechanism	Evidence supporting	Evidence refuting	Mechanism underlying
(1) Predation risk	Werner & Gilliam (1984); Werner & Hall (1988); Walters & Juanes (1993); Dahlgren & Eggleston (2000); Reñones *et al*. (2002); Kimirei *et al*. (2013)	–	To minimise predation risk and consequently mortality, fish change habitat use which, in turn, leads to changes in feeding because of changes in prey availability
(2) Competition	Werner & Hall (1988); Persson & Greenberg (1990); Persson & Hansson (1999); Huss *et al*. (2008); Choi & Suk (2012); Kimirei *et al*. (2013); Sánchez-Hernández & Cobo (2018)	–	Competitive interactions (both intra- and interspecific) promote ODSs, enabling coexistence in fish populations/communities
(3) Prey availability and suitability	Wu & Culver (1992); Hjelm *et al*. (2000); García-Berthou (2002); Takimoto (2003); Nunn *et al*. (2007); Choi & Suk (2012); Kimirei *et al*. (2013); Sánchez-Hernández & Cobo (2018)	–	Prey characteristics (availability, abundance and structure) impose the limitation of switching to an alternative food source (i.e. it requires that the new food resource becomes available)
(4) Habitat use	Werner & Hall (1988); McCormick (1998); Dahlgren & Eggleston (2000); Lukoschek & McCormick (2001); Knudsen *et al*. (2006); Choi & Suk (2012); Dixon *et al*. (2012); Hertz *et al*. (2016); Polte *et al*. (2017); Hammar *et al*. (2018)	Eggold & Motta (1992); Cocheret de la Morinière *et al*. (2003)	Many studies have corroborated ontogenetic changes in habitat use, but these shifts are linked to changes in diet as consequence of changes in prey availability
(5) Morphological constraints	Eggold & Motta (1992); Magalhães (1993); Mittelbach & Persson (1998); Hjelm *et al*. (2000); Scharf *et al*. (2000); Linde *et al*. (2004); Belinda *et al*. (2005); Sánchez-Hernández *et al*. (2013)	–	Allometric changes in morphological traits (mouth gape and gill rakers) make new food resources available and consequently ODSs
(6) Swimming ability	Juanes & Conover (1994*a*); Hasegawa *et al*. (2012); Sánchez-Hernández & Cobo (2018)	–	Ontogenetic improvements in swimming ability as a result of development enable improve attack success and reduce activity costs of preying on mobile prey
(7) Gut length	Davis *et al*. (2013)	Belinda *et al*. (2005); German & Horn (2006); German *et al*. (2014)	Ontogenetic changes in gut morphology and physiology can favour the switch to animal diets based on a biological principle (gut length and diet´s animal proportion are negatively related)
(8) Metabolism and enzymes	Sherwood *et al*. (2002); Drewe *et al*. (2004); Jackson *et al*. (2004)	German *et al*. (2004); Pradhan *et al*. (2013); German *et al*. (2014)	Genetically programmed ontogenetic changes in metabolism and enzymes can canalise the size at which ODSs occur
(9) Feeding behaviour and	Werner & Hall (1988); Browman & O'Brien (1992); Eggold & Motta	–	Behavioural changes across ontogeny can drive ODSs, but this seems to depend on prey availability and predation risk

foraging modes	(1992); Wu & Culver (1992); Persson & Brönmark (2002*a*,*b*); Linde *et al.* (2004); Gustafsson *et al.* (2010); Choi & Suk (2012); Sánchez-Hernández & Cobo (2018)

Figure legends

Fig. 1. Number of studies examining ontogenetic dietary shifts (black bars) or ontogenetic shifts (white bars) in fish species over the last three decades (1989–2018), as indicated by an *Web of Science* search. The search was performed using the key words: (*i*) "fish", "diet" and "ontogenetic shifts" (black bars), and (*ii*) "fish" and "ontogenetic shifts" (white bars). Note, although representative, this search might underestimate the real number of published studies to date.

Fig. 2. Conceptual view of the ontogenetic dietary shift in a freshwater species (brown trout *Salmo trutta* L.) and a marine species (Atlantic cod *Gadus morhua* L.).

Fig. 3. Drivers and consequences of ontogenetic dietary shifts (ODSs) of fishes. (A) Number of papers in the *Web Science* core collection (N = 926) supporting the potential influence of the identified drivers on ODSs. (B) Relative importance of factors based on the probability (%) of positive effect on ODSs obtained with the R package *qgraph* (Epskamp *et al*., 2012), with the length and colour of the arrows indicating the relative importance of the variables. (C) Conceptual view of the complexity of mechanisms influencing ODSs and its consequences at the individual, population, community and ecosystem levels. Dashed lines represent an unlikely direct effect of the driver on ODSs. Arrows indicate the direction of the effect.