

Feeding of twaite shad, *Alosa fallax* (Lacépède, 1803), during the upstream spawning migration in the River Ulla (NW Spain)

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Abstract. In order to contribute to a better understanding of feeding behaviour of adult twaite shad, *Alosa fallax*, in freshwater, we studied the stomach content composition of 147 *A. fallax* during their upstream spawning migration in the River Ulla (Galicia, NW Spain). The diet composition included 34 types of prey, aquatic invertebrates being the most important food. The present study is, to the best of our knowledge, the first record of *A. fallax* feeding on potamodromous *Pseudochondrostoma duriense*.

Additional keywords: *Alosa fallax*, diet, Iberian Peninsula, piscivorous, *Pseudochondrostoma duriense*.

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Introduction

There have been several studies dealing with the diet of *Alosa fallax* (Lacépède, 1803) (e.g. Aprahamian 1989; Taverny and Elie 2001; Maitland and Lyle 2005; Nunn *et al.* 2008; Ceyhan *et al.* 2011); however, the diet of *A. fallax* during their upstream spawning migration remains poorly understood. Until now, only two studies have reported the feeding and diet of adult *A. fallax* during the pre-spawning phase of their spawning migration. In fresh water, the stomach of those fish that had fed contained plastic, allochthonous plant material and emergent adult Trichoptera, suggesting that the fish had been feeding on relatively large particles in the drift or at the water surface (Bracken and Kennedy 1967; Aprahamian 1989). The aim of our work is to describe the diet and feeding activity of adult of *A. fallax* during their upstream spawning migration in a recently discovered spawning population in the River Ulla (Galicia, NW Spain).

Material and methods

The River Ulla has a catchment area of 2803 km² and a total length of 132 km and drains into the Atlantic Ocean in the Ría de Arousa. The River Ulla estuary extends from the town of Carril to the town of Padrón, the tidal limit (Prego *et al.* 2008). We selected two sampling stations (SS) upstream of the tidal limit (6.5 km and 2.5 km respectively) (Fig. 1) in resting areas for this species, at ~24 km (SS1, 29T533201 4732447) and (SS2, 29T530666 4731068) from the Atlantic Ocean.

Specimens were sampled between March and July in 2011 and 2012, coinciding with the spawning migration of this fish

species. Two trammel nets 40 m long (70 mm and 100 mm loose inner layer mesh size respectively) were used to obtain a good representation of all age classes, as mesh size affects the selectivity of the gear in terms of size and sex distribution (King and Roche 2008). All surveys were conducted at night to reduce gear visibility (Potter and Swain 1982). In total, 147 fish (mean fork length \pm s.e. = 39.3 \pm 0.38 cm; range: 28.3–49 cm) were captured and immediately killed by an overdose of anaesthetic (benzocaine), and transported in cool boxes (approx. 4°C) to the laboratory, where the fish were dissected and their stomachs removed for diet analysis. The stomachs were frozen at –30°C until processing. Fish with empty stomachs were excluded from diet analyses (50 in total). The degree of stomach fullness (f) was calculated for each fish as $f = (Ws/W) \times 100$, where Ws is the total stomach content wet weight (g) and W is the fish wet weight (g). Prey items were allocated to diet categories as follows: aquatic invertebrates, terrestrial invertebrates and other prey items. The abundance of plant materials was not quantified as it was impossible to count individual items, but the number of stomachs in which they appeared was noted. Fish remains were identified using reference material and published guides (Miranda and Escala 2002; Tuset *et al.* 2008). Animal prey items were identified to the lowest taxonomic level possible.

For the description of the diet, data were analysed in terms of relative abundance of prey ($A_i = (\Sigma S_i / \Sigma S_j) \times 100$, where S_i is the total number of prey i , and S_j the total number of all prey items) and frequency of occurrence of prey ($F_i = (N_i / N) \times 100$, where N_i is the number of fishes with prey i in their stomach and N is the total number of fishes with stomach contents of any kind).

might be related to two different motivational factors: (1) twaite shads could deliberately search for prey through activation of hypothalamic receptors (e.g. Lin *et al.* 2000; and references therein); or (2) it could be the consequence of prey entering their visual field and it acts as a stimulus to their predatory instinct. The question, however, remains whether this phenomenon yields a benefit or evolutionary advantages to those individuals. It is well documented that energy reserves and weight decrease in anadromous fishes during their spawning migration (e.g. Doucett *et al.* 1999; Walter and Olney 2003) and it is possible that the anecdotal active feeding behaviour observed in this study could help increase the somatic energy reserves and thus promote successful spawning and decrease post-spawning mortality.

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Prey trait analysis shows differences in summer feeding habitat use between wild YOY Atlantic salmon and brown trout

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Abstract

We evaluated the vertical use of the water column for feeding by young of the year (YOY) of brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) in a natural river during the summer. Prey trait analysis and diet composition demonstrated that brown trout showed a higher ability to feed on prey in the surface of the water column than Atlantic salmon. Hence, the differences in the ability to feed at different depths of the water column (surface vs. bottom) are important adaptive features that may reduce interspecific competition between the two sympatric fish species. Finally, results derived from the prey trait analysis provide useful information on resource partitioning between sympatric salmonid species.

Keywords: Diet, competition, water column, Iberian Peninsula, microhabitat

Introduction

Ecological interaction in streams between Atlantic salmon *Salmo salar* Linnaeus, 1758 and brown trout *Salmo trutta* Linnaeus, 1758 is well documented. A consequence of this knowledge is the great amount of literature on the habitat utilization of these species (e.g., Heggenes et al. 1999; Crisp 2000; Armstrong et al. 2003; Jonsson & Jonsson 2011). Previously and based on stream habitat selection studies, several researchers have stated that spatial niche overlap is considerable where the two species co-occur, although young Atlantic salmon tend to occupy faster flowing and shallower habitats (e.g., Baglinière & Arribé-Moutounet 1985; Heggenes et al. 1999). Moreover, when both fish species co-occur, habitat use by Atlantic salmon is restricted through interspecific competition with the more aggressive brown trout (Heggenes et al. 1999 and references therein). Indeed, Höjesjö et al. (2005) demonstrated in a controlled stream channel environment that trout held station by swimming actively in the central regions of food patches, whereas salmon occupied the margins.

The diet composition of brown trout and Atlantic salmon, according to field studies based on number,

volume and occurrence methods, is similar (e.g., Maitland 1965; Pedley & Jones 1978; Gibson & Cunjak 1986; Suárez et al. 1988). In the literature, there is an increasing number of studies under controlled laboratory conditions about the foraging competition between different salmonids species (e.g., Höjesjö et al. 2005 and references therein). These controlled studies provide invaluable preliminary information on feeding behaviour, but further studies under natural conditions are needed to increase ecological realism. In this context, prey trait analysis has been proposed as a functional approach to understand mechanisms involved in predator-prey relationships (de Crespín de Billy & Usseglio-Polatera 2002), and consequently it may be useful for understanding inter- and intra-species interactions and the mechanisms that determine food partitioning between them (Sánchez-Hernández & Cobo 2011, 2012; Sánchez-Hernández et al. 2011). So, assuming that age-0 Atlantic salmon and brown trout overlap for food and habitats, the most territorial or the most adaptive species will have prior access to the most profitable resources. Hence, the objective of this study was to analyse whether young of the year

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in sympatry (Gibson & Cunjak 1986; Coghlan et al. 2007). In a previous study in Spain, Suárez et al. (1988) found significant interspecific differences in the diet between *S. salar* and *S. trutta* in May and November, although they did not find differences in April and July. On the other hand, Pedley and Jones (1978) stated that interspecific competition between *S. salar* and *S. trutta* was only significant during the summer months when food was abundant. Our results, using the Schoener's index, suggest a remarkable similarity in prey utilization patterns between species as previously stated by other researchers (Gibson & Cunjak 1986; Coghlan et al. 2007). However, the high overlap values found in the present study might not indicate competition, for two reasons. First, as no data on potential preys (benthos and drift) are available, food could be so abundant that fishes might not compete for it. Second, fishes usually can adopt different strategies that overcome the effects of competition (Sánchez-Hernández & Cobo 2011; Sánchez-Hernández et al. 2011); in our case prey trait analysis and diet composition shows higher preference to feed on surface (terrestrial) drift for YOY brown trout.

Höjesjö et al. (2005) found in a controlled stream channel experiment that brown trout held station by swimming actively in the central regions of food patches, whereas Atlantic salmon occupied the margins, generally remaining stationary on the stream bed. Coghlan et al. (2007) found in subyearling fish that Atlantic salmon consumed a greater proportion of baetid mayflies than rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792), which fed more frequently on chironomid larvae and aerial-terrestrial invertebrates. In our study, differences in the number of terrestrial invertebrates consumed by both species on the stream surface are evident; observations are in agreement with Suárez et al. (1988), as during the summer season they found that terrestrial prey were more abundant in *S. trutta* than in *S. salar*. Hence, terrestrial prey constitute an important food item that may contribute greatly to reduce fish interactions between YOY of sympatric *S. trutta* and *S. salar*, as found in other fish species (e.g., Sánchez-Hernández et al. 2011 and references therein). Accordingly, prey trait analysis demonstrates that differences in habitat utilization between both fish species are related to the ability to feed at different depths of the water column (surface vs. bottom) due to the higher contribution in specific abundance of terrestrial invertebrates in the diet of brown trout.

In conclusion, our study supports the hypothesis that differences in the ability to feed at different depths of the water column in the same riffle sections between *S. salar* and *S. trutta* may reduce trophic

competition, and may be seen as important adaptations in feeding behaviour when these fish species co-occur. Additionally, we show that prey trait analysis provides extremely valuable ecological information on the mechanisms involved in predator-prey relationships, and complements traditional diet analysis (Sánchez-Hernández & Cobo 2011; Sánchez-Hernández et al. 2011, 2012). However, future studies might extend the present work and investigate the uses of microhabitat feeding patches by snorkel observations to corroborate if the vertical distribution between species for feeding is evident.

Supplementary Material

Supplementary material for this article is available from

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AQ1

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AQ2

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Prey trait analysis shows differences in summer feeding habitat use between wild YOY Atlantic salmon and brown trout

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Abstract

We evaluated the vertical use of the water column for feeding by young of the year (YOY) of brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) in a natural river during the summer. Prey trait analysis and diet composition demonstrated that brown trout showed a higher ability to feed on prey in the surface of the water column than Atlantic salmon. Hence, the differences in the ability to feed at different depths of the water column (surface vs. bottom) are important adaptive features that may reduce interspecific competition between the two sympatric fish species. Finally, results derived from the prey trait analysis provide useful information on resource partitioning between sympatric salmonid species.

Keywords: Diet, competition, water column, Iberian Peninsula, microhabitat

Introduction

Ecological interaction in streams between Atlantic salmon *Salmo salar* Linnaeus, 1758 and brown trout *Salmo trutta* Linnaeus, 1758 is well documented. A consequence of this knowledge is the great amount of literature on the habitat utilization of these species (e.g., Heggenes et al. 1999; Crisp 2000; Armstrong et al. 2003; Jonsson & Jonsson 2011). Previously and based on stream habitat selection studies, several researchers have stated that spatial niche overlap is considerable where the two species co-occur, although young Atlantic salmon tend to occupy faster flowing and shallower habitats (e.g., Baglinière & Arribé-Moutounet 1985; Heggenes et al. 1999). Moreover, when both fish species co-occur, habitat use by Atlantic salmon is restricted through interspecific competition with the more aggressive brown trout (Heggenes et al. 1999 and references therein). Indeed, Höjesjö et al. (2005) demonstrated in a controlled stream channel environment that trout held station by swimming actively in the central regions of food patches, whereas salmon occupied the margins.

The diet composition of brown trout and Atlantic salmon, according to field studies based on number,

volume and occurrence methods, is similar (e.g., Maitland 1965; Pedley & Jones 1978; Gibson & Cunjak 1986; Suárez et al. 1988). In the literature, there is an increasing number of studies under controlled laboratory conditions about the foraging competition between different salmonids species (e.g., Höjesjö et al. 2005 and references therein). These controlled studies provide invaluable preliminary information on feeding behaviour, but further studies under natural conditions are needed to increase ecological realism. In this context, prey trait analysis has been proposed as a functional approach to understand mechanisms involved in predator-prey relationships (de Crespín de Billy & Usseglio-Polatera 2002), and consequently it may be useful for understanding inter- and intra-species interactions and the mechanisms that determine food partitioning between them (Sánchez-Hernández & Cobo 2011, 2012; Sánchez-Hernández et al. 2011). So, assuming that age-0 Atlantic salmon and brown trout overlap for food and habitats, the most territorial or the most adaptive species will have prior access to the most profitable resources. Hence, the objective of this study was to analyse whether young of the year

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in sympatry (Gibson & Cunjak 1986; Coghlan et al. 2007). In a previous study in Spain, Suárez et al. (1988) found significant interspecific differences in the diet between *S. salar* and *S. trutta* in May and November, although they did not find differences in April and July. On the other hand, Pedley and Jones (1978) stated that interspecific competition between *S. salar* and *S. trutta* was only significant during the summer months when food was abundant. Our results, using the Schoener's index, suggest a remarkable similarity in prey utilization patterns between species as previously stated by other researchers (Gibson & Cunjak 1986; Coghlan et al. 2007). However, the high overlap values found in the present study might not indicate competition, for two reasons. First, as no data on potential preys (benthos and drift) are available, food could be so abundant that fishes might not compete for it. Second, fishes usually can adopt different strategies that overcome the effects of competition (Sánchez-Hernández & Cobo 2011; Sánchez-Hernández et al. 2011); in our case prey trait analysis and diet composition shows higher preference to feed on surface (terrestrial) drift for YOY brown trout.

Höjesjö et al. (2005) found in a controlled stream channel experiment that brown trout held station by swimming actively in the central regions of food patches, whereas Atlantic salmon occupied the margins, generally remaining stationary on the stream bed. Coghlan et al. (2007) found in subyearling fish that Atlantic salmon consumed a greater proportion of baetid mayflies than rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792), which fed more frequently on chironomid larvae and aerial-terrestrial invertebrates. In our study, differences in the number of terrestrial invertebrates consumed by both species on the stream surface are evident; observations are in agreement with Suárez et al. (1988), as during the summer season they found that terrestrial prey were more abundant in *S. trutta* than in *S. salar*. Hence, terrestrial prey constitute an important food item that may contribute greatly to reduce fish interactions between YOY of sympatric *S. trutta* and *S. salar*, as found in other fish species (e.g., Sánchez-Hernández et al. 2011 and references therein). Accordingly, prey trait analysis demonstrates that differences in habitat utilization between both fish species are related to the ability to feed at different depths of the water column (surface vs. bottom) due to the higher contribution in specific abundance of terrestrial invertebrates in the diet of brown trout.

In conclusion, our study supports the hypothesis that differences in the ability to feed at different depths of the water column in the same riffle sections between *S. salar* and *S. trutta* may reduce trophic

competition, and may be seen as important adaptations in feeding behaviour when these fish species co-occur. Additionally, we show that prey trait analysis provides extremely valuable ecological information on the mechanisms involved in predator-prey relationships, and complements traditional diet analysis (Sánchez-Hernández & Cobo 2011; Sánchez-Hernández et al. 2011, 2012). However, future studies might extend the present work and investigate the uses of microhabitat feeding patches by snorkel observations to corroborate if the vertical distribution between species for feeding is evident.

Supplementary Material

Supplementary material for this article is available from

Acknowledgements

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AQ1

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AQ2

NOTE

Life cycle of the sea lamprey *Petromyzon marinus*: duration of and growth in the marine life stage

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ABSTRACT: Little is known about the marine life-history phase of the anadromous sea lamprey *Petromyzon marinus*. The most widely accepted hypothesis suggests a hematophagous feeding phase of 2.5 yr. We captured and tagged (individually numbered T-bar anchor tags) 408 postmetamorphic sea lampreys during the onset of the hematophagous feeding phase in the River Ulla and its estuary (NW Spain). One marked sea lamprey was recaptured during its spawning migration (total length: 895 mm, weight: 1218 g). This individual had been marked 13.5 mo before recapture, and had measured 218 mm and 20 g. Our results suggest that at least a portion of the sea lamprey population can reach adult size in 1 yr of hematophagous feeding. This further suggests a period between completion of metamorphosis and reproduction of 1.5 yr (18 to 20 mo).

KEY WORDS: Growth · Adult · Feeding · Anadromous · Hematophagous · Estuary

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INTRODUCTION

The sea lamprey *Petromyzon marinus* L., 1758 is an anadromous species that, after several years in freshwater habitats as larvae (Beamish & Potter 1975, Hardisty 1979, Quintella et al. 2003, Taverny et al. 2005), undergoes metamorphosis that allows young postmetamorphic lampreys to migrate to the sea and begin hematophagous feeding (Youson 1980). In the River Ulla (NW Spain), metamorphosis is completed between October and November, and downstream migration occurs between October and May (Silva et al. 2013). After an unknown time at sea, individuals return to spawning areas in the river to reproduce. Upstream migration in the River Ulla occurs between December and May, and spawning occurs between May and July (Silva et al. 2013), which is similar to the timing of these events in Portuguese rivers (Quintella et al. 2004).

At present, only the freshwater part of the biological cycle of the sea lamprey is partially known and, as is often the case with diadromous fish species, knowledge of biology and distribution during the marine portion of the life cycle is practically nonexistent (OSPAR 2009). The overall picture of the distribution, growth and duration of the marine stage has been inferred from ca. 100 specimens from sporadic and isolated captures (Beamish 1980, Halliday 1991). Based on data obtained from these specimens, Beamish (1980) proposed a hematophagous feeding period of 2 to 2.5 yr, whereas Halliday (1991) suggested the possibility of a reduced feeding period (1.5 yr). Previously, using interspecific comparisons, Hardisty & Potter (1971) proposed that all the large anadromous lamprey species, including sea lamprey, have a hematophagous feeding period of at least 2.5 yr.

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$\{[\ln(W_2) - \ln(W_1)]/\Delta t\} 100$ and $G_{TL} = \{[\ln(TL_2) - \ln(TL_1)]/\Delta t\} 100$ (Ricker 1975, 1979), where W_1 and W_2 and TL_1 and TL_2 were recorded at the time of tagging and recapture, respectively, and Δt is the time period (d).

RESULTS

On 26 March 2012, we recaptured one tagged sea lamprey (TL: 895 mm, W: 1218 g) at E1 during its upstream migration. This individual had been tagged in the estuary on 1 February 2011 and measured 218 mm and 20 g, which indicates an increase of 311% in TL and 5990% in W in 13.5 mo. This results in a G_{TL} of 0.340% d^{-1} and a G_W of 0.988% d^{-1} . This individual was recaptured 4 mo after the start of the upstream migration period in the River Ulla (December to May), and it was not feeding when it was recaptured.

DISCUSSION

The size of this lamprey at the time of tagging was close to the size of the postmetamorphic individuals captured during the downstream migration in the River Ulla (Silva et al. 2013), most of which were not feeding (Silva et al. 2013). Assuming the growth rate observed for the recaptured lamprey and the difference in size between this individual and the postmetamorphics captured before the start of feeding, its size at the time of tagging (1 February 2011) would have required a previous feeding period of approx. 1 to 2 mo. Moreover, the spawning migration period in the area began 4 mo prior to recapture. During this migration, and probably 1 to 2 mo earlier, individuals do not feed (Beamish 1980, Johnson & Anderson 1980), so this sea lamprey may have been fasting for 1 to 4 mo before recapture. After consideration of this information, we estimated that the hematophagous feeding period for this individual is 10.5 to 14.5 mo. Indeed, during this migration lampreys decrease, both in W and TL, by roughly 5.7% (Beamish 1980), suggesting that this individual may have reached a larger size during that short time and that the growth rate is probably underestimated.

Given that the metamorphosis in this region ends in October–November, while spawning occurs between May and July (Silva et al. 2013), our results suggest a period between completion of metamorphosis and reproduction of 18 to 20 mo.

Our data suggest that the duration of hematophagous feeding is shorter than hypothesized by

Hardisty & Potter (1971) and Beamish (1980), although in both cases, the authors indicated that 23 to 28 mo of feeding was weakly supported by their data. Hardisty & Potter (1971) used comparisons among lamprey species to propose that all the large anadromous lamprey species, which include sea lamprey (excepting the Great Lakes), may have a hematophagous feeding period of at least 2.5 yr. Beamish (1980) used scattered information of a few individuals captured in the ocean, and referred also to the work of Farmer et al. (1977), who studied growth of landlocked lampreys of the Great Lakes in the laboratory, which exhibited lower growth rates and sizes than anadromous lampreys (Applegate 1950, Johnson & Anderson 1980). Halliday (1991) discussed the previous hypothesis using sea captures off the coast of Canada, and suggested a shorter feeding period of ~1.5 yr. Halliday noted that acceptance of this hypothesis of 1.5 yr of hematophagous feeding requires that individuals captured in early summer, which range in TL from 12 to 65 cm, be considered as from the same cohort. Size variation within a cohort can be explained by individual differences in the onset of feeding. Some young postmetamorphics migrate downstream in late autumn and begin feeding on fish, while others stay in the river and overwinter without feeding, and migrate to the estuary to begin feeding the following spring (Beamish & Potter 1975, Potter & Beamish 1977). Similarly, in the River Ulla, postmetamorphic individuals migrate to the estuary anywhere from 0 to 6–7 mo after metamorphosis, and most begin hematophagous feeding when they reach the estuary (Silva et al. 2013). This observation, together with the absence of postmetamorphic individuals in the river during the summer months (Cobo et al. 2010), and the limited time period during which it is possible to observe postmetamorphics in the River Ulla estuary (November–May), support the hypothesis that these individuals belong to the same cohort.

Mark-recapture studies of other anadromous populations throughout the geographic range might help to clarify this question.

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BRIEF COMMUNICATION

Haematophagous feeding of newly metamorphosed European sea lampreys *Petromyzon marinus* on strictly freshwater species

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Approximately 6% of the freshwater living northern straight-mouth nase *Pseudochondrostoma duriense* in two Spanish rivers had attached post-metamorphic sea lamprey *Petromyzon marinus*. Minimum prey size was 16.1 cm fork length and 56.3 g mass. The condition factor of attacked *P. duriense* was 16% lower than that of unattacked conspecifics.

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Key words: anadromous; cyprinid; downstream migration; host; parasite; prey size.

After several years in fresh water (Quintella *et al.*, 2003) sea lamprey *Petromyzon marinus* L. 1758 ammocoetes undergo metamorphosis that allows post-metamorphics to migrate to the sea and start haematophagous feeding (Potter, 1980). The long fasting period during and after the metamorphosis makes this a critical survival stage (Swink, 2003). Thus, it is important for post-metamorphics to obtain a food source as soon as possible to recover energy reserves (Beamish, 1980).

Until now, the occurrence of post-metamorphic *P. marinus* feeding in rivers has been assumed to result from attacks on migrating teleosts in marine or estuarine waters (Bird *et al.*, 1994). It was recently observed in European populations, however, that some post-metamorphics (10–30%) had already started feeding in the river before they reached the sea (Silva *et al.*, 2013). A similar behaviour was observed by Beamish (1980) for North American anadromous populations.

The available information on the haematophagous phase of *P. marinus* is mainly from landlocked populations suggesting a low selectivity in prey choice, apparently limited to a preference for larger individuals (Bence *et al.*, 2003).

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The present results support earlier findings of low prey selection by post-metamorphics, apparently limited to a preference for larger individuals (Bence *et al.*, 2003). Swink (2003) reported that, when all potential prey exceeded a minimum size threshold, *P. marinus* attach to prey randomly (in proportion to their surface area). The observations described here provide probably the smallest size of prey described for post-metamorphic anadromous *P. marinus* under natural conditions, and this size establishes the potential prey species depending on whether this threshold is exceeded. In the sampled rivers, these were *S. trutta*, *A. anguilla* and translocated *T. tinca* (Table SI, Supporting Information). Smolts of *S. salar* and *S. trutta* are also potential prey, as they can reach a L_F of 22 cm for *S. salar* and 30 cm for *S. trutta* in the River Ulla (Hervella & Caballero, 1999; Caballero *et al.*, 2006).

Studies on landlocked populations provide robust information for anadromous population studies, and they should not be ignored. They must be treated with caution, however, and results cannot be directly extrapolated because of the important ecological differences between these two forms (Clemens *et al.*, 2010).

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Supporting Information

Supporting Information may be found in the online version of this paper:

Table SI: Mean \pm s.e. (range) of total or fork length (L_T or L_F), mass (M) and condition factor (C_F) of species caught in the River Umia, except *Petromyzon marinus*. For *Pseudochondrostoma duriense*, only individuals not attacked by *P. marinus* have been included.

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NOTE

Life cycle of the sea lamprey *Petromyzon marinus*: duration of and growth in the marine life stage

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$\{[\ln(W_2) - \ln(W_1)]/\Delta t\} 100$ and $G_{TL} = \{[\ln(TL_2) - \ln(TL_1)]/\Delta t\} 100$ (Ricker 1975, 1979), where W_1 and W_2 and TL_1 and TL_2 were recorded at the time of tagging and recapture, respectively, and Δt is the time period (d).

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On 26 March 2012, we recaptured one tagged sea lamprey (TL: 895 mm, W: 1218 g) at E1 during its upstream migration. This individual had been tagged in the estuary on 1 February 2011 and measured 218 mm and 20 g, which indicates an increase of 311% in TL and 5990% in W in 13.5 mo. This results in a G_{TL} of 0.340% d⁻¹ and a G_W of 0.988% d⁻¹. This individual was recaptured 4 mo after the start of the upstream migration period in the River Ulla (December to May), and it was not feeding when it was recaptured.

DISCUSSION

The size of this lamprey at the time of tagging was close to the size of the postmetamorphic individuals captured during the downstream migration in the River Ulla (Silva et al. 2013), most of which were not feeding (Silva et al. 2013). Assuming the growth rate observed for the recaptured lamprey and the difference in size between this individual and the postmetamorphics captured before the start of feeding, its size at the time of tagging (1 February 2011) would have required a previous feeding period of approx. 1 to 2 mo. Moreover, the spawning migration period in the area began 4 mo prior to recapture. During this migration, and probably 1 to 2 mo earlier, individuals do not feed (Beamish 1980, Johnson & Anderson 1980), so this sea lamprey may have been fasting for 1 to 4 mo before recapture. After consideration of this information, we estimated that the hematophagous feeding period for this individual is 10.5 to 14.5 mo. Indeed, during this migration lampreys decrease, both in W and TL, by roughly 5.7% (Beamish 1980), suggesting that this individual may have reached a larger size during that short time and that the growth rate is probably underestimated.

Given that the metamorphosis in this region ends in October–November, while spawning occurs between May and July (Silva et al. 2013), our results suggest a period between completion of metamorphosis and reproduction of 18 to 20 mo.

Our data suggest that the duration of hematophagous feeding is shorter than hypothesized by

Hardisty & Potter (1971) and Beamish (1980), although in both cases, the authors indicated that 23 to 28 mo of feeding was weakly supported by their data. Hardisty & Potter (1971) used comparisons among lamprey species to propose that all the large anadromous lamprey species, which include sea lamprey (excepting the Great Lakes), may have a hematophagous feeding period of at least 2.5 yr. Beamish (1980) used scattered information of a few individuals captured in the ocean, and referred also to the work of Farmer et al. (1977), who studied growth of landlocked lampreys of the Great Lakes in the laboratory, which exhibited lower growth rates and sizes than anadromous lampreys (Applegate 1950, Johnson & Anderson 1980). Halliday (1991) discussed the previous hypothesis using sea captures off the coast of Canada, and suggested a shorter feeding period of ~1.5 yr. Halliday noted that acceptance of this hypothesis of 1.5 yr of hematophagous feeding requires that individuals captured in early summer, which range in TL from 12 to 65 cm, be considered as from the same cohort. Size variation within a cohort can be explained by individual differences in the onset of feeding. Some young postmetamorphics migrate downstream in late autumn and begin feeding on fish, while others stay in the river and overwinter without feeding, and migrate to the estuary to begin feeding the following spring (Beamish & Potter 1975, Potter & Beamish 1977). Similarly, in the River Ulla, postmetamorphic individuals migrate to the estuary anywhere from 0 to 6–7 mo after metamorphosis, and most begin hematophagous feeding when they reach the estuary (Silva et al. 2013). This observation, together with the absence of postmetamorphic individuals in the river during the summer months (Cobo et al. 2010), and the limited time period during which it is possible to observe postmetamorphics in the River Ulla estuary (November–May), support the hypothesis that these individuals belong to the same cohort.

Mark-recapture studies of other anadromous populations throughout the geographic range might help to clarify this question.

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BRIEF COMMUNICATION

Haematophagous feeding of newly metamorphosed European sea lampreys *Petromyzon marinus* on strictly freshwater species

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Approximately 6% of the freshwater living northern straight-mouth nase *Pseudochondrostoma duriense* in two Spanish rivers had attached post-metamorphic sea lamprey *Petromyzon marinus*. Minimum prey size was 16.1 cm fork length and 56.3 g mass. The condition factor of attacked *P. duriense* was 16% lower than that of unattacked conspecifics.

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Key words: anadromous; cyprinid; downstream migration; host; parasite; prey size.

After several years in fresh water (Quintella *et al.*, 2003) sea lamprey *Petromyzon marinus* L. 1758 ammocoetes undergo metamorphosis that allows post-metamorphics to migrate to the sea and start haematophagous feeding (Potter, 1980). The long fasting period during and after the metamorphosis makes this a critical survival stage (Swink, 2003). Thus, it is important for post-metamorphics to obtain a food source as soon as possible to recover energy reserves (Beamish, 1980).

Until now, the occurrence of post-metamorphic *P. marinus* feeding in rivers has been assumed to result from attacks on migrating teleosts in marine or estuarine waters (Bird *et al.*, 1994). It was recently observed in European populations, however, that some post-metamorphics (10–30%) had already started feeding in the river before they reached the sea (Silva *et al.*, 2013). A similar behaviour was observed by Beamish (1980) for North American anadromous populations.

The available information on the haematophagous phase of *P. marinus* is mainly from landlocked populations suggesting a low selectivity in prey choice, apparently limited to a preference for larger individuals (Bence *et al.*, 2003).

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The present results support earlier findings of low prey selection by post-metamorphics, apparently limited to a preference for larger individuals (Bence *et al.*, 2003). Swink (2003) reported that, when all potential prey exceeded a minimum size threshold, *P. marinus* attach to prey randomly (in proportion to their surface area). The observations described here provide probably the smallest size of prey described for post-metamorphic anadromous *P. marinus* under natural conditions, and this size establishes the potential prey species depending on whether this threshold is exceeded. In the sampled rivers, these were *S. trutta*, *A. anguilla* and translocated *T. tinca* (Table SI, Supporting Information). Smolts of *S. salar* and *S. trutta* are also potential prey, as they can reach a L_F of 22 cm for *S. salar* and 30 cm for *S. trutta* in the River Ulla (Hervella & Caballero, 1999; Caballero *et al.*, 2006).

Studies on landlocked populations provide robust information for anadromous population studies, and they should not be ignored. They must be treated with caution, however, and results cannot be directly extrapolated because of the important ecological differences between these two forms (Clemens *et al.*, 2010).

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Supporting Information

Supporting Information may be found in the online version of this paper:

Table SI: Mean \pm s.e. (range) of total or fork length (L_T or L_F), mass (M) and condition factor (C_F) of species caught in the River Umia, except *Petromyzon marinus*. For *Pseudochondrostoma duriense*, only individuals not attacked by *P. marinus* have been included.

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