



## Partial migration in fishes: definitions, methodologies and taxonomic distribution

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Partial migration, where populations are composed of both migratory and resident individuals, is extremely widespread across the animal kingdom. Researchers studying fish movements have long recognized that many fishes are partial migrants, however, no detailed taxonomic review has ever been published. In addition, previous work and synthesis has been hampered by a varied lexicon associated with this phenomenon in fishes. In this review, definitions and important concepts in partial migration research are discussed, and a classification system of the different forms of partial migration in fishes introduced. Next, a detailed taxonomic overview of partial migration in this group is considered. Finally, methodological approaches that ichthyologists can use to study this fascinating phenomenon are reviewed. Partial migration is more widespread amongst fishes than previously thought, and given the array of techniques available to fish biologists to study migratory variation the future of the field looks promising.

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### INTRODUCTION

The importance of animal migration is reflected in its long history of study by biologists. Bird migration has received the most research effort, most likely due to the conspicuous seasonal presence and absence of many bird species, and the relative ease of marking and observing individuals. Yet migration is extremely widespread and has been documented in a diverse range of taxa, from wildebeest to whales, and from water fleas to fishes (Chapman *et al.*, 2011a). Of all the migratory animals, the migration of fishes is perhaps the most enigmatic. Fish migration is difficult to observe, and individuals can be very difficult to track as they migrate often vast distances beneath the water's surface. As technology has advanced and the capacity to follow the movements of individuals has improved, the sheer diversity of

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migratory behaviour in fishes has become apparent. A remarkable range of migratory behaviours occur in nature, varying from the daily vertical movements of coregonids (Mehner & Kasprzak, 2011) and the short-distance migration of cyprinids in and out of shallow lakes (Skov *et al.*, 2008) to the vast oceanic journeys of Atlantic bluefin tuna *Thunnus thynnus* (L. 1758) (Block *et al.*, 2005). Migratory patterns can also vary between populations and even among individuals within populations. Such intraspecific variation in migratory behaviour is extremely widespread, and appears to be the rule rather than the exception (Newton, 2008; Chapman *et al.*, 2011*b*). Fish from different populations can vary in their likelihood of migrating, or in the distance they migrate and also in the migratory destination. For example, brown trout *Salmo trutta* L. 1758 can have populations composed entirely of anadromous migrants or entirely of freshwater residents (Bohlin *et al.*, 2001). Yet perhaps the most intriguing intraspecific variation can be found within populations. In a growing number of examples, individuals from the same population show differences in migratory behaviour, with some migrating on seasonal or diel time scales between habitats whilst others remain resident in a single habitat (Dingle, 1996). This within-population migratory dimorphism is known as partial migration and is ubiquitous amongst migratory taxa, with many examples of partially migratory invertebrates, fishes, birds and mammals documented in the wild (Hansson & Hylander, 2009; Boyle, 2011; Cagnacci *et al.*, 2011; Grayson *et al.*, 2011).

The most recent review of partial migration in fishes describes just 11 species as exhibiting partial migration (Jonsson & Jonsson, 1993), and of these, seven were salmonids. Advances in techniques to study fish migration in the past two decades, however, have revealed how taxonomically widespread partial migration is amongst fishes. One of the factors that has masked the prevalence of this type of migration in fishes in the past is that partial migration has a varied lexicon, with many researchers using different terms to describe the same kinds of migratory behaviours (Secor & Kerr, 2009). Here, definitions and fundamental concepts in partial migration are reviewed, followed by an updated taxonomic overview of this phenomenon in fishes. The review closes with a discussion of the techniques that can be used to study partial migration. The aims of this review are to (1) suggest a unified series of terminology to stimulate research and promote understanding between ichthyologists of different backgrounds, (2) demonstrate the taxonomic breadth and hence general importance of partial migration for fishes, and finally (3) give a brief introduction to the methods currently employed to collect data on partial migration in fishes. Throughout the review terminology from both migration biologists and also fisheries scientists is adopted in the hope that by doing so interactions between researchers from these different fields can be encouraged and future semantic confusion avoided (Table I). A second paper in this thematic addresses the causes and consequences of partial migration in fishes (Chapman *et al.*, 2012).

Upon reviewing the literature it is clear that the study of partial migration in fishes is in its infancy. Research has been taxonomically skewed to certain groups, so much more is known about salmonid partial migration (Jonsson & Jonsson, 1993; Hendry *et al.*, 2004) but very little about partial migration in other fishes [although there are a growing number of studies into cyprinid partial migration (Brodersen *et al.*, 2008*a*; Skov *et al.*, 2010; Chapman *et al.*, 2011*c*)]. In particular partial migration has received little attention for marine fishes (*i.e.* oceanodromous migrants) and also Neotropical and African species.

TABLE I. A lexicon of partial migration in fishes

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Anadromy: a widespread migratory life history in fishes where spawning occurs in fresh water and individuals migrate to the sea as juveniles and adults.

Catadromy: a type of migration where fish spawn in marine habitats and migrate to freshwater as juveniles and adults.

Contingent: a term to collectively describe groups of migratory or resident individuals within a partially migratory population (Secor 1999). Hence a partially migratory population is composed of a migratory contingent and a resident contingent. Note that this does not necessarily imply that migratory status is fixed for individual fishes (Chapman *et al.*, 2012).

Diel vertical migration (DVM): a behaviour often documented in pelagic oceanic or lake-dwelling fishes, where individuals migrate from the deep waters to the epipelagic waters. Usually DVM is on a diurnal timescale, with vertical migration to the epipelagic occurring at night.

Life-history polymorphism or diversity (also alternative life history strategies, life cycle diversity): these are general terms to describe intraspecific variation in life history strategies. They are non-specific, however, and can refer to various forms of non-migratory life-history variation (for example alternative reproductive strategies).

Migrant: a migratory individual; a member of a migratory contingent. Other terminology has been used in previous studies (*e.g.* disperser, ocean type and stray).

Oceanodromy: migration between marine habitats.

Partial anadromy: a form of partial migration where the migratory contingent move from fresh water to the sea, returning to spawn, whilst residents remain in fresh water for the entire cycle (partial catadromy is this situation reversed, *i.e.* residents remain all year round in the marine environment).

Partial migration: a prevalent form of animal migration, which occurs when a population contains both migratory and resident individuals.

Potamodromy: migration between freshwater habitats, *e.g.* migration from adult habitat in lakes to spawning habitats in streams.

Resident: a term to describe an individual within a partially migratory population that does not make migratory movements (also referred to as retentive or sedentary).

Semi-anadromy: migration from fresh water to brackish (*e.g.* estuarine) habitats.

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## DEFINING AND CATEGORIZING PARTIAL MIGRATION IN FISHES

Partial migration describes the phenomenon where a population consists of both migratory and resident individuals. Therefore any population with between 1 and 99% migrants can be considered to be a partially migratory population. It is likely that many migratory fish populations are in fact partially migratory. For example, even in species such as *T. thynnus*, which is often used to exemplify long distance aquatic migration, some individuals may remain resident around the spawning grounds throughout the entire year (Baker, 1978). Especially in fishes, progress in understanding patterns of partial migration has been hampered by variation in terminology for different species, however, many recent studies into partial migration have begun to overcome this, with studies into perciformes (Kerr & Secor, 2010), cypriniformes (Chapman *et al.*, 2011c) and salmoniformes (Olsson *et al.*, 2006) using similar terminology to investigate this phenomenon (which is also adopted here and integrated into the broader fisheries terminology: see Table I).

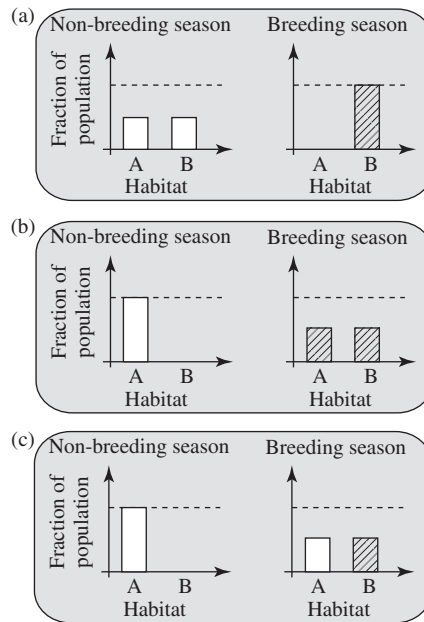


FIG. 1. Schematic of three different types of seasonal partial migration: (a) non-breeding partial migration: residents and migrants share a breeding habitat but spend the non-breeding season apart, (b) breeding partial migration: residents and migrants share a non-breeding habitat and breed apart, and (c) skipped breeding partial migration where residents and migrants are apart during the breeding season, but as migration is required for reproduction only migrant individuals reproduce. Each panel shows the fraction of the population in each of the two habitats (A and B) during each of two seasons (non-breeding and breeding). ▨, individuals that are reproducing. Reproduced with permission from Shaw & Levin (2011).

Three types of seasonal partial migration have been commonly described in the literature (Chapman *et al.*, 2011b; Fig. 1): (1) migrants and residents breed sympatrically, but overwinter apart (*e.g.* three-spined sticklebacks *Gasterosteus aculeatus* L. 1758 Kitamura *et al.*, 2006). This form of partial migration is in a sense the classic form of partial migration. This is referred to as non-breeding partial migration [Fig. 1(a)]; (2) migrants and residents overwinter together whereas they breed allopatrically [*e.g.* pike *Esox lucius* L. 1758 (Engstedt *et al.*, 2011)]. This is referred to as breeding partial migration [Fig. 1(b)]; (3) individuals migrate to breed, but not every year (Rideout *et al.*, 2005) leading to partial migration [*e.g.* shortnose sturgeon *Acipenser brevirostrum* LeSueur 1818 (Dadswell, 1979)]. This form of partial migration, where some individuals forgo breeding each year and hence forgo migration, has rarely been considered in the partial migration literature until recently (Shaw & Levin, 2011). Despite this it appears to be widespread in fishes, especially in oceanodromous species and species that make long and costly migrations to spawn. This is referred to as skipped breeding partial migration [Fig. 1(c)].

In addition, a fourth form of partial migration can be recognised, which occurs over shorter temporal and spatial scales: (4) Partial diel vertical migration (DVM): some individuals migrate vertically (usually at night) whilst others remain at the same place in the water column. This has been noted in a number of fish species, including coregonids (Mehner & Kasprzak, 2011) and Bear Lake sculpin *Cottus*

*extensus* Bailey & Bond 1963 (Neverman & Wurtsbaugh, 1994). This is referred to as partial DVM.

Classically, partial migration has been considered in the context of avian migration, where populations of birds can be relatively well defined. For many fishes, especially oceanic species, however, populations can range across vast areas of habitat, and so partial migration at a scale relevant to the particular species in question must be considered. Additionally, often fishes will undertake substantial journeys from nursery areas to adult habitats and it is upon reaching these habitats that some individuals migrate from and some remain resident [*e.g.* European eels *Anguilla anguilla* (L. 1758) (Tsukamoto *et al.*, 1998)]. In this example all individuals are in a sense migratory (as they migrate as larvae from the spawning grounds and return as adults to breed), but within a specific life stage only part of the population will migrate. Here, an inclusive approach is taken and migratory polymorphism within a particular life stage is also defined as partial migration, even when all individuals have migrated as larvae. It is of note that the categories of partial migration described above are not necessarily mutually exclusive of one another. For example, consider a case whereby a migratory contingent of fishes moves between two spatially segregated resident contingents A and B, feeding at site A and spawning at site B. These migrants could thereby be classed as breeding partial migrants when related to site A residents and non-breeding partial migrants when related to site B residents. Such a case exists for herring *Clupea harengus* L. 1758 populations which can be classified as displaying both breeding and non-breeding partial migration, depending upon the perspective (Ruzzante *et al.*, 2006). In addition, mature *C. harengus* do not migrate to spawn each year [skipped breeding partial migration (Engelhard & Heino, 2005)]. Finally, young-of-the-year (YOY) *C. harengus* also display a bimodal vertical distribution and can hence also be classified as exhibiting partial DVM (Jensen *et al.*, 2011). This example highlights the complexity evident in migratory and movement patterns in fishes in the wild, which (unfortunately for ichthyologists) defies neat and exclusive categorization.

## PARTIAL MIGRATION IN FISHES: A TAXONOMIC OVERVIEW

Partial migration has now been documented in a remarkably wide range of fishes, and has been described for all major types of migratory behaviour (anadromy, catadromy, oceanodromy and potamodromy). In this section some of the many examples of partial migration in fishes in the wild are described. The goal here is not to provide an exhaustive list of partially migratory fishes, but rather to highlight how taxonomically widespread intrapopulation migratory diversity is by giving examples of species from the many different orders that exhibit partial migration.

### ANGUILLIFORMES

Until relatively recently, freshwater anguillid eels were synonymous with obligate catadromy, whereby mature adults migrate from freshwater habitats to spawn in the sea. A landmark study, however, showed that *A. anguilla* are actually composed of two distinct migratory contingents: the first with individuals that make the catadromous journey from marine to fresh water (migrants) and the second with

individuals that never migrate into fresh water but spend their whole lives in the sea [marine residents (Tsukamoto *et al.*, 1998)]. Other species of eel have since been shown to display similar patterns of partial migration, including the Japanese eel *Anguilla japonica* Temminck & Schlegel 1846 and American eel *Anguilla rostrata* (LeSueur 1817) (Daverat *et al.*, 2006), and also a tropical species, the Indonesian shortfin eel *Anguilla bicolor bicolor* McClelland 1844 (Chino & Arai, 2010).

#### ACIPENSERIFORMES

There are a number of examples of breeding partial migration in the sturgeon order. Male *A. brevirostrum* make spawning migrations just one out of every two years (Dadswell, 1979), and female Atlantic sturgeon *Acipenser oxyrinchus* Mitchill 1814 breed just once every 2–5 years (Smith 1985). No reports of other forms of migratory dimorphism in this group, however, could be found.

#### BERCIFORMES

This order is composed of mostly deep-sea fishes and is poorly studied. The orange roughy *Hoplostethus atlanticus* Collett 1889 is a bathypelagic marine fish which makes oceanodromous spawning migrations. Not all individuals in a population, however, breed each year [skipped breeding partial migration (Bell *et al.*, 1992)].

#### CHARACIFORMES

The migratory behaviour of characiformes is not well understood at an individual level, partly as this group is prevalent in the Neotropics and Africa where information about fish migration is scarce. Studies of two species, however, are suggestive of different forms of partial migration in this group. Populations of the coporo *Prochilodus mariae* Eigenmann 1922 are composed of both migratory and resident individuals, with some individuals migrating from lagoons into rivers following the breeding season [non-breeding partial migration (Saldana & Venables, 1983)]. Furthermore, a recent study of a fish from the same genus, the zulega *Prochilodus argenteus* Spix & Agassiz 1829, a freshwater fish found in Brazilian rivers, showed that this species is a potamodromous partial migrant. Twenty-one % of tagged individuals remained resident within a limited area and the remainder migrated to spawn [breeding partial migration (Godinho & Kynard, 2006)].

#### CLUPEIFORMES

This order includes many economically important food species from the herring and anchovy families. There have been a number of reports of partial migration from this group, including *C. harengus*, blueback herring *Alosa aestivalis* (Mitchill 1814) and tapertail anchovy *Colia mystus* (L. 1758). For example, molecular analysis of *C. harengus*, from the North Sea and adjacent areas revealed that there were genetic differences between fish from three regions (Ruzzante *et al.*, 2006). *Clupea harengus*, from these regional contingents share common feeding grounds but migrate to spawn in distinct areas [breeding partial migration (Ruzzante *et al.*, 2006)], with some fish remaining resident in a single region to feed and spawn whilst others migrated to spawn in a different region. *Clupea harengus* are thought to exhibit

strong natal homing to spawning grounds (Iles & Sinclair, 1982), and this factor may be important in breeding partial migration if good feeding grounds are not patchily distributed. Additional reports analysing otolith annuli shape suggest that the Celtic Sea *C. harengus* population is also partially migratory, with the migratory contingent moving into the Irish Sea. In this population, migrants grow more slowly and hence recruit later to the adult population than residents (Burke *et al.*, 2008). Further evidence from scale analysis shows that herring may skip breeding migrations in certain years (Engelhard & Heino, 2005). The YOY *C. harengus* also exhibit partial DVM (Jensen *et al.*, 2011).

In anadromous *A. aestivalis*, recent analysis using otolith microchemistry to infer patterns of migration between freshwater habitats and the sea showed evidence for a small (c. 4%) resident contingent for this species (Limburg *et al.*, 2001). A similar analysis for anadromous *C. mystus* from the Changjiang Estuary in China also revealed that freshwater residents exist in this species, which was previously thought to be entirely anadromous (Yang *et al.*, 2006).

## CYPRINIFORMES

A recent increase in research effort into cyprinid partial migration means that this group of fishes is probably the best studied example of potamodromous partial migration available (Jepsen & Berg, 2002; Brodersen *et al.*, 2008a, 2011, 2012; Brönmark *et al.*, 2008; Skov *et al.*, 2008, 2010, 2011; Chapman *et al.*, 2011c). Various cyprinid species partially migrate out of shallow lakes into connecting streams over winter (non-breeding partial migration). In a study in a Swedish lake, Lake Krankesjön, patterns of cyprinid partial migration in roach *Rutilus rutilus* (L. 1758), white bream *Blicca bjorkna* (L. 1758) and rudd *Scardinius erythrophthalmus* (L. 1758). All three species exhibited partial migration, with 55% of tagged *B. bjorkna*, 40% of *R. rutilus* and 5% of *S. erythrophthalmus* migrating (Skov *et al.*, 2008). *Rutilus rutilus* and *B. bjorkna* mostly migrated overwinter, with a second peak in the spring, whilst the few *S. erythrophthalmus* that migrated did so in spring. The migratory behaviour of this particular population of *R. rutilus* has now been studied intensively for almost a decade, and it is clear that the proportion of migrants varies substantially between years (Brodersen *et al.*, 2011). Migrant *R. rutilus* show consistency both in terms of site fidelity and the timing of migration (Brodersen *et al.*, 2012), and also migratory status (B. B. Chapman unpubl. data). This case of partial migration has also been shown to have considerable effects on the lake ecosystem, for example by influencing the zooplankton population dynamics (Hansson *et al.*, 2007) or potentially the dynamics of the entire system (Brönmark *et al.*, 2010). Partial migration has also been documented in the common bream *Abramis brama* (L. 1758) in a study in two Danish lakes (Skov *et al.*, 2011). The evidence here is strongly suggestive that *A. brama* (partially) migrate from shallow lakes into the surrounding streams overwinter to refuge from piscivorous predators such as *E. lucius*. Predation risk has been implicated as playing an important role in the migratory dynamics of a number of fish species (Chapman *et al.*, 2012).

## ELASMOBRANCHII

There are a number of reports that spiny dogfish *Squalus acanthias* L. 1758 populations are partially migratory. Whilst around 90% of the *S. acanthias* caught

and tagged in the waters around Newfoundland were recovered in the same region, the remaining 10% were recaptured much further afield, in the Gulf of St Lawrence, Nova Scotia and U.S. waters (Campana *et al.*, 2009). These patterns, along with data from a north-east Pacific Ocean population, where 85% remained resident, are strongly suggestive of partial migration in this species (McFarlane & King, 2003). Some sharks perform skipped breeding partial migrations, for example the Australian school shark *Galeorhinus australis* Macleay 1881 (Olsen, 1954; in Shaw & Levin, 2011). Whilst evidence to suggest that other elasmobranchs engage in breeding or non-breeding partial migrations is lacking, there are some candidate species that deserve further attention. Euryhaline bull sharks *Carcharhinus leucas* (Müller & Henle 1839) that were studied in an early tagging project were found to have contingents that migrate from the Caribbean Sea into Lake Nicaragua (Thorson, 1971). Little is known, however, about the periodicity of these movements or what proportion of the population makes these catadromous forays from the sea into lakes.

## ESOCIFORMES

Lake dwelling *E. lucius* have been shown to partially migrate into connected streams in very low numbers during spring in a study by Skov *et al.* (2008). Thus, freshwater *E. lucius* potentially partake in a breeding partial migration, although the evidence here is scarce and further studies are required. Observations of large *E. lucius* in the streams in spring around the same lake over recent years also support this idea (B. B. Chapman pers. obs.). *Esox lucius* have partially migratory populations that inhabit brackish environments such as the Baltic Sea. These populations are composed of resident individuals that spawn in the bays of the Baltic Sea and of migrants that swim into freshwater habitats to spawn [breeding partial migration (Engstedt *et al.*, 2011)].

## GADIFORMES

The gadiformes are mostly marine fishes that comprise a number of food fishes, including the Atlantic cod *Gadus morhua* L. 1758. *Gadus morhua* are an exceptionally important commercial species and a number of studies suggest that some populations are partially migratory. For example, acoustic telemetry research into the movements and habitat use of juvenile (age 2 – 3 year) *G. morhua* in a Newfoundland fjord showed that *c.* 70% from this age class made winter migrations to deeper waters, whilst 30% remained resident (Cote *et al.*, 2004). Migrant *G. morhua* were in better condition than resident fish, which suggests that residency could be a best-of-a-bad-job strategy for individuals that cannot pay the energetic costs associated with migration. Others have also reported similar proportions of migrants and residents for this species (Comeau *et al.*, 2002). Sympatric *G. morhua* can also display striking colour variation. For example, an offshore population in the Gulf of Maine comprises two colour variants, with red and olive-coloured fish inhabiting the same area. A recent study showed that colouration correlated with body shape, and the authors suggest that the two different colour morphs (which differ in their diet), represent different migratory contingents, with both residents (red fish) and migrants (olive fish) coexisting in sympatry (Sherwood & Grabowski, 2010). Further research on this interesting system will clarify whether the partial migration hypothesis holds for red and olive *G. morhua* in the Gulf of Maine.



## GASTEROSTIFORMES

*Gasterosteus aculeatus* inhabits many different habitats, from freshwater ponds and streams to brackish estuaries and coastal marine environments. The Pacific Ocean form of this species is composed of both anadromous migratory and freshwater resident individuals. These groups differ morphologically but allozyme analysis suggests that they form a single breeding population (Higuchi *et al.*, 1996). A study of juvenile *G. aculeatus* from a nursery pond in Hokkaido, Japan, showed that fish from this population contained both resident individuals and also anadromous migrants [non-breeding partial migration (Kitamura *et al.*, 2006)]. Furthermore, the authors show that smaller juveniles adopt the migratory strategy. A second study is suggestive of breeding partial migration in this species. Kedney *et al.* (1987) reported that *G. aculeatus* in the St Lawrence Estuary comprised both anadromous fish that migrated to spawn in fresh water and estuarine residents.

## MYCTOPHIFORMES

This order is composed of deep-sea fishes that mostly belong to the lanternfish family, *Myctophidae*. In one species in this family, the northern lampfish *Stenobrachius leucopsarus* (Eigenmann & Eigenmann 1890), a bimodal distribution of fish was documented at night. The first peak of abundance occurred at 100 m depth, and the second at 300–500 m depth [partial DVM (Pearcy *et al.*, 1979)]. Other studies also suggest that partial DVM is common in this group, and occurs in other myctophids besides *S. leucopsarus* (Pearcy *et al.*, 1979).

## OSMERIFORMES

There are scattered reports of potential migratory dimorphism in the smelts, all of which are suggestive of partial migration (more specifically partial anadromy), and all of which require more study. The New Zealand smelt *Retropinna retropinna* (Richardson 1848) has been shown to have two distinct morphological types, which have been inferred to be river migratory (anadromous) and lake resident forms (Northcote & Ward, 1984). These ecotypes show a bimodal distribution for many meristic characteristics, and differ in gill raker and vertebral number in addition to mass and length relationships and fecundity measurements. Circumstantial evidence is presented that bimodal morphological distributions for gill raker and vertebral counts are only present in open lowland lakes, and not in closed lakes, rivers or coastal waters (Northcote *et al.*, 1992). Isotope studies to investigate whether this species is partially anadromous, however, have been inconclusive and so a conclusive assessment of partial migration in this species is not possible. Another stable isotope study based in New Zealand showed that a species previously considered to be diadromous, the koaro *Galaxias brevipinnis* Günther 1866, contained fish that had never migrated to sea (Hicks *et al.*, 2005). Again, this study is suggestive of partial migration, however, it is difficult to conclude this on the basis of a study with such a low sample size ( $n = 6$ , with just a single individual showing no microchemical signature of sea migration). The wasagi (ice-fish) *Hypomesus nipponensis* McAllister 1963 has also been reported to exhibit partial migration, with anadromous and freshwater resident forms coexisting (Arai *et al.*, 2006). Populations of *H. nipponensis* are also composed of estuarine residents that do not enter freshwater

habitats, highlighting the diversity of life history strategies in this species. A final example of an osmerid partial migrant is the shiraou *Salangichthys microdon* (Bleeker 1860), an important species in eastern Asian fisheries. Stable-isotope analysis of *S. microdon* from Hokkaido, Japan, indicate that this lake population are partially migratory, with the majority of fish exhibiting anadromous behaviour and a minority (c. 15%) remaining as lacustrine residents (Arai *et al.*, 2003).

## PERCIFORMES

There are many diverse examples of partial migration amongst perciformes, but most studies simply document that migratory and resident contingents occur. One exception to this is white perch *Morone americana* (Gmelin 1789), which has been the focus of detailed research in recent years. *Morone americana* partially migrate from their natal freshwater habitats into brackish estuaries in North America (Kerr & Secor, 2011), with the majority of fish (>90%) migrating (Kerr *et al.*, 2009). These alternative life history strategies are influenced by early life conditions, with early spawned larval cohorts making up the majority of the migratory contingent (Kerr & Secor, 2010). Early spawned fish had low growth rates compared to late spawned fish, most likely due to temporal variation in food (zooplankton) abundance (Kerr & Secor, 2010). Striped bass *Morone saxatilis* (Walbaum 1792) have also been shown to have a variety of migratory modes within populations (Secor *et al.*, 2001). In this species, as with many other partially anadromous fishes, males dominated the resident contingent, and females the oceanic migratory contingent. Dorsal colouration in this species has also been linked to migratory strategy, with black dorsal colouration for freshwater residents and green for oceanic migrants (Paramore & Rulifson, 2001).

Perch *Perca fluviatilis* L. 1758 populations have also been observed making partial migrations out of shallow lakes in Northern Europe (Skov *et al.*, 2008), and the proportion of migrants varies significantly between lakes (C. Skov, unpubl. data). In marine fishes there is some evidence for partial migration in oceanodromous perciformes such as spotnape cardinalfish *Apogon notatus* (Houttuyn 1782) and *T. thynnus*. *Apogon notatus* are found in the coastal waters of the north-western Pacific Ocean. They spawn in neritic breeding grounds, and most migrate overwinter into deeper waters, whilst some remain resident (Fukumori *et al.*, 2008). Finally for this group, *T. thynnus* have been reported as potentially exhibiting patterns similar to partial migration [non-breeding partial migration (Baker, 1978)]. Following spawning in the Mediterranean Sea, some fish remain in this area whilst others migrate out into the Atlantic Ocean, migrating northwards to Norway and making a return journey during winter. These inferences are based on an old study which used the identification of fishermen's hooks from different regions to study *T. thynnus* migration (Sella, 1930). More recent work which is currently in progress using modern tagging techniques, however, suggests that the classification of the Mediterranean population of *T. thynnus* as partial migrants may indeed be accurate (J. M. Fromentin pers. comm.). Furthermore, geolocation data from 330 electronically tagged *T. thynnus* shows that fish tagged in the western Atlantic Ocean have overlapping foraging grounds in the North Atlantic Ocean but form two geographically distinct breeding groups, with individuals migrating to spawn in the Mediterranean Sea and the Gulf of Mexico [breeding partial migration (Block *et al.*, 2005)].

## PETROMYZONTIFORMES

This order comprises entirely of lamprey, which are one of the most ancient and successful orders of living fishes. Whether or not lamprey are partial migrants cannot currently be concluded, as this is still a topic of debate. Most genera of lamprey include species pairs of parasitic anadromous lamprey and freshwater non-parasitic residents (Zanandrea, 1959). During the juvenile stage the larvae of the two species are morphologically similar but the adults adopt different life-history strategies. Furthermore, species pairs have sympatric distributions, with freshwater residents being found within the distribution of parasitic anadromous lamprey (Hardisty, 1986). Given that it is now known how environmentally labile migratory strategy can be in fishes (Olsson *et al.*, 2006), it seems plausible that the two putative species are actually distinct life-history forms within partially anadromous populations, such as has been documented in many other fishes. This idea is supported by the lack of genetic differentiation between species pairs. Some commentators (Salewski, 2003) suggest that this is because the species are very recently diverged whilst others (Schreiber & Engelhorn, 1998) argue that this is supportive of the life-history dimorphism hypothesis. Currently the molecular evidence does not exclude either hypothesis (Espanhol *et al.*, 2007), and so whether this is truly a case of partial anadromy remains to be seen.

## PLEURONECTIFORMES

The flatfishes contain a number of commercially important marine species, including plaice *Pleuronectes platessa* L. 1758. A recent study into the stock structure of *P. platessa* is suggestive that some populations may be partially migratory. Based on data from >2700 tag recaptures of fish from populations on the west coast of England and Wales, Dunn & Pawson (2002) describe a variety of movements from these fish. Their analysis of *P. platessa* tagged and released in the southeast Irish Sea suggests that some individuals dispersed to the Bristol Channel. Of the dispersed contingent, a small proportion remained resident in the Bristol Channel whilst the majority (>70%) made feeding migrations to the Irish Sea (Dunn & Pawson, 2002), which is suggestive of oceanodromous non-breeding partial migration in this species. Other potential partial migrants include starry flounder *Platichthys stellatus* (Pallas 1787), which is a coastal flatfish that spawns in sea water but juveniles can sometimes be found in rivers (Quinn & Brodeur, 1991). Similarly, populations of European flounder *Platichthys flesus* (L. 1758) also display comparable patterns of facultative amphidromy, with freshwater migrants attaining a larger body size at age than marine residents (Beaumont & Mann, 1984).

## SALMONIFORMES

Amongst the fishes, the salmonids probably best exemplify migration in the public imagination. Many of the species in this group are extremely important to mankind, in both a cultural and commercial sense. The wealth of literature describing and analysing migratory patterns of salmonids makes reviewing such a body of work a daunting prospect, and so here the account is limited to providing a handful of examples of partial migration in this order, and direct interested readers to other more complete reviews (Jonsson & Jonsson, 1993; Hendry *et al.*, 2004).

Many salmonids have partially anadromous populations containing both a resident freshwater contingent and a migratory marine contingent that spawn in the same area. For example, *Oncorhynchus mykiss* (Walbaum 1792) populations contain both resident rainbow trout and anadromous steelhead trout (McPhee *et al.*, 2007). These divergent migratory strategies are thought to be a product of phenotypic plasticity (McPhee *et al.*, 2007), however, recent evidence points to genetic differentiation between these forms (Pearse *et al.*, 2009). One seemingly general pattern in the salmonids is that females dominate the migratory contingent (Jonsson & Jonsson, 1993). This is likely because there is a positive relationship between body size and fecundity in female fishes, but not males, hence migrating to a highly productive marine environment can significantly increase reproductive capacity in this sex *via* an increase in growth rate relative to freshwater forms (Jonsson & Jonsson, 1993). Males may also benefit from the greater body size associated with marine migration, as sexual selection is strong in many salmonids, both for female choice and also male–male competition. The costs of migration, however, are also considerable, potentially balancing fitness returns for migrants and residents (Chapman *et al.*, 2012).

Potamodromous partial migrations have also been reported in this group. Arctic charr *Salvelinus alpinus* (L. 1758) that inhabit Lake Visjön in north-west Sweden contain lacustrine residents and also migrants that enter the streams in summer and make opportunistic feeding migrations to other lakes in the vicinity (Näslund *et al.*, 1993). Similarly, *S. trutta* partially migrate from rivers to lakes (Olsson & Greenburg, 2004).

Migratory salmonids have been reported skipping annual spawning migrations, most likely to conserve the energy costs of long distance migration to spawn in fresh water. Hence breeding partial migration is also evident in this group, for example in Atlantic salmon *Salmo salar* L. 1758 (Schaffer & Elson, 1975). Finally, fishes from the salmoniformes also exhibit partial DVM. Mapping of the vertical distribution of zooplanktivorous lake dwelling ciscoes *Coregonus* spp. in German lakes showed that some individuals migrate into the upper waters in the night, whilst others remain resident in the deep pelagic throughout the daily cycle (Mehner & Kasprzak, 2011).

## SCORPAENIFORMES

Whilst some species within this group show diverse migratory histories between populations [*e.g.* Japanese sculpin *Cottus pollux* Günther 1873 (Goto & Arai, 2003)], varying from amphidromy to resident fluvial strategies, strong evidence for within population diversity (*i.e.* partial migration) is scarce. One species in this group which may potentially show partial migration, however, is sablefish *Anoplopoma fimbria* (Pallas 1814). Data from a tagging study carried out on this species were interpreted as showing that whilst the majority of fish remain resident, a minority travel much greater distances (Beamish & McFarlane, 1988). Whether this is truly a case of partial migration, or whether the long distance movements were more akin to unidirectional dispersal remains to be seen.

Despite a lack of examples of seasonal partial migration, there is an example from this group of partial DVM. Juvenile *C. extensus* (<30 mm in standard length) carry out partial DVMs in American lakes, whilst larger fish remain resident in deeper waters (Neverman & Wurtsbaugh, 1994). Laboratory trials suggest that this partial migration may be a strategy for smaller fish to increase their growth rate

via increasing their digestion rate in the warmer surface waters (Neverman & Wurtsbaugh, 1994).

## SILURIFORMES

There is scant evidence that catfish species are partial migrants. A recent study of female piscivorous catfish, spotted sorubim *Pseudoplatystoma corruscans* (Spix & Agassiz 1829), suggested that both migrant and resident behaviours were evident (Godinho *et al.*, 2007). The authors state that migratory and resident fish were of similar size, and also that individuals can switch between strategies between different years, although data on these aspects were not presented.

## CURRENT TECHNIQUES IN PARTIAL MIGRATION STUDIES

The primary goal of researchers who study migration is to understand when, where, why, and how animals migrate. Partial migration adds an additional dimension: who migrates? In some cases, such as many salmonids, migrants and residents differ phenotypically, and so identifying fish from different migratory contingents is relatively straightforward. In most other groups, however, morphological differences are either subtle or absent, and so other methods must be used to study partial migration. Information regarding which individuals migrate and also the timing and destination of migration can be collected in various ways, either directly or indirectly (Durbec *et al.*, 2010). Direct information acquisition can occur by following individuals using some form of visible or electronic marker, or by visual encounters or hydroacoustics (Lucas & Baras, 2001). Information can be indirectly gathered by deducing a fish's movements using natural, intrinsic biological or biogeochemical markers (Rubenstein & Hobson, 2004). A range of different methods has been involved in studies of partial migration in fishes which are briefly reviewed here.

## DIRECT TECHNIQUES TO STUDY PARTIAL MIGRATION

Telemetry is a common name for studies where some kind of electronic tag is placed internally or externally on the animal, after which the animal is followed over time and space with a resolution depending on the type, size and longevity of the tag used (Lucas & Baras, 2001). Telemetry has recently been used to great effect in partial migration research to study phenotypic differences between migrants and residents, *i.e.* which individuals stay and which migrate (Brodersen *et al.*, 2008a; Skov *et al.*, 2011, Chapman *et al.*, 2011c). Telemetry can be divided into active and passive telemetry where in the former the fishes are actively tracked whereas in passive telemetry data are collected from stationary (passive) listening stations. Whilst active telemetry has the obvious advantage of providing researchers with a fine-scale individual track of changes in location, this is not always necessary in partial migration studies to assess whether a fish is a migrant or resident. For fishes that migrate via distinct migratory corridors [for example up streams as many cyprinids do in the winter migration (Skov *et al.*, 2008)], passive telemetry can provide information upon which individuals migrate and hence which individuals remain resident, in addition to timing and migratory destination. Passive telemetry is more suited

for studies that require a high sample size due to the high effort involved in active telemetry work. Passive telemetry can also be used in more open systems (*e.g.* lakes or lagoons) where listening stations can be placed on buoys and individuals' positions can be estimated from multiple records of the same tag at different stations. These kind of set-ups, however, pose a greater logistical and financial challenge than stations placed in small streams. Choosing whether to use active or passive telemetry depends not only on the system but also upon the question. For example, passive telemetry would be suitable for investigations into the proportion of migratory fishes, or between year comparisons of individual migratory consistency or timing. If how migrants and residents use habitat during the non-migratory period in a lake is of interest, or estimating individual survival probabilities of migration *v.* residency or active telemetry would be potentially more suitable. A combination of the two methods can prove very effective, since one method complements the other (Brodersen *et al.* 2008b), but unfortunately this approach is rarely used.

The types of electronic tags available differ, and can be with or without internal power supply (batteries), and can be based on radiofrequency or acoustic signals. Normally the size of the tag is determined by the size of the battery which in turn strongly influences tag longevity, meaning that longitudinal studies normally require relatively large tags. Consequently many studies have focused on larger and older individuals whereas telemetry studies of small individuals are scarce. This may mask patterns of age or size-specific partial migration, and also potentially lead to an underestimation of the prevalence of partial migration in species of smaller body size. The smallest telemetry tags available are passive integrated transponder tags (PIT tags) which can be as small as 8 mm long with a mass <0.03 g. PIT tags have no internal battery but are energized when close to special reader units which create electromagnetic fields. The miniature PIT tags are advantageous compared to the larger tags with batteries as they are much cheaper and can be used in smaller fishes but their use is restricted to systems where migrating fishes pass a confined area (Aarestrup *et al.*, 2003; Skov *et al.*, 2008).

Another type of tag that could be used in studies of partial migration is an archival or data storage tag (DST). These tags sample information about one or several different environmental signals in the vicinity of the tagged fish, such as conductivity, temperature, oxygen, pressure (depth), light intensity or salinity (Neuenfeld *et al.*, 2007; Aarestrup *et al.*, 2009; Reddin *et al.*, 2011), from which it is potentially possible to geolocate the fishes and consequently determine differences in migration patterns and habitat preferences between individuals (Pedersen *et al.*, 2008; Neuenfeld *et al.*, 2007). This technique has mostly been used in marine environments, where variations in environmental signals allow relatively accurate geolocation. DST tags can also sample internal physiological information from the fish such as heart rate and electro cardiograms (Muramoto *et al.*, 2004), muscle activity (Quintella *et al.*, 2004), acceleration (Nakamura *et al.*, 2011), or a combination of these (Clark *et al.*, 2010), which could be used to shed light on (for example) the energetic costs of migration *v.* residency. DST tags are most often dependent on being retrieved from the tagged fish, which can be a challenge. In its simplest form, data retrieval from the DST tags requires recaptures of the fish (Neuenfeld *et al.*, 2007). Alternatives to this are pop-up tags which are DST tags that include devices which allow the tag to pop off the fish at some pre-programmed time and float to the surface, where data are uploaded *via* satellite (Aarestrup *et al.*, 2009). Tags have also been developed

that can recognize and store information about other tagged individuals within a certain proximity [proximity tags (Guttridge *et al.*, 2010)]. These tags have great potential to study social structure and partial migration, and answer questions about the importance of social interactions in migratory behaviour, and about how migrants and residents interact during the non-migratory period.

A final direct technique that has recently been utilized with great success to study partial DVM is hydroacoustic technology. Hydroacoustic techniques provide a useful technique to monitor the spatial distribution and migration of fish populations and is based on equipment that directs acoustic beams either vertically (Busch & Mehner, 2009) or horizontally in the water. When the acoustic energy hits an object in the water, such as schools of fishes or even individual fish, some of the energy is back-scattered to the equipment, called transducers, and converted into a quantifiable electrical signal (Lucas & Baras, 2001). In a recent study, Mehner & Kasprzak (2011) used this technology to demonstrate that *Coregonus* spp. perform partial DVM in a German lake.

## INDIRECT TECHNIQUES TO STUDY PARTIAL MIGRATION

The use of indirect techniques to study partial migration has also undergone somewhat of a revolution in recent years. Techniques such as otolith microchemistry, stable isotope and molecular (*e.g.* microsatellite) analysis have proliferated and provided many useful insights into migratory behaviour in fishes. Indirect techniques have many benefits over direct techniques, such as active tracking of fishes. For example using otolith microchemistry the migratory history of an individual fish over its entire lifetime (Secor, 2010) can be potentially viewed. Here, each method is briefly described and an example of its utility in partial migration research given.

Otolith microchemistry based on either trace element ratios (often Sr:Ca ratios) or stable isotopes has frequently been used to establish the migration history of different individuals within a population (Gillanders, 2005). For example, Sr:Ca ratios were used to establish the occurrence of partial breeding migration in *E. lucius* from the Baltic Sea where a contingent migrates to spawn in freshwater areas whereas others remain resident to spawn in the saline environment [breeding partial migration (Engstedt *et al.*, 2011)]. This technique is particularly suited to studies of partial anadromy and catadromy, where freshwater and marine microchemical signatures are highly divergent (Tsukamoto *et al.*, 1998). In addition to their chemical composition, otoliths can also carry useful information in the shape of their annuli. A recent study showed that the shape of the juvenile portion of *C. harengus* otoliths could be used to differentiate between migrants and residents with 95% accuracy (Burke *et al.*, 2008). Likewise, migratory and resident individuals in a population can be potentially distinguished from each other based on isotopic signatures sampled from soft tissue samples. The stable-isotope approach is based on the fact that food-web isotopic signatures are reflected in the tissues of organisms. Since isotopic signatures can vary spatially, based on a variety of biogeochemical processes, organisms moving between isotopically distinct food webs can carry with them information on the location of previous feeding (Hobson, 1999). In addition to their chemical composition, otoliths can also carry useful information in the shape of their annuli.

Partial migration can also be investigated with molecular genetic analyses such as microsatellite and restriction site associated DNA (RAD) sequencing techniques.

These may be especially useful for assessing breeding partial migration in which population genetic techniques could test whether migrants and residents spawn in geographically distinct areas (microsatellites), or potentially identifying genomic regions linked to migratory behaviour (RAD sequencing). Finally, parasite prevalence can also be used as an indirect indicator of varying migratory behaviour within populations, as migrants will potentially be exposed to parasites on the migratory grounds that residents do not encounter. For example, a study investigating *C. harengus* distinguished between individuals from two spawning populations using a comparison of endoparasites on fish (Campbell *et al.*, 2007).

### CONCLUDING REMARKS

This review suggests that partial migration is much more widespread amongst fishes than previously thought (Jonsson & Jonsson, 1993). Many species from a diverse series of orders partially migrate, and the true taxonomic distribution of this migratory mode is likely to be even broader than is reported here due to geographic and taxonomic gaps in the literature. One of the problems encountered when synthesizing the growing literature on partial migration in fishes was of the varied terminology adopted to describe migratory variation. Following earlier discussions of this issue (Secor & Kerr 2009) here an attempt has been made to clarify definitions and types of partial migration. It is hoped that the term partial migration will become the accepted term amongst ichthyologists of different backgrounds and research foci. In this way the understanding of this fascinating phenomenon, both among fish biologists and also more widely, can be promoted. Finally, many of the techniques now in use to help scientists find answers to the puzzle of partial migration have been outlined. It is hoped that this review will stimulate innovative and exciting future research projects, and inspire ichthyologists to apply partial migration thinking to their own studies of the movement and ecology of fishes.

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