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# 1 **Causes and consequences of ontogenetic dietary shifts: a** 2 **global synthesis using fish models**

3

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20

21 **ABSTRACT**

22 Ontogenetic dietary shifts (ODSs), the changes in diet utilisation occurring over the life  
23 span of an individual consumer, are widespread in the animal kingdom. Understanding  
24 ODSs provides fundamental insights into the biological and ecological processes that

25 function at the individual, population and community levels, and is critical for the  
26 development and testing of hypotheses around key concepts in trophic theory on model  
27 organisms. Here, we synthesise historic and contemporary research on ODSs in fishes,  
28 and identify where further research is required. Numerous biotic and abiotic factors can  
29 directly or indirectly influence ODSs, but the most influential of these may vary  
30 spatially, temporally and interspecifically. Within the constraints imposed by prey  
31 availability, we identified competition and predation risk as the major drivers of ODSs  
32 in fishes. These drivers do not directly affect the trophic ontogeny of fishes, but may  
33 have an indirect effect on diet trajectories through ontogenetic changes in habitat use  
34 and concomitant changes in prey availability. The synthesis provides compelling  
35 evidence that ODSs can have profound ecological consequences for fish by, for  
36 example, enhancing individual growth and lifetime reproductive output or reducing the  
37 risk of mortality. ODSs may also influence food-web dynamics and facilitate the  
38 coexistence of sympatric species through resource partitioning, but we currently lack a  
39 holistic understanding of the consequences of ODSs for population, community and  
40 ecosystem processes and functioning. Studies attempting to address these knowledge  
41 gaps have largely focused on theoretical approaches, but empirical research under  
42 natural conditions, including phylogenetic and evolutionary considerations, is required  
43 to test the concepts. Research focusing on inter-individual variation in ontogenetic  
44 trajectories has also been limited, with the complex relationships between individual  
45 behaviour and environmental heterogeneity representing a particularly promising area  
46 for future research.

47

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

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70

## 71 **I. INTRODUCTION**

72 Ontogenetic dietary shifts (ODSs), the changes in diet utilisation occurring over the life  
73 span of an individual consumer, are widespread in the animal kingdom. ODSs have  
74 been most extensively researched in insects, amphibians and fishes. The best-studied

75 examples in insects and amphibians are associated with metamorphosis and the  
76 sometimes extreme shifts in habitat use, such as between freshwater and terrestrial  
77 environments [Nakazawa (2015) and references therein]. By contrast, fishes typically  
78 inhabit the same environments throughout their lives (except for diadromous fishes),  
79 allowing an examination of other factors influencing ODSs and whether or not  
80 conclusions can be generalised among contrasting aquatic ecosystems (e.g. freshwater,  
81 brackish and marine). Fish have been useful model species in both empirical and  
82 theoretical studies of trophic ontogeny (e.g. Schellekens, De Roos & Persson, 2010;  
83 Nakazawa, 2015; Sánchez-Hernández & Cobo, 2018), with a steep increase in the  
84 number of publications over the last decade (Fig. 1). Despite this growing interest, the  
85 majority of research has addressed changes in diet composition during development or  
86 differences between size classes (e.g. Lukoschek & McCormick, 2001; Davis *et al.*,  
87 2011; Sánchez-Hernández & Cobo, 2016). In the early stages of the life cycle, many  
88 fish species prey upon phytoplankton, zooplankton or small macroinvertebrates, but  
89 may switch to larger macroinvertebrates, fish, plants or detritus later in development  
90 (Nunn, Tewson & Cowx, 2012; Huss *et al.*, 2013). Conversely, generalist species, such  
91 as most salmonids, often forage on a wide range of aquatic invertebrates when small,  
92 but may include terrestrial invertebrates, fish, amphibians or rodents at larger sizes  
93 (Eloranta, Kahilainen & Jones, 2010; Jensen, Kiljunen & Amundsen, 2012; Sánchez-  
94 Hernández *et al.*, 2013). Pronounced dietary shifts sometimes coincide with specific  
95 events in development, such as the transition from ‘finfold’ to ‘finformed’ larvae or  
96 from larvae to juveniles (Nunn, Harvey & Cowx, 2007), but few studies have attempted  
97 to disentangle the potentially confounding influences of ontogeny (i.e. processes scaling  
98 with body size) on ODSs.

99 Although ODSs in fishes are well documented (e.g. Amundsen *et al.*, 2003; Kolasinski  
100 *et al.*, 2009; Nunn *et al.*, 2012), the majority of research has focussed on a small number  
101 of economically important species, and our comprehension of the exact nature of ODSs,  
102 the driving mechanisms and their consequences is incomplete. Nunn *et al.* (2012)  
103 described the occurrence of ODSs in a review of the foraging ecology of larval and  
104 juvenile fishes, but adults and the causes and consequences of ODSs were not explored.  
105 In particular, attempts to separate the drivers and consequences of ODSs have been  
106 equivocal. For example, many researchers have concluded that ODSs are related to the  
107 specific habitat requirements of prey following ontogenetic changes in habitat use by  
108 fish (e.g. Lukoschek & McCormick, 2001; Choi & Suk, 2012), but habitat changes can  
109 be a consequence of other drivers, such as changing predation risk or prey availability  
110 (e.g. Werner & Hall, 1988; Wu & Culver, 1992). Theory predicts that ODSs are  
111 influential in community and food-web stability (Schellekens *et al.*, 2010; Miller &  
112 Rudolf, 2011; Rudolf & Lafferty, 2011; de Roos & Persson, 2013; van Leeuwen *et al.*,  
113 2013, 2014; Nilsson, McCann & Caskenette, 2018), but we currently lack a holistic  
114 understanding based on empirical evidence of their consequences for populations,  
115 communities, food-web dynamics and ecosystem processes and functioning. Because  
116 morphological, behavioural, physiological and life-history traits play an important role  
117 in foraging specialisation and define intra-specific trophic polymorphisms where they  
118 exist [Smith & Skúlason (1996) and references therein], identification of the role of  
119 traits linked with foraging should help to disentangle the causes and consequences of  
120 ODSs. However, little attention has been given to exploring specific events in fish  
121 ontogeny during which diets switch and during which rapid change in selection  
122 pressures could trigger evolutionary branching (Claessen & Dieckmann, 2002; ten  
123 Brink & de Roos, 2017). To overcome the challenges associated with this knowledge

124 deficit and equivocal conclusions, we aim to synthesise: (i) the biological concepts (i.e.  
125 the causes and consequences of ODSs), setting them in a broad ecological and  
126 evolutionary framework, and (ii) enhance our current understanding of the drivers and  
127 consequences of ODSs in fishes, using pertinent examples from marine and freshwater  
128 ecosystems. Understanding ODSs provides fundamental insights into the biological and  
129 ecological processes that function at the individual, population and community levels,  
130 and is critical to the development and testing of hypotheses around key concepts in  
131 trophic theory on model organisms.

132

## 133 **II. THE NATURE OF ODSs**

134 ODSs are often linked to other ontogenetic niche shifts, in particular habitat choice,  
135 which influences the availability of different prey types to the consumer (e.g. Werner &  
136 Hall, 1988). For organisms with distinct life stages, such as aquatic insects and  
137 amphibians, these shifts are typically abrupt and consist of complete switches between  
138 separate niches following metamorphosis (Claessen & Dieckmann, 2002; Bassar, Travis  
139 & Coulson, 2017). Most organisms, however, exhibit less-abrupt shifts in niche  
140 utilisation, but ODSs may nonetheless manifest as relatively distinct changes in prey  
141 choice or diet composition associated with shifts in habitat use during ontogeny, as is  
142 often seen in fish (Fig. 2; Werner, 1986). Most ODSs are size-related (Werner &  
143 Gilliam, 1984) as, for many species, the body size of a consumer significantly affects its  
144 feeding ability and the size range of prey that is available for consumption (Werner,  
145 1986; Mittelbach & Persson, 1998). Hence, ODSs are commonly observed in organisms  
146 that undergo large changes in body size (Werner & Gilliam, 1984; Werner, 1986). With  
147 the notable exceptions of birds and mammals, whose juveniles are typically  
148 approximately adult-sized when they commence independent foraging, individuals of

149 most animal taxa vary greatly in body size over their lifetime (Werner, 1986).  
150 Accordingly, ODSs are a common feature of the life cycles of a diverse range of  
151 organisms (Kimirei *et al.*, 2013), including most invertebrates, fishes, amphibians and  
152 reptiles (Werner & Gilliam, 1984). The relationship between body size and prey size is  
153 particularly strong in fish, which do not have any appendages to manipulate prey. Their  
154 ability to handle prey thus generally scales with mouth gape size, which, in turn, scales  
155 with body size (e.g. Dunic & Baum, 2017). Hence, unlike amphibians and aquatic  
156 insects, body size seems to play a critical role in ODSs in fishes, although there are a  
157 few exceptions (e.g. lampreys) in which ODS is linked to metamorphosis.

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



174 may exhibit such a switch [Sánchez-Hernández & Cobo (2018) and references therein].  
175 This phenomenon needs to be examined in other stream-dwelling species to be  
176 recognised as a general principle.

177 Profound multiple ODSs occurring over the life cycle are frequently seen in piscivorous  
178 fish species (e.g. Mittelbach & Persson, 1998; Hjelm, Persson & Christensen, 2000;  
179 Amundsen *et al.*, 2003; Hanson, 2011; Artero *et al.*, 2015). Typically, such dietary  
180 switches involve distinct shifts in prey sizes from millimetre to centimetre and finally to  
181 decimetre orders of magnitude. The prey size increases with predator size following  
182 allometric scaling theory (Mittelbach & Persson, 1998; Dunic & Baum, 2017). For  
183 example, juvenile largemouth bass [*Micropterus salmoides* (Lacépede, 1802)] and  
184 European perch (*Perca fluviatilis* L.) primarily feed upon zooplankton before switching  
185 to benthic invertebrates, and later to small and, subsequently, large fish prey (e.g. Hjelm  
186 *et al.*, 2000; García-Berthou, 2002; Amundsen *et al.*, 2003). Moreover, studies focused  
187 on stage-structured models have concluded that an early ODS from zooplankton to  
188 macroinvertebrates is necessary for individuals to reach sizes large enough to enable  
189 subsequent exploitation of the ultimate piscivorous niche (Huss *et al.*, 2013). Similar  
190 multiple ODSs from pelagic to benthic invertebrates and subsequently to increasingly  
191 larger fish prey are also seen in marine piscivorous fish, such as Atlantic cod (*Gadus*  
192 *morhua* L.) (Fig. 2; Link & Garrison, 2002), and benthic coastal marine fish, such as  
193 Atlantic John Dory (*Zeus faber* L.) (Stergiou & Fourtouni, 1991). Some cyprinids may,  
194 by contrast, follow a different dietary trajectory during their ontogeny (e.g. Penttinen &  
195 Holopainen, 1992; Sánchez-Hernández & Cobo, 2012a; Dadebo *et al.*, 2014). The first  
196 ODS in cyprinids is invariably from plankton to benthic invertebrates (Penttinen &  
197 Holopainen, 1992), but the contribution of detritus and plant material increases during  
198 ontogeny in some species, whereas others feed largely on insects (Sánchez-Hernández

199 & Cobo, 2012a; Dadebo *et al.*, 2014). A consequence of ODSs is that, whereas the diets  
200 of many fish species are frequently similar during the larval period, juveniles and adults  
201 often diverge into a broad spectrum of feeding strategies, such as herbivory, detritivory,  
202 omnivory and carnivory (see for example Davis *et al.*, 2011).

203 The current literature indicates that ODSs are flexible in nature. Indeed, considerable  
204 variation in ODSs can be observed even among conspecifics at the same life stage (e.g.  
205 Post, 2003; Sánchez-Hernández & Cobo, 2018). In addition to individual ontogenetic  
206 trajectories, many fish species experience gradual ODSs at the population level (e.g.  
207 Stergiou & Fourtouni, 1991; Cocheret de la Morinière *et al.*, 2003; Ramos-Jiliberto *et*  
208 *al.*, 2011), whereas they occur abruptly in others. Abrupt ODSs are most apparent in  
209 diadromous or amphidromous species (e.g. many salmonids, lampreys and galaxiids),  
210 which inevitably shift their diets (both in terms of prey size and species composition)  
211 when migrating between freshwater and marine environments, leading to marked  
212 changes in the origin of utilised carbon and nitrogen sources and concomitant changes  
213 in the trophic level at which they feed (Keeley & Grant, 2001; Dixon *et al.*, 2012; Hertz  
214 *et al.*, 2016). ODSs are generally more distinct when the switch occurs following  
215 migration between marine and freshwater ecosystems than within freshwater  
216 ecosystems (e.g. riverine *versus* lacustrine). Many ODSs in freshwater species involve  
217 life stages feeding mainly on insects, a prey category that, with the exception of river  
218 mouths, is not generally present in marine ecosystems. Based on the reviewed literature,  
219 we conclude that the dietary role occupied by insects in fresh water chiefly is filled by  
220 crustaceans and/or cephalopods in marine ecosystems (Fig. 2). Ontogenetic diet  
221 trajectories thus depend upon the type of ecosystem inhabited (e.g. freshwater *versus*  
222 marine), although a switch to piscivory, when fish become top predators, seems to be a  
223 common feature of many ecosystems (e.g. Winemiller, 1989; Jensen *et al.*, 2012; Artero

224 *et al.*, 2015). Species with highly specialised diets in the adult period invariably also  
225 experience abrupt ODSs. Many lampreys, for example, are filter feeders during the  
226 freshwater phase of their life cycle, but haematophagous (blood feeders) during the  
227 marine phase (Silva, Barca & Cobo, 2016). Some fish species, such as many  
228 Neotropical characids, undergo ODSs from terrestrial insects to fruits and leaves  
229 (Drewe *et al.*, 2004), and fish-scale consumption by facultative scale feeders usually  
230 increases with fish size (Peterson & Winemiller, 1997; Hahn, Pavanelli & Okada,  
231 2000).

232 In recent decades, there has been a strong interest in the period of ontogeny in which  
233 fish become piscivorous (Mittelbach & Persson, 1998; Hanson, 2011; Sánchez-  
234 Hernández *et al.*, 2017). An early transition to piscivory may increase somatic growth,  
235 lead to early maturation or enhance lifetime fitness (Werner, 1986; Olson, 1996;  
236 Mittelbach & Persson, 1998; Post, 2003), but the size-related timing of the switch is  
237 highly variable among freshwater fishes (see Mittelbach & Persson, 1998). Brown trout  
238 is a widely distributed and extensively studied species that provides a good example of  
239 ODSs to piscivory (Fig. 2). Although it has been claimed that brown trout become  
240 piscivorous at a minimum body length of 200–300 mm, the switch may occur at smaller  
241 sizes [Sánchez-Hernández *et al.* (2017) and references therein]. Importantly, the size-  
242 related timing of the switch seems to be dependent upon the presence of small-sized  
243 prey fish and competition with other species (Sánchez-Hernández *et al.*, 2017).

244 Similarly, fish species typically become piscivorous above a threshold size in the  
245 marine environment (Hanson, 2011; Artero *et al.*, 2015). For example, Hanson (2011)  
246 observed that white hake [*Urophycis tenuis* (Mitchill, 1814)] and Atlantic cod become  
247 piscivorous when they are greater than 350 and 450 mm in length, respectively. By  
248 contrast, other marine species can become piscivorous very early in ontogeny (e.g.

249 Reglero *et al.*, 2011; Llopiz, 2013). It is possible that an early switch to piscivory is  
250 connected to water temperature, as higher temperatures tend to promote a higher  
251 frequency of piscivory (Reglero *et al.*, 2011). This was corroborated by Llopiz (2013),  
252 who found that piscivory in the early development of fish was most frequent at lower  
253 latitudes, but a mechanistic understanding of how water temperature influences the size-  
254 related timing of ontogenetic switches to piscivory is missing. Factors other than  
255 temperature, such as prey-encounter rates and size-selective predation, probably also  
256 influence piscivory and growth in the larval and early juvenile periods of species  
257 displaying ODSs (e.g. Huss, Byström & Persson, 2010). Thus, we conclude that the  
258 nature of ODSs can differ among ecosystem types as a consequence of differences in  
259 food availabilities and the inherent food preferences of particular species which is most  
260 likely linked to phylogenetic relatedness.

261

### 262 **III. DRIVING MECHANISMS**

263 The potential drivers of ODSs in coral reef fish have been thoroughly reviewed by  
264 Kimirei *et al.* (2013). Here, we attempt to identify the general mechanisms that drive  
265 ODSs in fish in riverine, lacustrine and marine systems, as well as the most directional  
266 drivers involved. It should be kept in mind that there are numerous biotic and abiotic  
267 factors, both known and unknown, that have the potential to influence directly or  
268 indirectly ontogenetic diet trajectories, and consequently affect the timing and nature of  
269 ODSs in fishes (Fig. 3). These include competitive interactions, prey availability,  
270 predation risk and internal mechanisms (Werner, 1986; Olson, 1996; Sherwood *et al.*,  
271 2002; Galarowicz, Adams & Wahl, 2006; Kimirei *et al.*, 2013). With so many factors  
272 that directly or indirectly influence ODSs, separating the most important driving

273 mechanisms is a complex task, especially as many factors seem inter-related (see  
274 Sánchez-Hernández & Cobo, 2018).

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

298 disentangle the most important drivers of ODSs, we calculated the prevalence  
299 (percentage of reviewed articles) of positive effects (evidence supporting) for each of  
300 the nine potential drivers of ODSs. This enabled us to estimate the relative importance  
301 of the nine potential drivers on ODSs (Fig. 3B).

302

### 303 **(1) Predation risk**

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

323 the trophic ontogeny of fishes, but it can have an indirect effect on diet trajectories  
324 through predation risk-driven changes in habitat use (e.g. previously risky habitats  
325 becoming available during ontogeny).

326

## 327 **(2) Competition**

328 Fish abundance, assumed to be a principal mediator of intra- and interspecific  
329 competition, can play a role in driving ODSs in fishes (e.g. Persson & Hansson, 1999;  
330 Kimirei *et al.*, 2013; Sánchez-Hernández & Cobo, 2018). Theoretical approaches to the  
331 relationship between competition and diet trajectories posit that competition is a key  
332 variable that forces individuals to shift their foraging behaviour to alleviate intra- and  
333 interspecific competition (see Section IV). However, this mechanism is likely relevant  
334 only for consumers with overlapping trophic niche requirements (Persson & Hansson,  
335 1999; Huss, Byström & Persson, 2008).

336 ODSs can be influenced by competition (e.g. Werner & Hall, 1988; Choi & Suk, 2012;  
337 Kimirei *et al.*, 2013). In an illustrative example, Persson & Greenberg (1990) observed  
338 that the body length-related timing of an ODS from zooplankton to macroinvertebrate  
339 feeding in juvenile European perch changed (that is switched to earlier) in response to a  
340 competitor [roach *Rutilus rutilus* (L.)] with a superior efficiency when foraging on  
341 zooplankton. Similarly, Persson & Hansson (1999) showed that common bream  
342 [*Abramis brama* (L.)] shifted to benthic organisms earlier in ontogeny following a  
343 reduction in fish abundance, although it was not clear whether the change was  
344 associated with a reduction in intra- or interspecific competition. Huss *et al.* (2008)  
345 provided experimental evidence that in the initial stages of fish ontogeny (juveniles),  
346 size-related morphological constraints prevented European perch from making an early  
347 shift from zooplankton to macroinvertebrates at high levels of intraspecific competition.

348 Based on our literature review, we conclude that competition is a major driver of ODSs  
349 in fishes (Fig. 3B).

350

### 351 **(3) Prey availability and suitability**

352 There is considerable evidence that prey availability and suitability are important  
353 mechanisms driving ODSs in fishes (e.g. Hjelm *et al.*, 2000; Choi & Suk, 2012; Kimirei  
354 *et al.*, 2013; Sánchez-Hernández & Cobo, 2018). For example, the switch in summer by  
355 many juvenile cyprinids to aufwuchs (the periphyton and associated microfauna that  
356 grow on underwater surfaces), considered a poor food resource because of its low  
357 digestibility and nutritive value (e.g. Lemke & Bowen, 1998), is probably linked to a  
358 lack of suitable animal prey; the evidence for this is that the switch may not occur if  
359 sufficient invertebrates are available [Nunn *et al.* (2007) and references therein].

360 Similarly, Wu & Culver (1992) observed that juvenile yellow perch [*Perca flavescens*  
361 (Mitchill, 1814)] shift from zooplankton to benthic prey in response to a decline in the  
362 abundance of zooplankton in summer. In addition to species composition, García-  
363 Berthou (2002) observed that the ODS to piscivory by largemouth bass can be  
364 influenced by the size structure of the prey fish assemblage. Specifically, a dominance  
365 of centrarchids within the body length range 75–150 mm with anti-predator mechanisms  
366 (e.g. spiny rays in the dorsal and anal fins) can have a strong negative influence on the  
367 ontogenetic shift to piscivory, preventing the switch occurring (García-Berthou, 2002).  
368 Takimoto (2003) concluded that an early shift to the next ontogenetic niche can occur  
369 when the abundance of prey in the first niche is low. Thus, the evidence suggests that  
370 prey availability and suitability impose important limitations on the timing and extent of  
371 ODSs (Fig. 3B).

372



373 **(4) Habitat use**

374 Ontogenetic changes in habitat use is a clear example of where a process may be driving  
375 an ODS or where the ODS may be a consequence of other drivers, such as changing  
376 predation risk or prey availability (see Sections III.1 and III.3), and thus the ontogenetic  
377 habitat change may be a simple consequence of an ODS driven by other factors. Thus,  
378 in both marine and freshwater systems, many prey taxa frequently have specific habitat  
379 requirements (Chapman, 1999; Tachet *et al.*, 2010) and, consequently, ontogenetic  
380 changes in habitat use by a predator may lead to unavoidable changes in diet. This is  
381 particularly evident in diadromous species (that migrate between freshwater and marine  
382 ecosystems; Dixon *et al.*, 2012; Hertz *et al.*, 2016) and lacustrine migrants (moving  
383 between littoral and pelagic or profundal habitats; Werner & Hall, 1988; Knudsen *et al.*,  
384 2006).

385 The habitat preferences of fishes commonly change during development (e.g. from  
386 nursery to adult habitats), and may provide new foraging opportunities (McCormick,  
387 1998; Dahlgren & Eggleston, 2000; Choi & Suk, 2012). For example, Werner & Hall  
388 (1988) demonstrated that a switch of bluegill sunfish from littoral prey to zooplankton  
389 coincided with a shift from the littoral to the pelagic zone during ontogeny. Cocheret de  
390 la Morinière *et al.* (2003) postulated that ODSs may crucially influence changes in  
391 habitat use and promote nursery-to-coral-reef migrations. Notwithstanding, for some  
392 fish species, such as the striped mullet (*Mugil cephalus* Linnaeus, 1758), changes in  
393 habitat use during ontogeny do not necessarily lead to changes in diets (Eggold &  
394 Motta, 1992). This may underline the difficulty in identifying the role of habitat use as a  
395 driving mechanism of ODSs. It is possible that ontogenetic changes in habitat use are  
396 drivers of ODSs in some species, but a consequence of ODSs in others. The relatively

397 sparse literature on this topic suggests that this would be a fruitful area for future  
398 research.

399 In addition to horizontal habitat shifts (e.g. between the littoral and pelagial of lentic  
400 systems), which are common in both marine and freshwater fish species (Werner &  
401 Hall, 1988; Polte *et al.*, 2017), changes in diet composition can occur in response to  
402 vertical habitat shifts (i.e. through the water column). Although such patterns do not  
403 apply to all species, there are some common themes from both marine and freshwater  
404 systems that are informative. It seems that vertical and resource-driven ontogenetic  
405 habitat shifts are frequently driven by differential predation risk in differing water  
406 depths regardless of ecosystem type. For example, Choi & Suk (2012) concluded that  
407 ontogenetic shifts from the upper to the lower water column often occur in marine  
408 species, with the common pattern being that large individuals feed closest to the benthic  
409 zone. In lacustrine ecosystems, this type of vertical habitat shift during ontogeny has  
410 been identified in smelt [*Osmerus eperlanus* (L.)], with this species undergoing a  
411 habitat shift towards deeper water as individuals grow (Hammar *et al.*, 2018). However,  
412 the common ontogenetic theme of shifting through the water column may change across  
413 ecosystem type and fish species. Regarding differences among fish species inhabiting  
414 the same ecosystem, Hammar *et al.* (2018) observed that Arctic charr [*Salvelinus*  
415 *alpinus* (Linnaeus, 1758)] have the opposite vertical ontogenetic habitat shift than that  
416 of its prey (smelt). Similarly, the pattern in marine ecosystems is not always replicated  
417 in freshwater as small Arctic charr frequently make ontogenetic habitat shifts to the  
418 profundal zone in the ice-free season (Knudsen *et al.*, 2006; Hammar *et al.*, 2018),  
419 contrasting with the behaviour observed in the serpentine goby [*Pterogobius elapoides*  
420 (Gunther, 1872)] (Choi & Suk, 2012). Rather than these habitat shifts being driven by  
421 differences in predation risk *per se*, it is likely that differences in water-column use

422 between marine and freshwater fishes and among fish species might be explained by a  
423 trade-off between predation risk and prey availability. Our reasoning is that predation  
424 risk is usually lower near the bottom or in the profundal zone than at the surface in  
425 freshwater systems (Knudsen *et al.*, 2006; Sánchez-Hernández & Cobo, 2018), whereas  
426 the water column, a potentially risky habitat in marine systems, seems to be optimal for  
427 small marine individuals to catch abundant small pelagic organisms (Choi & Suk,  
428 2012). It is possible that predation risk is highest in the water column in marine  
429 ecosystems but near the water surface in fresh waters. However, species undergoing  
430 vertical habitat shifts during ontogeny with zooplankton as the first prey type, such as  
431 for example in smelt (Hammar *et al.*, 2018), are forced simply to contend with this  
432 higher predation risk. Thus, a decision by small fish to utilise the water column as a  
433 habitat may be driven by prey availability regardless of, or in combination with,  
434 predation risk. This corroborates our earlier conclusion that prey availability and  
435 predation risk are key drivers of ODSs.

436 Dahlgren & Eggleston (2000) provided another example of ontogenetic habitat  
437 segregation where a foraging–predation trade-off is evident. These authors observed  
438 ontogenetic habitat shifts from the interstices of macroalgal clumps (a safe habitat) to  
439 outside of the algal habitat in the Nassau grouper [*Epinephelus striatus* (Bloch, 1792)],  
440 with small fish showing higher foraging rates (number of prey items ingested per 72 h)  
441 than larger fish in the macroalgal habitat. Additionally, Lukoschek & McCormick  
442 (2001) observed that large individuals of a marine benthic carnivorous fish preferred to  
443 forage at the reef edge and base, whereas small individuals tended to feed on the reef  
444 flat and slope. It is worth noting that habitat variation among species and individuals  
445 provides an indication to understand the causes of variations in ODSs in fishes, but the  
446 true role of habitat as a driver of ODSs is not yet clearly resolved.

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

462

### 463 **(5) Morphological constraints**

464 Body size determines a suite of morphological traits that can affect the transition among  
465 prey types across the lifetime of fish. Indeed, changes in body morphology, such as  
466 mouth gape and gill raker size or density, during ontogeny can be a determinant of  
467 ODSs in fishes. Mouth gape certainly imposes limitations on ODSs in fishes through its  
468 effect on prey-handling ability. Thus, gape is closely correlated with body size-related  
469 changes in diet during ontogeny (Magalhães, 1993; Scharf *et al.*, 2000; Linde *et al.*,  
470 2004; Sánchez-Hernández *et al.*, 2013). In fish species that consume whole prey,  
471 increasing mouth dimensions are generally closely and positively related to mean and

472 maximum prey size (Scharf *et al.*, 2000; Sánchez-Hernández *et al.*, 2013). This effect is  
473 most easily observed in the switch to piscivory, with fish species with larger mouth  
474 gapes typically becoming piscivorous at smaller body sizes (Mittelbach & Persson,  
475 1998). This pattern is repeated within species as ontogenetic changes in mouth  
476 dimensions account for diet shifts such as, for example, the switch to cephalopods or  
477 fish prey at larger individual size (Scharf *et al.*, 2000; Linde *et al.*, 2004; Belinda,  
478 Ward-Campbell & Beamish, 2005). Additionally, changes in mouth dimensions with  
479 body size may drive changes from generalist to more specialised feeding in some  
480 species (Linde *et al.*, 2004). Thus, prey-handling characteristics impose important  
481 limitations on the timing and extent of ODSs.

482 In many filter-feeding fish species, gill raker length and inter-raker spacing increase  
483 with body size, and prey particle size increases concomitantly (Eggold & Motta, 1992;  
484 Gerking, 1994). The number of gill rakers can also increase with fish size (Hjelm *et al.*,  
485 2000). Therefore, any variation in the size and structure of the gill rakers during  
486 ontogeny can have direct consequences for ontogenetic dietary trajectories and, thereby,  
487 on the timing of ODSs (Eggold & Motta, 1992; Hjelm *et al.*, 2000). It has been widely  
488 accepted that individuals with a large number of gill rakers are better adapted to  
489 zooplankton feeding because dense gill raker spacing is assumed to be most efficient for  
490 retaining small prey in the mouth cavity [Kahilainen *et al.* (2011) and references  
491 therein]. Ontogenetically, one consequence of having a large number of gill rakers is an  
492 increase in the size at which a shift from zooplankton to other prey may occur,  
493 presumably because of the relatively higher foraging efficiency on zooplankton of  
494 individuals with a higher density of gill rakers (Hjelm *et al.*, 2000). This conclusion was  
495 based on a freshwater model organism, the European perch, and may not apply to all  
496 fish species. In addition, some marine species seem to change feeding strategies with

497 increasing fish size, which may be related to gill raker length and inter-raker spacing  
498 (Gerking, 1994; Hirota, Uehara & Honda, 2004). It is possible that small individuals are  
499 often more selective in their feeding strategy (showing selective browsing) than larger  
500 conspecifics, which frequently rely more on grazing feeding strategies (Eggold &  
501 Motta, 1992).

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

522

523 **(6) Swimming ability**

524 Improvements in swimming ability during ontogeny have the potential to lead ODSs,  
525 thereby poor swimming ability may be a constraint on ODSs in some cases. Although  
526 more pronounced during early ontogeny, the swimming ability of fishes tends to  
527 increase with fish length through the development of fins, body shape and muscle  
528 anatomy (e.g. Ojanguren & Braña, 2003; Koumoundouros *et al.*, 2009; Butler *et al.*,  
529 2012). Based on the principle that prey species have specific habitat requirements and  
530 behaviours (Chapman, 1999; Tachet *et al.*, 2010), increased swimming ability enables  
531 access to additional habitat types and/or new foraging opportunities (Hasegawa *et al.*,  
532 2012; Sánchez-Hernández & Cobo, 2018). For example, many salmonid species are  
533 able to exploit higher velocity and deeper water as they develop and grow (e.g.  
534 Hasegawa *et al.*, 2012). Additionally, improvements in swimming ability during  
535 ontogeny can lead to ODSs because (i) the capture success of mobile prey may increase  
536 (e.g. Juanes & Conover, 1994a), and (ii) improved escape swimming performance may  
537 release individuals from former constraints of predation (Gibb *et al.*, 2006). Thus,  
538 swimming performance usually improves during ontogeny, which, in turn, indirectly  
539 impacts on the diets of fishes.

540

541 **(7) Gut length**

542 Generally, gut length in fishes increases as a consequence of increasing body size  
543 during ontogeny, although there is some evidence that ontogenetic changes in relative  
544 gut length (i.e. gut length independent of body size) generally differ between  
545 herbivorous and carnivorous species (German & Horn, 2006; Davis *et al.*, 2013). There  
546 is considerable evidence that gut length changes in response to exposure to different

547 prey (Belinda *et al.*, 2005; German & Horn, 2006; Davis *et al.*, 2013; German,  
548 Gawlicka & Horn, 2014), but little support for the hypothesis that gut length may drive  
549 ODSs. Belinda *et al.* (2005), for example, could find no evidence for gut length being a  
550 driver of ODSs in snakehead [*Channa limbata* (Cuvier, 1831)], but showed that mouth  
551 dimensions were influential.

552

### 553 **(8) Metabolism and enzymes**

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



571 ontogenetic development of digestive enzymes from the pancreas, stomach and intestine  
572 of fishes (e.g. German *et al.*, 2004; Pradhan *et al.*, 2013).  
573 Size-scaling metabolic theory predicts allometric relationships between metabolic rate  
574 and body mass in fishes [Yagi & Oikawa (2014) and references therein], and such  
575 ontogenetic changes in metabolic rate may improve swimming ability and lead to  
576 ODSs. Indeed, Jackson *et al.* (2004) concluded that changes in metabolic rate may  
577 determine the size at which diet shifts occur, playing a key role, alongside handling  
578 time, in determining prey choice. Other factors, such as muscle enzymatic activity, also  
579 appear to change during ontogeny. For instance, it has been observed that wild fish  
580 show changes in muscle enzymatic activity, such as lactate dehydrogenase activity, with  
581 diet switches to planktivory, benthivory, and piscivory (Sherwood *et al.*, 2002). This  
582 enzyme has an important role in glycolysis, and concentrations seem to be higher in  
583 fishes exhibiting dietary shifts (Sherwood *et al.*, 2002). Enzymes that enhance  
584 glycolysis in the white muscle during exercise can have a positive impact on swimming  
585 ability, and thus theoretically may affect prey capture ability (see Section III.6).  
586 Notwithstanding, it is doubtful that either metabolic rate or enzyme activity (either  
587 digestive or muscle physiology) are direct drivers of ODSs.

588

### 589 **(9) Feeding behaviour and foraging modes**

590 The feeding behaviour strategies (e.g. planktivory, benthivory and piscivory) and  
591 foraging modes, i.e. the type of prey-search behaviour [‘ambush’ (sit-and-wait) or  
592 ‘cruise’ (active) *sensu lato*], of fishes can change during ontogeny (e.g. Werner & Hall,  
593 1988; Browman & O’Brien, 1992; Sánchez-Hernández & Cobo, 2018). A number of  
594 laboratory and field studies have identified size-dependent effects on the foraging  
595 modes of fishes and, ultimately, on ODSs (e.g. Nakano *et al.*, 1999; Persson &

596 Brönmark, 2002*a,b*; Gustafsson, Bergman & Greenberg, 2010; Sánchez-Hernández &  
597 Cobo, 2018). Gustafsson *et al.* (2010) noted that large brown trout used the upper water  
598 column to forage on surface-drifting prey (drift foraging) more often than did smaller  
599 individuals, which remained closer to the bottom and fed on aquatic prey. In another  
600 example, Sánchez-Hernández & Cobo (2018) demonstrated size-related changes in  
601 foraging modes, namely an increasing probability of switching to drift foraging with  
602 increasing fish size. Although it is possible that these foraging shifts (i.e. from the  
603 benthos to the water surface) may be triggered by intrinsic features linked to body size,  
604 they seem to be influenced by a number of inter-related factors in addition to intrinsic  
605 features, such as environmental variation (mainly benthic invertebrate density and water  
606 current velocity) and competition (Sánchez-Hernández & Cobo, 2018). Similarly, there  
607 are several examples from lacustrine and marine ecosystems supporting the view that  
608 feeding behaviour and foraging modes change during ontogeny through ontogenetic  
609 habitat shifts (see Section III.4). A common ontogenetic pattern amongst lacustrine fish  
610 is a switch in foraging along the littoral–pelagic axis (i.e. from littoral to pelagic  
611 foraging or *vice-versa*) (e.g. Werner & Hall, 1988; Wu & Culver, 1992). From marine  
612 ecosystems, it has been observed that the foraging behaviour of many species changes  
613 from planktivory to benthivory (Choi & Suk, 2012) or browsing to grazing (Eggold &  
614 Motta, 1992). In addition, Linde *et al.* (2004) observed ontogenetic changes from a  
615 passive (preying on sedentary taxa) to an active (preying on nekton) behaviour in the  
616 foraging strategy of the dusky grouper [*Epinephelus marginatus* (Lowe, 1834)].  
617 Because foraging specialisation and fish ontogeny are closely linked, we tentatively  
618 conclude that changes in foraging strategy related to ontogenetic shifts in specialisation  
619 can be a mechanism driving ODSs, but that such changes are likely ultimately driven by  
620 predation risk, competition and/or prey availability.

621 To summarise, the *Web of Science* core collection indicated that habitat use emerged as  
622 the most recurrent topic in explaining ODSs (Fig. 3A), but that competition, prey  
623 availability, feeding behaviour, foraging modes and predation risk also seem to be  
624 influential. It is doubtful that some putative drivers (gut length, metabolism and  
625 enzymes) are direct drivers of ODSs (Fig. 3B), but their true roles are not yet clearly  
626 resolved and represent fruitful areas of future research. Based on the reviewed literature,  
627 we posit that habitat use, feeding behaviour and foraging mode are a consequence of  
628 other drivers, such as changes in predation risk, competition and prey availability (Fig.  
629 3C). Although prey-handling constraints can play a significant role in the timing of  
630 ODSs (see Section III.5), we conclude that any impacts may be masked by inter- or  
631 intraspecific competition through density-dependent effects on developmental processes  
632 and, in particular, the body size of fishes. Similarly, we suggest that morphological  
633 constraints, swimming ability, gut length, metabolism and enzymes are consequences of  
634 body size and not drivers of ODSs *per se* (Fig. 3C). Prey availability, predation risk and  
635 competition emerged as the most important drivers of ODSs in fishes, with prey  
636 availability providing the potential for other factors to influence ODSs. Thus, it is  
637 reasonable to posit that the transition among prey types across the lifetime of fishes is  
638 closely related to their availability, but that other drivers may be responsible for the  
639 size-related timing and/or magnitude (i.e. some or all individuals of a population) of the  
640 ontogenetic switches. Consistent with this view, predation risk and competition do not  
641 impact directly on the trophic ontogeny of fishes, but can have indirect effects on diet  
642 trajectories through ontogenetic changes in habitat use and concomitant changes in prey  
643 availability (Fig. 3C). Notwithstanding this, we still lack a clear understanding of the  
644 true drivers of ODSs and require new and integrative approaches to identify possible  
645 false-positive drivers.

646

## 647 **IV. CONSEQUENCES**

### 648 **(1) Individuals, populations and communities**

649 ODSs in fishes often coincide with increases in individual growth rates (Fig. 3C), and  
650 many studies have suggested that the relationship is causal (e.g. Olson, 1996;  
651 McCormick, 1998; Mittelbach & Persson, 1998; Jensen *et al.*, 2012). A key challenge,  
652 however, is to disentangle the true relationship between ODSs and fish growth, as ODSs  
653 can be a consequence of, as well as a contributor to, growth (Fig. 3C). Most studies  
654 indicate that increases in growth rates can be caused by switches to more profitable food  
655 resources. For example, growth rates can increase substantially after switching from  
656 invertebrates to fish in many marine (e.g. Juanes & Conover, 1994*b*; Bromley, Watson  
657 & Hislop, 1997; Tanaka *et al.*, 2014) and freshwater (e.g. Olson, 1996; Mittelbach &  
658 Persson, 1998; Pazzia *et al.*, 2002; Persson & Brönmark, 2002*b*) fish species. Indeed,  
659 the growth rates of individuals that become piscivorous early in development can be  
660 almost double those of conspecifics that switch later (Post, 2003; Tanaka *et al.*, 2014).  
661 Other ODSs, such as from zooplankton to macroinvertebrates, may also have  
662 consequences, as growth is often faster in zoobenthivorous than zooplanktivorous  
663 individuals (Persson & Brönmark, 2002*a*; Svanbäck & Eklöv, 2002). ODSs can have a  
664 positive influence on growth, when prey-handling efficiency conforms with allometric  
665 scaling theories, otherwise ODSs can be a consequence of growth (e.g. when prey is  
666 outside of the optimal predator–prey size ratio) as we outlined in Section III.5.  
667 Alternatively, ODSs may be overridden by lifestyle in species whose feeding-behaviour  
668 strategies does not change much but which show growth. This is exemplified by many  
669 species undergoing discrete ODSs; with no ontogenetic shifts in prey-type consumption  
670 but shifts in maximum prey-width consumption (e.g. Egan *et al.*, 2017). In addition,

671 herbivorous species; for example, grass carp [*Ctenopharyngodon idella* (Valenciennes,  
672 1844)] can absorb plant-derived nutrients and undergo rapid growth during ontogeny  
673 (Wang *et al.*, 2015). Using the behavioural traits and life histories of fish to examine the  
674 consequences (and causes) of ODSs (see Hin *et al.*, 2011) is a promising area for future  
675 research.

676 The survival and recruitment of many fish species is positively associated with growth  
677 and successful dietary shifts in the first year of life (Myers, 1995; Houde, 1997; Nunn *et*  
678 *al.*, 2010). ODSs therefore have the potential to influence the lifetime fitness of  
679 individual fish and population dynamics, and other size-dependent processes, *via* their  
680 impacts on growth (Olson, 1996; Post, 2003; Huss *et al.*, 2013; Tanaka *et al.*, 2014).

681 Depending upon resource availability, individuals that undertake ODSs can accrue an  
682 advantage over competitors that do not (Pazzia *et al.*, 2002; Post, 2003; Schellekens *et*  
683 *al.*, 2010). Alternatively, and on the basis of resource partitioning theory (Schoener,  
684 1974), ODSs may allow individuals to avoid potential recruitment bottlenecks caused  
685 by competition for food resources (e.g. Polis, 1984; Olson, 1996; Cowan, Rose &  
686 DeVries, 2000; King, 2005) and facilitate the coexistence of consumers (e.g. Amundsen  
687 *et al.*, 2003; Sánchez-Hernández & Cobo, 2012*b*; Wollrab, de Roos & Diehl, 2013;  
688 Pereira *et al.*, 2015). Reductions in the intensity of competition could lead to increases  
689 in growth rates and, consequently, in survival and recruitment (Post, 2003). ODSs,  
690 especially early transitions to profitable food sources (e.g. fish), could also have  
691 implications for the lifetime fecundity of individual fish (Post, 2003), because several  
692 important maternal traits (e.g. egg quality and quantity) frequently increase with body  
693 size (Mittelbach & Persson, 1998; Venturelli *et al.*, 2010). Size differences among  
694 individuals produced by ontogenetic variation in the transition to piscivory are  
695 commonly maintained at later ages (Pazzia *et al.*, 2002; Post, 2003), so fish that grow

696 large relative to their conspecifics may have a disproportionately strong influence on  
697 population dynamics through enhanced recruitment success.

698 As demonstrated by previous studies, ODSs are a key factor in determining how  
699 ecological communities are structured (e.g. de Roos & Persson, 2013; van Leeuwen *et*  
700 *al.*, 2013, 2014). These theoretical studies focussed on stage-structured models and did  
701 not address evolutionary dynamics, but nonetheless provided the basis for empirical  
702 work to increase ecological realism and identified promising evolutionary research  
703 directions to explore the consequences of ODSs in population and community ecology.  
704 Indeed, ten Brink & de Roos (2017) recently demonstrated that ODSs are evolutionary  
705 advantageous when switches to alternative food sources involve higher intake rates for  
706 consumers. Thus, a strategy to understand ODSs better in an evolutionary framework  
707 would be to take foraging specialisation and trophic polymorphisms into account (Fig.  
708 3C). Our reasoning is that previous studies have assumed that switching niches during  
709 ontogeny can lead to trophic polymorphisms (e.g. Adams & Huntingford, 2002;  
710 Knudsen *et al.*, 2006, 2010) and/or evolutionary branching (see Claessen & Dieckmann,  
711 2002) in population ecology. Based on the premise that niche shifts and trophic  
712 polymorphisms are genetically determined (Adams & Huntingford, 2002; Claessen &  
713 Dieckmann, 2002), ODSs may constitute an early phase in the evolution of trophic  
714 polymorphisms leading to ecologically distinct sub-populations due to foraging  
715 specialisation. Indeed, several studies have highlighted the evolutionary implications of  
716 the combination of ODSs and the environment (Claessen & Dieckmann, 2002;  
717 Whiteley, 2007; ten Brink & de Roos, 2017). Especially relevant are the theoretical  
718 considerations of Claessen & Dieckmann (2002) that foraging differences determine the  
719 type of feeding trajectory (i.e. monomorphic, ontogenetic generalist or polymorphism)  
720 adopted in fish populations. Whiteley (2007) observed that eco-evolutionary traits

721 responsible for stage-specific developmental switches in feeding in the mountain  
722 whitefish [*Prosopium williamsoni* (Girard, 1856)] can occur late in ontogeny. This was  
723 supported by ten Brink & de Roos (2017), who highlighted that individuals usually  
724 display a dietary shift late in ontogeny to maximise food intake. Thus, it is reasonable to  
725 assume that ODSs are a strong candidate for a mechanism of divergence within fish  
726 populations, but the trade-off between early and late foraging success can impede the  
727 evolution of an ODS (ten Brink & de Roos, 2017). We suggest that the eco-evolutionary  
728 consequences of ODSs on fish populations are a promising area for further investigation  
729 and should not be neglected.

730

## 731 **(2) Food webs and ecosystem processes**

732 It has long been recognised that fishes can have a major influence on the abundance and  
733 species and size composition of prey assemblages through top-down mechanisms (e.g.  
734 Mehner & Thiel, 1999; Rosenfeld, 2000; Baum & Worm, 2009; van Leeuwen *et al.*,  
735 2013). Knowledge of ODSs is therefore vital to understand how they influence food  
736 webs and ecosystem processes (e.g. respiration and primary productivity). Network-  
737 based approaches have demonstrated that the functional role of fish is developmental-  
738 stage specific (Ramos-Jiliberto *et al.*, 2011; Sánchez-Hernández, 2016). ODSs,  
739 therefore, have the potential to have important effects on energy pathways and food-  
740 web structure and dynamics (Woodward *et al.*, 2005; Miller & Rudolf, 2011;  
741 Nakazawa, 2015).

742 ODSs usually result in individuals feeding higher up food chains, which increases food-  
743 web complexity (e.g. the number of feeding linkages) as different functional groups  
744 occupy alternative positions (i.e. alternative stable states) in the food web (Amundsen *et*  
745 *al.*, 2003; Takimoto, 2003; Nakazawa, 2011*a*, 2015; van Leeuwen *et al.*, 2014;

746 Sánchez-Hernández, 2016). However, it may not be possible to identify alternative  
747 positions in food webs clearly when predators undergo multiple ODSs (i.e. feeding on  
748 additional resources before switching to piscivory) (van Leeuwen *et al.*, 2013). Thus,  
749 there may be interspecific differences in the influence of ODSs, with generalist species  
750 expected to increase food-web complexity in comparison to specialist species. Indeed,  
751 niche breadth and diet modularity (the subgroup of predators and prey interacting in a  
752 network) can decrease following ODSs in some fishes [e.g. Spanish toothcarp  
753 (*Aphanius iberus* Valenciennes, 1846)] (Ramos-Jiliberto *et al.*, 2011), especially in  
754 species that switch from animal resources to plants or detritus, such as grass carp,  
755 fathead minnow (*Pimephales promelas* Rafinesque, 1820) and thin-lipped grey mullet  
756 [*Liza ramada* (Risso, 1810)]. As ODSs can involve littoral, pelagic and profundal  
757 resources in lentic ecosystems (e.g. Knudsen *et al.*, 2006; Kolasinski *et al.*, 2009;  
758 Eloranta *et al.*, 2010), there can be direct and indirect consequences for energy  
759 pathways and the dynamics of food webs and ecosystem processes through cascading  
760 (both top-down and bottom-up) effects (Nakazawa, 2011*b*, 2015).

761 Understanding stability in stage-structured food webs is an emerging field in ecology,  
762 and much attention is being paid to identify and disentangle the contributing factors (de  
763 Roos & Persson, 2013; Caskenette & McCann, 2017; Nilsson *et al.*, 2018). Theory  
764 predicts that ODSs and stage-structured populations are key determinants of food-web  
765 stability (de Roos & Persson, 2013; Nilsson *et al.*, 2018). Indeed, in accordance with  
766 biomass reallocation theory (see de Roos & Persson, 2013), Caskenette & McCann  
767 (2017) recently demonstrated that stage-structured predators increase the stability of  
768 food webs. Size-structured predator–prey models have demonstrated that predatory size  
769 effects are species specific and that food webs can be dynamically stable (Emmerson &  
770 Raffaelli, 2004). Importantly, there are stabilising and destabilising aspects of stage



771 structure that need to be taken into consideration (see Nilsson *et al.*, 2018). For  
772 example, predators feeding on the same food resource can strongly destabilise a system,  
773 whereas size- or stage-specific feeding can have a stabilising effect when predators feed  
774 selectively on one consumer stage or at high interaction strength (Nilsson *et al.*, 2018).  
775 However, exactly how ODSs affect food-web stability in nature is still unclear and  
776 under debate. It seems reasonable to posit that ODSs can have a stabilising or  
777 destabilising effect depending upon what is studied (population, community or food  
778 web). More precisely, whereas ODSs generally seem to stabilise consumer–resource  
779 dynamics and, through resource partitioning, can increase population and community  
780 stability by reducing inter- or intraspecific competition (Amundsen *et al.*, 2003;  
781 Schellekens *et al.*, 2010; Sánchez-Hernández & Cobo, 2012*b*), the effect at the food-  
782 web level is variable. For example, ODSs commonly reduce the stability of complex  
783 trophic networks (Miller & Rudolf, 2011; Rudolf & Lafferty, 2011), but can increase  
784 food-web stability when the resources used by adults are less abundant than those used  
785 by juveniles (Schellekens *et al.*, 2010). The influence (positive or negative) of ODSs  
786 can be complex and reversible, however, as fish that appear to be generalists at the  
787 species level can sometimes function as sequential specialists (see Rudolf & Lafferty,  
788 2011). Models applied to developmental-stage-structured communities have  
789 demonstrated that ODSs may also affect community resilience and disturbance  
790 responses (Nakazawa, 2015), but this has yet to be tested in natural ecosystems.

791

## 792 **V. CONCLUSIONS**

793 (1) Although ODSs in fishes are well documented, our comprehension of their exact  
794 nature and driving mechanisms is incomplete because the knowledge is biased towards  
795 economically important species, and we currently lack a holistic understanding of their

796 consequences for population, community, consumer–resource and food-web dynamics,  
797 and ecosystem processes and functioning. Studies attempting to address these  
798 knowledge gaps (e.g. Takimoto, 2003; Schellekens *et al.*, 2010; Nakazawa, 2011*b*;  
799 Wollrab *et al.*, 2013; Nilsson *et al.*, 2018) have largely focused on theoretical  
800 approaches. Although some empirical attempts have been made to explore the  
801 implications of ODSs on consumer–resource and food-web dynamics (e.g. Persson &  
802 Greenberg, 1990; Persson & Hansson, 1999; Persson & Brönmark, 2002*a*), it is  
803 recommended that empirical research under natural conditions is instigated to  
804 corroborate the theory-based concepts behind the consequences of ODSs on the  
805 dynamics, processes and functioning at the population, community and ecosystem  
806 levels. It is also recommended that large-scale patterns in ODSs and common drivers in  
807 the animal kingdom are examined, so that novel ecological theories can be formulated  
808 and tested.

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

817 (3) Numerous biotic and abiotic factors can directly or indirectly influence ODSs, but  
818 the most influential likely vary spatially, temporally and interspecifically. We confirm  
819 that the major drivers of ODSs in fishes are prey availability, predation risk and  
820 competition. This review provides novel insights into trophic ontogeny theory,

821 highlighting that some of the most influential drivers (predation risk and competition)  
822 do not impact directly on the trophic ontogeny of fishes, but can have an indirect effect  
823 on diet trajectories through ontogenetic changes in habitat use and concomitant changes  
824 in prey availability.

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

834 (5) ODSs can have profound ecological consequences for fishes, in particular by  
835 enhancing individual growth and lifetime reproductive output or reducing the risk of  
836 mortality (Fig. 3C). ODSs also have the potential to promote ecological release,  
837 facilitating the coexistence of sympatric species. It should be kept in mind that this  
838 conclusion may be context dependent as environmental conditions can change  
839 temporally or spatially. For example, factors impacting on prey-encounter rate, such as  
840 vegetation and turbidity, can influence ontogenetic trajectories (see Vejříková *et al.*,  
841 2017) and consequently ecological release.

842 (6) Research focusing on inter-individual variation in ontogenetic diet trajectories  
843 (Olson, 1996; Post, 2003; Svanbäck *et al.*, 2015; Sánchez-Hernández & Cobo, 2018)  
844 has been limited, and it is recommended that the complex relationships between  
845 individual behaviour and environmental heterogeneity, including the relative

846 importance of environmental factors and heritable traits (see Shedd *et al.*, 2015), should  
847 be prioritised in future research. Such research may benefit from the use of a  
848 combination of methodical approaches, such as traditional diet, stable isotope, DNA  
849 metabarcoding, RNA–DNA ratio and tissue stoichiometry analyses (e.g. Boros, Saly &  
850 Vanni, 2015; Nielsen *et al.*, 2018).

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

863

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869

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- 1290

1291 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 <i>et al.</i> (2002); Kimirei <i>et al.</i> (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 <i>et al.</i> (2008); Choi & Suk (2012); Kimirei <i>et al.</i> (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 <i>et al.</i> (2000); García-Berthou (2002); Takimoto (2003); Nunn <i>et al.</i> (2007); Choi & Suk (2012); Kimirei <i>et al.</i> (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 <i>et al.</i> (2006); Choi & Suk (2012); Dixon <i>et al.</i> (2012); Hertz <i>et al.</i> (2016); Polte <i>et al.</i> (2017); Hammar <i>et al.</i> (2018)	Eggold & Motta (1992); Cocheret de la Morinière <i>et al.</i> (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 <i>et al.</i> (2000); Scharf <i>et al.</i> (2000); Linde <i>et al.</i> (2004); Belinda <i>et al.</i> (2005); Sánchez-Hernández <i>et al.</i> (2013)	–	Allometric changes in morphological traits (mouth gape and gill rakers) make new food resources available and consequently ODSs
(6) Swimming ability	Juanes & Conover (1994a); Hasegawa <i>et al.</i> (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 <i>et al.</i> (2013)	Belinda <i>et al.</i> (2005); German & Horn (2006); German <i>et al.</i> (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 <i>et al.</i> (2002); Drewe <i>et al.</i> (2004); Jackson <i>et al.</i> (2004)	German <i>et al.</i> (2004); Pradhan <i>et al.</i> (2013); German <i>et al.</i> (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)

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1292



1293 **Figure legends**

1294 **Fig. 1.** Number of studies examining ontogenetic dietary shifts (black bars) or  
1295 ontogenetic shifts (white bars) in fish species over the last three decades (1989–2018),  
1296 as indicated by an *Web of Science* search. The search was performed using the key  
1297 words: (i) “fish”, “diet” and “ontogenetic shifts” (black bars), and (ii) “fish” and  
1298 “ontogenetic shifts” (white bars). Note, although representative, this search might  
1299 underestimate the real number of published studies to date.

1300

1301 **Fig. 2.** Conceptual view of the ontogenetic dietary shift in a freshwater species (brown  
1302 trout *Salmo trutta* L.) and a marine species (Atlantic cod *Gadus morhua* L.).

1303

1304 **Fig. 3.** Drivers and consequences of ontogenetic dietary shifts (ODSs) of fishes. (A)  
1305 Number of papers in the *Web Science* core collection ( $N = 926$ ) supporting the potential  
1306 influence of the identified drivers on ODSs. (B) Relative importance of factors based on  
1307 the probability (%) of positive effect on ODSs obtained with the R package *qgraph*  
1308 (Epskamp *et al.*, 2012), with the length and colour of the arrows indicating the relative  
1309 importance of the variables. (C) Conceptual view of the complexity of mechanisms  
1310 influencing ODSs and its consequences at the individual, population, community and  
1311 ecosystem levels. Dashed lines represent an unlikely direct effect of the driver on ODSs.  
1312 Arrows indicate the direction of the effect.