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Partial migration in fishes: causes and consequences

B. B. CHAPMAN*†, K. HULTHÉN*, J. BRODERSEN*‡, P. A. NILSSON*,
C. SKOV§, L.-A. HANSSON* AND C. BRÖNMARK*

**Department of Biology, Lund University, Ecology Building, 223 62 Lund, Sweden and*
§*National Institute of Aquatic Resources, Technical University of Denmark (DTU), Vejlsøvej*
39, 8600 Silkeborg, Denmark

Partial migration, where only some individuals from a population migrate, has been widely reported in a diverse range of animals. In this paper, what is known about the causes and consequences of partial migration in fishes is reviewed. Firstly, the ultimate and proximate drivers of partial migration are reflected upon: what ecological factors can shape the evolution of migratory dimorphism? How is partial migration maintained over evolutionary timescales? What proximate mechanisms determine whether an individual is migratory or remains resident? Following this, the consequences of partial migration are considered, in an ecological and evolutionary context, and also in an applied sense. Here it is argued that understanding the concept of partial migration is crucial for fisheries and ecosystem managers, and can provide information for conservation strategies. The review concludes with a reflection on the future opportunities in this field, and the avenues of research that are likely to be fruitful to shed light on the enduring puzzle of partial migration in fishes. © 2012 The Authors

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Migration is perhaps nature's most spectacular event. Each year billions of animals set out on a seasonal journey to find food or mates, avoid predators or escape severe winter weather conditions. These cyclical movements occur over a vast array of spatial and temporal scales and have mystified and inspired mankind for >2000 years (Aristotle, c. 350 BC). The intrinsic interest in migration has generated a great deal of research aimed at understanding the causes and consequences of this phenomenon (Alerstam, 1990; Dingle, 1996; Newton, 2008). Understanding migration is important as it is a powerful force shaping the distribution of animals across space and time, and influences processes at all scales, from individuals to entire ecosystems. Unravelling the mystery of migration is therefore critical for a broad understanding of ecological and evolutionary processes, in addition to being central to many applied issues, such as species conservation and fisheries stock management.

Migration is a heterogeneous phenomenon, varying both between and within species. Arguably, the most common form of migration is known as partial migration

†Author to whom correspondence should be addressed. Tel.: +46 736 643 608; email: ben.chapman@biol.lu.se

‡Present address: Department of Fish Ecology and Evolution, EAWAG Swiss Federal Institute of Aquatic Science and Technology, Center of Ecology, Evolution and Biochemistry, Seestrasse 79, CH-6047 Kastanienbaum, Switzerland

(Chapman *et al.*, 2011a). Partial migration occurs when just a fraction of a population migrates and the remainder stay resident, and has been widely documented across a wide range of taxa, including fishes (Jonsson *et al.*, 1993; Chapman *et al.*, 2012). Partial migration in fishes has long been recognized amongst salmonid species, where some individuals migrate to the sea from fresh water (anadromy) and others remain resident in their natal streams (Jonsson & Jonsson, 1993). Recent reports, however, have revealed that partial migration is extremely widespread, including not just anadromous but also catadromous, potamodromous and oceanodromous fishes. It is also widely distributed across orders, with examples in many species from Perciformes to Pleuronectiformes (Table I; Chapman *et al.*, 2012). Many studies now show that populations of fishes can contain both migratory and resident individuals, and that partial migration occurs in a variety of habitats and spatial scales.

Whilst the number of studies in this area continues to grow, many of these studies merely describe patterns of migratory dimorphism, or even simply show that it occurs for a given population, and offer little analysis into the factors that promote this fascinating behavioural variation, or assess the potential consequences. The proximate and ultimate mechanisms underlying partial migration in fishes are vague, and knowledge of the ecological and evolutionary consequences of partial migration is extremely limited. Partial migration also provides a real opportunity to gain an insight into physiological and behavioural migratory adaptations and is critically important in developing management strategies for stocks, as many commercially important species are partial migrants.

This paper reviews what is currently known about the causes and consequences of partial migration with a special focus on fishes. It begins with an introduction to partial migration, and then considers the causes and consequences of partial migration. This review firstly assesses the ultimate and proximate causes of partial migration: what ecological factors may be important as drivers of migratory dimorphism and what are the proximate control mechanisms of migration? Following this, the conundrum of how partial migration can be maintained over evolutionary time spans is discussed. Next, the ecological and evolutionary consequences of partial migration in fishes are considered, along with the applied implications of partial migration in the context of conservation, biomanipulation and fisheries management. The paper concludes with a reflection upon future opportunities in partial migration research, both in the context of technological advances and also research areas of interest that perhaps deserve greater attention over the coming years.

WHAT IS PARTIAL MIGRATION?

A multitude of terminology has been used to describe migratory dimorphism in fishes (Secor & Kerr, 2009), which has hampered understanding and synthesis of this field in the past. In a sister review from this thematic, the different terms used and the various forms partial migration can take are discussed (Chapman *et al.*, 2012), and so these ideas are not addressed in detail here. In this review, the term partial migration is used to describe the phenomenon where a population is composed of both migratory and resident individuals.

Partial migration is also diverse: it can be seasonal, and either driven by migrants breeding or overwintering allopatrically to residents, or alternatively it can arise from

TABLE I. A taxonomic summary of partially migratory fishes. For each order a single species example of partial migration is included, and the migratory type and classification, and the evidence for partial migration are detailed

Order	Common name	Latin name	Migratory type	Migratory classification	Evidence for partial migration	Per cent migrants	Proposed ecological mechanism	Reference
Anguilliformes	European eel	<i>Anguilla anguilla</i>	Partial non-breeding migration	Partial catadromy	Otolith microchemistry	Unknown	Unknown, linked to body condition	Tsukamoto <i>et al.</i> (1998)
Acipenseriformes	Shortnose sturgeon	<i>Acipenser brevirostrum</i>	Partial skipped breeding migration	Partial anadromy	Tag (capture–recapture)	Unknown	Costly spawning migration	Dadswell (1979)
Berciformes	Orange roughy	<i>Hoplostethus atlanticus</i>	Partial skipped breeding migration	Partial oceanodromy	Demersal trawling	Unknown	Costly spawning migration	Bell <i>et al.</i> (1992)
Characiniiformes	Zulega	<i>Prochilodus argenteus</i>	Partial breeding migration	Partial potamodromy	Active and passive telemetry	79	Costly spawning migration	Godinho & Kynard (2006)
Clupeiformes	Atlantic herring	<i>Clupea harengus</i>	Partial breeding migration	Partial oceanodromy	Genetic markers and otolith morphology	Unknown	Unknown	Ruzzante <i>et al.</i> (2006)
Cypriniformes	Roach	<i>Rutilus rutilus</i>	Partial non-breeding migration	Partial potamodromy	Passive telemetry	High variation between years (7–60)	Predation risk	Chapman <i>et al.</i> (2011c)
Elasmobranchii	Spiny dogfish	<i>Squalus acanthias</i>	Unknown – probably partial non-breeding migration	Partial oceanodromy	Tag (capture–recapture)	<i>c.</i> 15	Unknown	McFarlane & King (2003)
Esociformes	Pike	<i>Esox lucius</i>	Partial breeding migration	Partial anadromy	Passive telemetry and otolith microchemistry	Unknown	Unknown	Engstedt <i>et al.</i> (2011)
Gadiformes	Cod	<i>Gadus morhua</i>	Probably partial non-breeding migration	Partial oceanodromy	Acoustic telemetry	70	Unknown, some evidence for a role of body condition	Cote <i>et al.</i> (2004)
Gasterostiformes	Three-spined stickleback	<i>Gasterosteus aculeatus</i>	Partial non-breeding migration	Partial anadromy	Frequent sampling (dip-net, trap net)	Unknown	Unknown, potentially competition	Kitamura <i>et al.</i> (2006)
Osmeriformes	New Zealand smelt	<i>Retropinna retropinna</i>	Partial non-breeding migration	Partial anadromy	Shore seining	Unknown	Unknown	Northcote & Ward (1984)

TABLE I. Continued

Order	Common name	Latin name	Migratory type	Migratory classification	Evidence for partial migration	Per cent migrants	Proposed ecological mechanism	Reference
Perciformes	White perch	<i>Morone americana</i>	Partial non-breeding migration	Partial semi-anadromy (<i>i.e.</i> migration from fresh water to estuaries)	Otolith microchemistry	High variation between years (0–96)	Food abundance and availability	Kerr <i>et al.</i> (2009)
Pleuronectiformes	Plaice	<i>Pleuronectes platessa</i>	Partial non-breeding migration	Partial oceanodromy	Tag (capture–recapture)	Estimates of > 70 of dispersive contingent	Unknown	Dunn & Pawson (2002)
Salmoniformes	Rainbow trout	<i>Oncorhynchus mykiss</i>	Partial non-breeding migration	Partial anadromy	Frequent sampling (hook and line, gillnets)	56 in this study population	Fecundity and mortality trade-off	Mephee <i>et al.</i> (2007)
Scorpaeniformes	Bear Lake sculpin	<i>Cottus extensus</i>	Partial DVM	Partial potamodromy	Mid-water and bottom trawls	Unknown	Size-dependent physiological differences	Neverman & Wurtsbaugh (1994)
Siluriformes	Spotted sorubim	<i>Pseudoplatystoma cortuscanis</i>	Partial breeding migration	Partial potamodromy	Active and passive telemetry	Unknown	Unknown	Godinho <i>et al.</i> (2007)

DVM, diel vertical migration.

patterns driven by individuals skipping spawning and therefore migration (Chapman *et al.*, 2011b, 2012; Shaw & Levin, 2011). Partial migration can also occur over shorter timescales, as many fishes make diel vertical migrations (DVM) in marine and lacustrine systems (*e.g.* ciscoes *Coregonus* spp. Mehner & Kasprzak, 2011). Here, this is referred to as partial DVM. In a complementary review a thorough taxonomic overview of partial migration in fishes is presented (Chapman *et al.*, 2012); this review simply summarizes the diverse array of species which display partial migration to highlight its general importance as a migratory mode amongst fishes (Table I).

CAUSES OF PARTIAL MIGRATION IN FISHES

The most obvious (and perhaps interesting) question when considering the problem of partial migration is why only some individuals migrate and others stay resident. What are the underlying causes of this phenomenon? This question can be answered on a number of levels: the following section addresses both ultimate and proximate causation, and additionally considers how this kind of migratory polymorphism can be maintained within populations over evolutionary timescales.

STAY OR GO? INDIVIDUAL PHENOTYPIC DIFFERENCES AND THE ECOLOGICAL DRIVERS OF PARTIAL MIGRATION

Fishes migrate to breed, feed and seek refuge from predators. These descriptive categories of migration type, however, are not necessarily useful when assessing the drivers of partial migration in fishes, which often involve trade-offs between multiple factors. Here, a more mechanistic view of the ultimate ecological drivers of partial migration is taken, and what factors shape an individual's 'decision' to migrate are considered. What are the costs and benefits of migration and residency, and what factors are important in determining these? As individuals are the currency of natural selection, understanding what drives differences in individual migratory tendency is paramount and can give clues to the ultimate factors responsible for the evolution of partial migration. In fishes, studies at this level are not common, but recent work has begun to compare migratory and resident phenotypes in order to try and understand which ecological factors promote the evolution of partial migration (Chapman *et al.*, 2011c; Skov *et al.*, 2011). This approach is more common in the study of partial migration in other animal groups, particularly in birds (Nilsson *et al.*, 2011). From the patterns documented in these kinds of studies a variety of hypotheses regarding the ecological factors underpinning the evolution of partial migration have been developed, which are discussed in the following section of this review. Essentially, all are based on that migratory behaviour is an adaptive response to temporally (seasonally and daily) fluctuating resources or predators, and that an individual will attempt to maximize their evolutionary fitness by migrating or remaining resident. Most of these hypotheses have been developed to understand breeding or non-breeding partial migration (where individuals migrate to breed or overwinter respectively), but the same rationale could be equally well applied to partial DVM. In skipped breeding partial migration, residency is thought to be a strategy in years when individuals do not have sufficient energy stores to migrate and also invest in gonad and egg

production, and is hence relatively common in fishes that undertake energetically costly and long-distance spawning migrations, or migrations between marine and fresh water that require the capacity to switch between osmoregulatory modes.

Body size and physiological tolerance

A common observation in partial migration studies in fishes is that migrants and residents differ in body size (ciscoes *Coregonus* spp.: Mehner & Kasprzak, 2011; Bear Lake sculpin *Cottus extensus* Bailey & Bond 1963; Neverman & Wurtsbaugh, 1994; three-spined stickleback *Gasterosteus aculeatus* L. 1758: Kitamura *et al.*, 2006). These differences in size can give clues to the drivers of partial migration, although in some cases they are difficult to interpret as multiple hypotheses can explain why differences in size occur. One example of body size differences between different contingents is in partially anadromous *G. aculeatus*. *Gasterosteus aculeatus* were observed spawning in a freshwater pond, but only a subset of the juveniles migrated out to sea (Kitamura *et al.*, 2006). More detailed analysis of the body length of fish from this population showed a bimodal distribution, with smaller juveniles migrating and larger fish remaining resident. It is likely that smaller individuals migrate to take advantage of the highly productive marine environment to increase their growth rate and are forced to take this risky strategy to maximize future fitness returns. Oceanic migrants often have a much greater growth rate and hence fecundity (for females), and size is also linked to males having a higher competitive ability in foraging and reproductive scenarios. Migration to the marine environment, however, is energetically costly, both in terms of the journey itself and also the physiological changes required to adapt to the saline habitat (Gross, 1987). Hence, this could be an example of a 'best of a bad job' scenario. Evidence in salmonids suggests that metabolic and growth rates can be important in determining which individuals become migrants (Jonsson & Jonsson, 1993). Therefore, body size differences which result in migratory dimorphism could be shaped by intraspecific competitive interactions and be density dependent (the competitive release hypothesis), or alternatively growth rate could be intrinsic, and be a maternally or genetically transmitted trait.

In the broader partial migration literature, especially in studies of non-breeding bird partial migration, it has been shown that body size can have a strong influence upon which individuals migrate, with smaller individuals commonly migrating. A number of interesting hypotheses have been postulated to explain this pattern. First, animals with a larger body size are more physiologically resistant to the cold, and hence residency is less costly to larger individuals (as many birds migrate overwinter to southerly and warmer climes: the thermal tolerance hypothesis: Chapman *et al.*, 2011b). Second, body size differences could also be suggestive of intraspecific competition for food or breeding sites (the competitive release hypothesis: Chapman *et al.*, 2011b, and arrival time hypothesis: Ketterson & Nolan, 1976, respectively). Studies to test these hypotheses in fishes are lacking, and would potentially be of great benefit in identifying more general, cross-taxonomic patterns to explain the phenomenon of partial migration. As previously discussed, the competitive release hypothesis could potentially apply to partial anadromy in *G. aculeatus*. Thermal tolerance may be important in partial DVM, or in habitats where temperatures differ overwinter such as deep lakes and shallow streams. Furthermore, fishes of different body sizes may experience different metabolic consequences at different temperatures (Mehner & Kasprzak, 2011), and so body size variation may reflect individual

variation in physiology. There is some evidence to support this idea for partial DVM in juvenile *C. extensus* (Neverman & Wurtsbaugh, 1994). Within populations of *C. extensus*, juveniles of <30 mm in standard length (L_S) vertically migrate 30–40 m from the bottom of the lake to the epilimnion during the night, whilst larger fish do not migrate into the water column and instead remain resident at the bottom of the lake. Stomach content analysis showed that the function of this migration was not to feed, but potentially instead to utilize the warmer upper waters to increase digestion rate and hence allow juveniles to feed on consecutive days to maximize growth rate (Neverman & Wurtsbaugh, 1994). The authors suggest that adult resident fish, which do not migrate, differ metabolically to juveniles and hence do not benefit in the same way as juveniles from this kind of thermotactic vertical migration. However, this hypothesis remains to be explicitly tested.

Similarly, intrapopulation variation in individuals' physiological tolerance to cope with other environmental extremes such as anoxia may shape patterns of partial winter migration in potamodromous fishes, although this is rarely considered in such studies. The fact that often multiple hypotheses can be suggested to explain the body size differences often evident between fishes of the same species but different migratory strategies highlights the need for carefully planned studies, whereby different hypotheses generate different predictions that can be tested.

Predation risk–growth potential trade-off

The role of predators in shaping patterns of partial migration has been historically neglected. This is at least partly because properly assessing the role of predation in partial migration in fishes is not easy, as predator-induced mortality rates for migrants *v.* residents are very difficult to quantify accurately. A number of recent studies into cyprinid partial migration, however, provide circumstantial evidence that predation may be of key importance in determining which fish within a species migrate and which remain resident. For example, in a cross-population comparison of common bream *Abramis brama* (L. 1758), Skov *et al.* (2011) showed that whether an individual migrated out of shallow Danish lakes into the connecting streams could be predicted by its size-dependent predation vulnerability. Individuals with a high vulnerability of predation risk also had a high probability of migration (Fig. 1). To quantify predation vulnerability the authors calculated what proportion of the piscivorous predators in the lake could prey successfully upon each *A. brama* to generate an individual vulnerability score. This was possible as the predators in this system (pike *Esox lucius* L. 1758) are gape-limited, and gape size can be estimated from an individual's body size. They also collected data from two lakes that differed in the predator size distributions and so each individual *A. brama*'s predation vulnerability score was specific to the predator environment in the lake they inhabited. This cross-population approach made it possible to focus upon size-dependent predation risk *per se* and avoid some of the problems with interpretation of body size effects mentioned in the previous section (*i.e.* that multiple hypotheses can potentially explain why migrants and residents may differ in body size).

Further evidence from individual-based studies that supports the role of predation in shaping the dynamics of partial migration includes a recent study into roach *Rutilus rutilus* (L. 1758) partial migration. In this study, Chapman *et al.* (2011c) showed that migrants and residents differ behaviourally, with migrants exhibiting bolder, more risk-prone behaviour than residents. The authors suggest that this may

FIG. 1. Individual migration propensity ($\square$) and size-specific predation vulnerabilities ($\bullet$) of *Abramis brama* in two Danish lakes: (a) Søgård and (b) Loldrup. Both lakes show the same pattern: predation risk and migratory propensity decrease with increasing total length (L_T) body size. Reproduced with permission from Skov *et al.* (2011).

implicate predation risk as an important factor in partial migration in this species, as bold individuals may migrate overwinter in order to avoid predation when food resources and hence the benefits of residency are reduced.

In both these examples, essentially what drives the polymorphic element of the migratory behaviour of the cyprinids is a trade-off between growth potential (g) and predation risk (p), with resident fishes occupying a relatively high growth, high predation environment during winter and migrants moving to a relatively low growth, low risk habitat (Brönmark *et al.*, 2008). During the winter in the shallow lakes the cyprinids inhabit, food availability is massively decreased compared with the summer, but still remains higher than the streams the migrants occupy. Hence, individuals fleeing predation do so at a cost to their food consumption during winter. This cost is traded off against the benefit of a lower predation risk in the streams (Brönmark *et al.*, 2008). Thus, partial migration can be considered in the same $p:g$ framework developed by Werner & Gilliam (1984) to explain ontogenetic habitat shifts in fishes. In some salmonids, the same $p:g$ trade-off may have explanatory power in explaining patterns of partial anadromy, although the pattern is reversed, with migration being the more perilous strategy. In such cases, migrants to marine environment experience a more profitable food environment, but one which also incurs a higher predation risk, whilst residents encounter lower predation risk and also have lower growth potential. A number of studies show that sea migrants have a higher mortality risk than freshwater residents, although the source of mortality is of course very difficult to infer (Elliot, 1993).

Skipped-breeding partial migration is usually explained by the energetic costs of migration. If individuals cannot afford to migrate and spawn they will remain resident (Rideout *et al.*, 2005). Predation risk, however, may also be important: for example, Norwegian spring-spawning herring *Clupea harengus* L. 1758 face high predation risk at the spawning grounds due to a variety of coastal predators (Fernö *et al.*, 1998).

In addition to partial seasonal migration, a recent longitudinal study over 10 years in a deep German lake has shown that DVM in fishes can also be partial, and populations can be composed of both residents and vertical migrants (Mehner &

Kasprzak, 2011). This study documented partial DVM in two species of freshwater zooplanktivores (*Coregonus* spp.). Migration to the upper hypolimnetic layers results in higher feeding rates, and whilst there is no direct data on differences in predation risk between shallow and deep waters at dusk, the authors showed differences in body size between migrants and residents. One explanation for these differences is that larger fish within species were less vulnerable to predation and could thus take advantage of the more productive feeding habitat, and hence this partial DVM can potentially be explained using the $p:g$ framework. The body size data, however, were from a single sample and in addition size differences were not extreme, and so Mehner & Kasprzak (2011) highlight that this is by no means conclusive evidence of the role of a predation and growth potential trade-off in driving partial DVM. Body size differences between migrant and resident coregonids could also reflect differences in the costs of respiration at different temperature regimes. If smaller fish within a species pay a greater metabolic cost for feeding in warmer waters this may reduce the benefit of migration and hence be an important factor in shaping patterns of partial DVM in these species.

Research into other species also highlights the importance of predation risk in shaping partial migratory patterns in fishes, e.g. bull trout *Salvelinus confluentus* (Suckley 1859) (Monnot *et al.*, 2008); Arctic charr *Salvelinus alpinus* (L. 1758) (Näslund *et al.*, 1993) and also in animals from other taxonomic groups, from water fleas *Daphnia magna* (Hansson & Hylander, 2009) to Canadian elk *Cervus elaphus* (Hebblewhite & Merrill, 2009). In the future, it is likely that many more studies will implicate predation as a key ecological factor in the partial migration of fishes. One notable lacuna from work on predation on fishes is the importance of avian and mammalian predators in shaping fish behaviour. Most studies focus solely upon the importance of piscivorous fish predation (Skov *et al.*, 2010). An important next step will be to factor in the role of endothermic predators to patterns of partial migration in fishes. These predators may be particularly important during winter, when piscivorous fish predation is reduced due to lower temperatures reducing the predator's metabolic rates and hence feeding requirements, whereas ectotherms such as birds and mammals sustain a high predation rate all year round.

Competitive release

Intraspecific competition can also play an important role in driving partial migration in fishes. In environments that have a seasonally limited food resource it might be predicted that competitively inferior individuals would be forced to pay the costs of migration in order to seek new foraging opportunities (known as the competitive release hypothesis: Chapman *et al.*, 2011b). There is some evidence for the role of competition in fish partial migration, but as an individual's competitive ability is difficult to measure usually surrogates such as body condition are used (Näslund *et al.*, 1993). Several studies show a link between body condition and migratory tendency in fishes; for example, within a population of landlocked *S. alpinus*, fish that migrated into streams were found to have a significantly lower body condition than lake residents (Näslund *et al.*, 1993). Furthermore, in an experimental study, *S. alpinus* that were fed reduced rations were more likely to migrate from a northern Swedish lake (Näslund, 1991). These migrations were carried out during the spring months and are thus likely to be feeding migrations. Brodersen *et al.* (2008a) also reported an effect of body condition upon migratory tendency in the cyprinid *R.*

rutilus. By manipulating individual condition *via* enhanced feeding or starvation, they showed that fish with higher body condition scores were more likely to make a winter migration out of shallow lakes into the surrounding streams (Brodersen *et al.*, 2008a). Here, the fish made a winter migration which is thought to function as a refuge migration, with migrants escaping from the high predation risk in the lake over the winter months whilst food availability was low (Brönmark *et al.*, 2008). Thus, fish with a low body condition are thought to be unable to afford to pay the energetic costs of surviving overwinter in the streams and must hence remain in the relatively higher predation lake habitat. In both examples here, fish of low condition were forced into a potentially suboptimal strategy.

More compelling evidence for the role of competition comes from recent work where brown trout *Salmo trutta* L. 1758 were reciprocally transplanted from high-density river sections with low specific-growth rates to low-density sections with high specific-growth rates (Olsson *et al.*, 2006). Fish that were transplanted into high-density conditions behaved similarly to local fish, and exhibited a much higher rate of migration than fish either transplanted to, or originating from, low-density river sections. Laboratory trials also showed that fishes reared under low food conditions were more likely to develop the migratory phenotype (Olsson *et al.*, 2006), a pattern also documented in feeding experiments with *S. alpinus* (Nordeng, 1983). Despite elegantly combining field translocations with laboratory work, the authors could not exclude the influence of predation risk, as migrating fish from the low-density section would have to swim through a lake filled with predators whilst fish from the high-density section did not. It is perfectly plausible that competition and predation act in synergy to shape patterns of partial migration, and future work could address the complexities of wild environments by studying multiple ecological factors simultaneously.

In addition to individual condition, body size has been used as an index of competitive ability. It is important to recognize, however, that within a certain age or size class individual fish can differ in their competitive ability. Recent studies have shown that competitive ability can be a component of a fish's personality (Ward *et al.*, 2004), or that variation can be due to differences in metabolic rate (McCarthy, 2001). Future work could test the role of individual differences in competitive ability and migratory tendency to circumvent more indirect measures such as condition or size. Whilst such studies are undoubtedly logistically demanding, recent work linking animal personality to migratory tendency in fishes suggests that this approach may be rewarding (Chapman *et al.*, 2011c).

Trophic polymorphism and niche shifts

In fishes, there are many examples of resource polymorphism (also known as trophic polymorphism), whereby populations are composed of individuals that specialize upon different food items (Smith & Skúlason, 1996). This form of life history polymorphism has been widely described in *G. aculeatus*, perch *Perca fluviatilis* L. 1758, bluegill sunfish *Lepomis macrochirus* Rafinesque 1819, and many other species, including partial migrants such as *R. rutilus* (Bolnick *et al.*, 2003). If such intrapopulation variation in dietary optima exists in partially migratory populations, and there is also temporal and spatial variation in the abundance or availability of different food types, trophic polymorphism could play a role in partial migration. In other words, individuals that vary in which food items they prefer may

adopt different migratory strategies if the abundance of the preferred prey differs seasonally between two habitats. Trophic niche shifts can also be ontogenetic, and many species go through ontogenetic niche shifts during development (Werner & Gilliam, 1984). Therefore age or size-structured partial migration may also be influenced by trophic polymorphism. This class of explanation for partial migration is known as the trophic polymorphism hypothesis (Chapman *et al.*, 2011b). Whilst this is an intriguing idea, as yet few studies have addressed this. Stable isotopic analyses comparing the diet of migrants and residents could elucidate the importance of resource polymorphism in partially migratory fishes. The scant evidence that is available is suggestive but circumstantial that dietary niche differences may play a role in partial migration. For example, in the coastal partial migrant *Apogon natus* (Houttuyn 1782), migratory fish differed in $\delta^{13}\text{C}$ compared with residents prior to migration, which suggests dietary differences between individuals with divergent migratory strategies (Fukumori *et al.*, 2008).

THE EVOLUTIONARY MAINTENANCE OF PARTIAL MIGRATION

Partial migration is a life-history polymorphism, and can evolve and be maintained when different life-history strategies produce the same lifetime fitness values, or as a result of conditional strategies. In other words, partial migration can be maintained over evolutionary time as either: (1) a frequency dependent evolutionary stable state (ESS), where the two strategies have equal fitness at an equilibrium point or (2) a situation where the best strategy is dependent upon an individual's phenotype (Chapman *et al.*, 2011b). The second scenario is often called a 'conditional strategy' in the partial migration literature (Lundberg, 1988) and occurs when an individual's migratory status is determined by a relatively fixed intrinsic state (*e.g.* age and sex), or a flexible extrinsic state (*e.g.* physical condition and dominance). Conditional migration may also be frequency dependent (as in the former ESS category), if for example migratory behaviour is driven by body condition, and food resources are limited by intraspecific competition. Yet whilst a great deal of the theoretical investigation of partial migration involves ESS models (Lundberg, 1987, Kaitala *et al.*, 1993), there is little empirical evidence for this mechanism from wild studies. Particularly in fishes, individual fitness data are extremely difficult to collect, and few if any studies have attempted to quantify the lifetime fitness of migrants compared to residents. Future studies should attempt to overcome the significant logistical issues surrounding such data collection and address this gap in present knowledge. Conversely, there are many partial migration studies that support the idea that migratory tendency is influenced by individual asymmetries such as sex or age. Many of these studies are on birds, and fewer use fishes as study organisms. For conditional partial migration, migration or residency can evolve as the 'best of a bad job' where fitness balancing between migrants and residents is not required (Lundberg, 1987). This can occur in systems where there is a significant energetic cost to migration, and individuals in poor physiological condition with low energy reserves are forced to remain resident. Some data suggest that this is at least partially the case for *R. rutilus*, as analysis showed that individuals with a low body condition score were less likely to migrate from shallow lakes into the connecting streams for the winter (Brodersen *et al.*, 2008a). In this species, however, the matter is more complicated,

as longitudinal analysis has shown that migratory tendency has both a fixed and a flexible component. It is important to note that in all these cases, fish making the best of a bad job can still be considered as choosing the best strategy to maximize their individual fitness.

NATURE AND NURTURE: THE PROXIMATE CONTROL MECHANISMS OF FISH MIGRATION

The factors which control the proximate expression of migratory status are of great interest in migration biology. Migratory status can be determined by a genetic polymorphism (*i.e.* a set of migratory alleles code for migration or residency), phenotypic plasticity (where migratory status is shaped by the environment), or it can be learnt (Chapman *et al.*, 2011b). Migratory tendency is either obligate, and fixed throughout an individual's lifetime, or facultative and the product of intrinsic or extrinsic factors (Terrill & Able, 1988), or in some cases can have both fixed and flexible components (B. B. Chapman, unpubl. data). If migratory tendency is fixed this is not necessarily the result of a genetic polymorphism: alternatively, early conditions could determine whether an individual is a migrant or a resident *via* the phenotypic canalization of a developmentally plastic trait. This would mean that all fish within a species could potentially be migratory or resident, with migratory status being determined by early life conditions; however, once a fish is either a migrant or a resident the behaviour is relatively fixed. This appears to be the case in white perch *Morone americana* (Gmelin 1789), whereby migratory contingent fish usually originate from early spawned cohorts (Kerr & Secor, 2010). Early spawned fish experience thermal conditions associated with poor food availability and low growth rates, which lead them to adopt a migratory strategy.

Similarly, migratory strategy can be highly plastic, with individual fish switching between migrant and resident in different years (*e.g.* in skipped breeding partial migration: Shaw & Levin, 2011), or migratory behaviour can be learnt. There is no strong empirical evidence for strong genetic determinism in migratory dimorphism in fishes, but rather many recent studies suggest that environmental influences are important (Olsson *et al.*, 2006; Kerr & Secor, 2010; Skov *et al.*, 2010). Recently, a model was proposed which integrates environmental and genetic influences to explain the control mechanisms involved in partial migration (the environmental threshold model: Pulido, 2011). The model states that there is a trait which underlies the expression of the migratory dimorphism (the liability), and a threshold which determines which phenotype is produced. If the liability of an individual is above the threshold an individual will express migratory behaviour. On the other hand, if the liability is lower than the threshold the individual will remain resident (Pulido, 2011). Hence, this model suggests that all individuals within partially migratory populations have the innate propensity to migrate, but just that some have such high threshold values that migratory behaviour is extremely unlikely to be expressed in that individual. This model can be used to address the developmentally canalized migratory behaviour that has been documented in partially anadromous fishes such as Atlantic salmon *Salmo salar* L. 1758, where individuals undergo a major physiological transition to prepare them for oceanic migration. Here, the threshold is essentially a developmental switch-point, following which an individual adopts a migratory or resident phenotype. This model may also have high explanatory power

for the *M. americana* system described above, where early environmental conditions shape an individual's migratory status (Kerr & Secor, 2010), which remains consistent over the fish's entire lifetime (Kerr *et al.*, 2009). The model can also be applied to highly plastic migratory behaviour determined by (for example) current energetic state (Brodersen *et al.*, 2008a). Whilst most evidence to support this model is from laboratory experiments with passerine birds (Pulido *et al.*, 1996), genetic variation in threshold reaction norms for different migratory phenotypes has been reported in *S. salar* (Piche *et al.*, 2008). Less evidence exists for learning as a proximate mechanism for migration in fishes, perhaps at least partly as most research effort is focused upon species with no parental care and demonstrating patterns of learning in the wild is not a straightforward task. Some data, however, hints that learning (also known as entrainment in a migratory context) could play a role in differential migratory behaviour in oceanodromous fishes (Petitgas *et al.*, 2010).

CONSEQUENCES OF PARTIAL MIGRATION IN FISHES

The majority of the analytical work into partial migration in fishes focuses upon the proximate or ultimate causes of variation in migratory tendency. Research into the consequences of partial migration is far rarer, although these are often speculated upon and discussed in the literature. In this section, the evidence for the ecological and evolutionary consequences of migratory dimorphism is reviewed and also potential avenues for future research discussed. Finally, the applied implications of partial migration are addressed, and the argument made that understanding partial migration is critical for the conservation and management of many species, ecosystems and fish stocks.

ECOLOGICAL EFFECTS OF PARTIAL MIGRATION

Partial migration drives spatial and temporal variation in the abundance of organisms and hence may have important ecological consequences, although empirical studies are uncommon. Despite this, theoretical models as well as some empirical work have shown that partial migration can be a powerful force shaping ecosystem dynamics (Hansson *et al.*, 2007; Brodersen *et al.*, 2008b; 2011). These ecological effects can roughly be divided into two categories: nutrient transport and trophic effects. For both, the effect size can be predicted to increase with the proportion of the population that is migratory and the time that the migratory individuals spend away from an ecosystem.

The importance of nutrient transport is well known in anadromous salmonids that transport marine-derived nutrients to freshwater ecosystems (Naiman *et al.*, 2002). This input is mediated through either the death of adult fishes or through egg deposition. Out-migrating fishes, however, also transport freshwater-derived nutrients in the opposite direction. Hence, the net-directional transport cannot necessarily be easily determined based on the type of migration. Whereas nutrient transport has been considered for a number of full migration systems, it has only recently been addressed for partial migration (Swanson *et al.*, 2010). Partial migration leads to a significant (and potentially temporally fluctuating) seasonal flow of nutrients in and out of ecosystems, which may influence ecosystem stability and dynamics. Parallel to

nutrient transport, anadromous fishes can also transport contaminants from marine- to freshwater ecosystems (Swanson & Kidd, 2010); a flux that will increase with the proportion of migratory individuals in the population.

From a trophic ecological point of view, partial migration means that a part of a population within that ecosystem is missing for part of the year (Brodersen *et al.* 2008a). Since many partially migratory fishes can be considered to be either keystone or dominant species, and thereby under normal circumstances have an ecological effect on other species in the ecosystem, it is very likely that the temporal absence of a part of such a population may also affect other species in the ecosystem. The most obvious effects are probably those that act upon the prey of the migratory species (*i.e.* top-down effects), which will experience a decrease in predation risk over the migratory period. For example, the migration of cyprinids from lakes to streams during winter can affect lacustrine plankton dynamics. In a recent study, the proportion of *R. rutilus* migrating overwinter and the timing of migration explained both the size-structure of zooplankton, and the phenology of spring zooplankton and potentially also phytoplankton (Brodersen *et al.*, 2011). This suggests that partial migration in cyprinids may not only have a direct effect upon the prey (zooplankton), but also have cascading effects down the food chain (Brodersen *et al.*, 2008b). In this example, the cascading effects of cyprinid partial migration have been speculated to play a critical role in regulating regime shifts for the entire lake ecosystem between a clear-water and turbid state (Hansson *et al.*, 2007; Brönmark *et al.*, 2010).

In addition to top-down effects and trophic cascades, the consequences of partial migration may transmit up the food chain. For example, the predators of partial migrants are likely to be affected by the seasonal loss of high numbers of prey. This effect, however, may be remediated or even made positive if partially migratory populations can achieve higher population sizes and further, if they migrate during the winter, when the food requirements of poikilothermic piscivorous predators are reduced, as is the case with many cyprinids (Skov *et al.*, 2011). Additional effects may be evident amongst the competitors of partial migrants, as the seasonal absence of a migratory species may lead to a temporary reduction in competition with non-migratory species. Another way in which partial migration can affect community structure is by reducing competition and hence allowing for the coexistence of a competitor. For example, relatively unproductive Arctic lakes can usually only support one large-bodied fish predator (Johnson, 1980). Hence *S. alpinus* only co-occur with lake trout *Salvelinus namaycush* (Walbaum 1792) if their populations are partially migratory, and are hence partially supported by the marine environment.

Predation from shared predators may also increase seasonally on non-migratory species during the absence of migratory species. Predation pressure for competitors may be strongly predicted to increase when predators display a type III functional response and switch diet dependent on relative abundance. Hence for competitors of partially migratory species, a high proportion of migrants can be predicted to lead to a seasonal decrease in competition for food, but to an increased predation pressure. Since the consequences of migration for competitors can be both positive and negative, the net effect cannot be easily predicted.

To summarize, partial migration in fishes may have significant ecological consequences on a number of levels, and it is hopeful that future work, both theoretical and empirical, will address the current lack of information in this area.

EVOLUTIONARY CONSEQUENCES OF PARTIAL MIGRATION

In addition to ecological effects, partial migration also has the potential to have evolutionary consequences, and these are dependent on the type of partial migration that occurs. Breeding partial migration, where migrants breed allopatrically to residents, migrants and residents spawn in geographically distinct areas, and so for this form of partial migration gene flow between migrants and residents has already been reduced, with allopatric spawning acting as a reproductive barrier. As fish of the same species share habitat for a major part of the year, however, this decreases the opportunity for local adaptation and hence reduces the potential for evolutionary divergence compared to allopatric spawning in non-partial migrants. In non-breeding partial migration the opposite may be true. In this form of partial migration, different migratory contingents may experience a differentiated adaptive landscape, leading to different selection pressures for residents and migrants. Such a differentiated adaptive landscape during the migratory period may lead to disruptive selection, where migrants are selected for traits related to migratory travel as well as for traits related to the environmental conditions in the habitat to which the fishes migrate. Whether this leads to assortative mating and population divergence is dependent upon a number of factors. For example, the proximate mechanism underlying migratory tendency plays an important role here. If migratory behaviour is genetically fixed in individuals there would probably be strong disruptive selection to occur in situations where migratory fish within a species experience different environmental conditions during the migratory period compared with residents. If migratory tendency is a phenotypically flexible trait and responsive to environmental conditions [such as is the case for *S. trutta* (Olsson *et al.*, 2006) and *M. americana* (Kerr & Secor, 2011)], this plasticity may decrease the power of disruptive selection.

If disruptive selection does occur, whether this leads to a diversification or in an extreme case an adaptive radiation is dependent upon the degree of assortative mating between migratory and resident fishes, *i.e.* the degree to which migrants are more likely to mate with other migrants as compared with residents. Such assortative mating can be the result of a number of mechanisms. Whilst with this form of partial migration migrants and residents are thought to breed in sympatry, cryptic barriers may still exist within the shared habitat. For example, in lake dwelling *Coregonus* spp., depth gradients in spawning sites are known to facilitate adaptive radiation (Vonlanthen *et al.*, 2008). Also the timing of spawning is likely to influence the degree of assortative mating between residents and migrants. Differences in spawning time between residents and migrants can be the result of a differentiated adaptive landscape for residents and migrants, where migrants are selected for either earlier or later spawning than residents. Alternatively, temporal spawning segregation could occur as a direct eco-physiological result of partial migration, where gonad maturation in one habitat proceeds faster than in the alternative habitat, for example due to differences in temperature or food availability. Lastly, assortative mating between migrants and residents can also be a result of direct mate choice, when residents are more likely to choose to mate with other resident fishes over migrants. In order for behavioural assortative mating to exist, there has to be phenotypic differences between migrants and residents at the time of spawning, which can be either behavioural or morphological.

The evolutionary consequences are thus mainly concerned with spawning segregation and disruptive selection between migrants and residents. For fishes, this

is exemplified in some Alaskan rivers, where anadromous sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) and the resident form (called the kokanee) compose a partially migratory population. Especially in males reproductive success is related to the degree of red skin colouration, where the pigment responsible for the colouration is attained mainly through crustaceans in the diet. Since the diet of the fish in the ocean contains more of the pigment, the resident form has evolved a more efficient use of the pigment. Although the two forms display mating preference for their own form, hybrids exist, but these perform less well and thus there is disruptive selection in the population.

APPLIED IMPLICATIONS OF PARTIAL MIGRATION IN FISHES

Understanding partial migration in fishes is not simply an academic exercise. It also has far-reaching and important applied implications. It is essential to know about a species' movement patterns through space and time to conserve populations, and also diversity within populations. In contrast to the conservationists' desire to keep some fishes in the water, the same species are removed in vast numbers by the fishing industry and also to biomanipulate lakes. Hence understanding partial migration can give clues on when and where to fish, and also what the consequences can be, which should be an important consideration for management decisions.

Species and phenotypic conservation

Maintaining biodiversity is recognized as a major goal globally, as anthropogenic activities have led to a wave of extinctions over recent centuries and at an increasing rate in past decades. Migratory species are especially in danger of population declines, as they rely on multiple habitats to complete their life cycle (Wilcove, 2008). Partial migrants may be buffered against extinction to some degree by the fact that they have multiple contingents of fishes that use different habitats within the same population. Migratory contingents have declined in some species (e.g. *S. confluentus*: Nelson *et al.*, 2002), which can have negative consequences for resident fish of the same species. For example, in years of high water flow the resident contingent of *M. americana*, whilst less productive than the migratory contingent, is thought to play an important role in stabilizing population dynamics in years of poor flow (Kraus & Secor, 2004). In addition, the loss of genetic diversity that would probably follow the loss of a migratory or resident contingent is thought to have adverse effects upon recruitment potential and population recovery (Ryman *et al.*, 1995).

The intraspecific diversity of partial migration can be at threat of being lost if the migratory habitat is degraded, or there are barriers to migration. The maintenance of intraspecific diversity forms part of the 1992 Rio Convention on Biodiversity (Ryman *et al.*, 1995), and so conserving all contingents of partially migratory populations is an important conservation goal. Hence, for situations where different migratory forms derive from the same gene pool, as with *Oncorhynchus mykiss* (Walbaum 1792), management actions should be focused upon the conservation of both forms (in this case both steelhead and rainbow trout). This reasoning is currently not accepted in all fisheries management circles. For example, in 2005 the U.S. National Marine Fisheries Service (NMFS) ruled that steelhead, but not rainbow trout, would be protected under the U.S. Endangered Species Act (NMFS, 2005). It is likely

that a deeper understanding of partial migration in fishes by managers and policy makers will help to avoid such biologically unsound management decisions in the future. Also practical considerations such as constructing effective fish passages to assist migratory fishes to pass man-made barriers such as dams can help preserve intraspecific diversity. It is likely that many partially anadromous and catadromous populations have suffered heavy losses of migratory contingents due to factors such as these, as in the case of white-spotted charr *Salvelinus leucomaenis* (Pallas 1814) (Morita *et al.*, 2000).

Bio-manipulation and lake ecosystem management

Fish migration provides an excellent opportunity for bio-manipulation fishing, *i.e.* where fish of a particular species are removed with the goal of maintaining a clear-water state for freshwater lakes (Hansson *et al.*, 2007). Eutrophic lakes are commonly dominated by zooplanktivorous fishes that reinforce a turbid state by the trophic consequences of zooplanktivory. The removal of zooplanktivores has proven a successful means in attempts to manipulate lakes from a turbid to a clear-water state, where the resulting clear water is upheld by a high piscivore to zooplanktivore ratio and top-down trophic cascades (Carpenter & Kitchell, 1993; Hansson *et al.*, 1998). The removal of unwanted fish types from lakes is, however, often labour intensive and financially costly. Moreover, in shallow European lakes, fish removal often needs to be repeated on a regular basis in order to maintain a permanent clear-water state (Søndergaard *et al.*, 2007). The spatio-temporal nature of fish migrations, where fishes aggregate on migration routes or at destinations, facilitates the efficient capture of focal fishes as they are more easily located and occur in high local densities. For instance, partially migrating *R. rutilus*, small *A. brama* and other zooplanktivorous cyprinids that leave lakes for connected streams over winter could easily be denied return to their lakes in spring, and removed from the system, by simply closing the streams with seines during the return migration period. The efficiency of this procedure assumes a reliable prediction of timing of return migration, which is largely governed by seasonal temperature progression and food availability during spring developments in lakes. This highlights why extensive knowledge of local migratory behaviours is necessary for effective bio-manipulation strategies.

Commercial and recreational fisheries management

The fisheries literature on migratory dimorphism is mostly bereft of the term partial migration, even though many important commercial species have partially migratory populations [*e.g.* *C. haringus* (Ruzzante *et al.*, 2006); cod *Gadus morhua* L. 1758 (Cote *et al.*, 2004); plaice *Pleuronectes platessa* L. 1758 Dunn & Pawson, 2002); shiraou *Salangichthys microdon* (Bleeker 1860) (Arai *et al.*, 2003)]. It is a concept, however, of critical importance in making decisions related to stock management. For example, residents and migrants can have significantly different growth rates and hence, achieve very different body sizes. If large-bodied migrants are overfished and not managed as a separate stock then a high population of unproductive residents may remain, as is the case for migratory brook trout *Salvelinus fontinalis* (Mitchill 1814) in Lake Superior (Schreiner *et al.*, 2004; Sherwood & Grabowski, 2010). Of course this is also dependent upon the proximate mechanisms that drive partial migration. In an interesting discussion of *C. harengus* stock management issues, Ruzzante *et al.*

(2006) argue that population sustainability, resistance to disturbance and potentially even the capacity to recover from low abundances following environmental change or climatic extremes can be negatively affected by the generalized management of diverse stocks. As many partial migrants are exploited, it is clearly of major importance to properly assess biological management units that take into account within-population migratory polymorphism. More research into the importance of population structure and life-history diversity in population persistence and rebuilding would be valuable, not least as this may explain why the recovery of collapsed stocks takes longer than many theoretical models predict.

Finally, any process which involves removing parts of populations (as in the harvesting of natural resources such as commercial or recreational fisheries and also biomanipulation) can be selective with consequences for community or population composition (Darimont *et al.*, 2009; Jorgensen *et al.*, 2009; Matsumura *et al.*, 2011). Hence, if migrants are more likely to be removed than residents, this can, for example, influence sex ratios if one sex dominates the migratory contingent, or age structure if migrants are from a certain age class. In other words, fishing out only migrating individuals could extensively reduce both phenotypic and genotypic diversity in partially migratory fish populations, with conservation and diversity issues at stake.

FUTURE DIRECTIONS, CHALLENGES AND OPPORTUNITIES

Partial migration is widespread amongst fishes (Table I; Chapman *et al.*, 2012). It is a fascinating field of enquiry on many levels, and has thrived as a research area in recent years. Many interesting, exciting and relevant research questions require more attention in the future. For example, techniques have advanced such that questions can be asked about migratory behaviour on a new frontier, and the ecology of individuals addressed. A growing interest in individual variation is not limited to migration biology, but has also received a great deal of recent attention in other fields such as behavioural and foraging ecology (Bolnick *et al.*, 2003; Sih *et al.*, 2004). Studies analysing individual patterns of migration or residency will probably shed light on the ultimate ecological factors involved in the evolution of partial migration in fishes. Additionally, few studies have sought to understand the synergies between different forms of alternative life-history strategies (*e.g.* trophic polymorphism and alternative reproductive tactics) and partial migration (with the exception of salmonids).

A focus upon certain taxonomic groups has given many insights into partial migration in fishes, however, many groups are poorly studied, and future work should address this to give a more complete taxonomic picture of the distribution of partial migration across genera and families (Chapman *et al.*, 2012). This will allow for phylogenetic analyses to assess the evolutionary origins of this phenomenon. A critical and contemporary question is how human activities have affected the dynamics of partial migration; for example, in the exploitation of fish stocks and climate change. Some work has begun in this area: Theriault *et al.* (2008) present a theoretical model of how human harvesting of partially anadromous *S. fontinalis* can have evolutionary effects on the migration reaction norm, with increasing harvesting rate reducing the probability of migration (with obvious consequences for fisheries and population productivity). Processes such as eutrophication within freshwater systems may result in increases in residency for partially anadromous species (Gross, 1987), just

as eutrophication in saline habitats such as the Baltic Sea may lead to increases in migratory contingents. Future changes in temperature *via* global warming may lead to changes in individual growth rate, which may be important in shaping individual decisions to migrate.

To assist researchers in the quest to understand the puzzle of partial migration, there are many opportunities. Technologies to track fishes are cheaper and smaller and more effective each year. In the future scientists can look forward to datasets potentially at the scale of entire populations. New molecular techniques are developed that allow finer and finer detail in the genetic mechanisms of many phenotypic traits to be understood. Finally, in potamodromous migrations, there is the possibility to manipulate whole ecosystems, and replicate at the lake and stream level. Whilst logistically challenging, these kinds of studies can offer unique insights into natural processes (Carpenter *et al.*, 2011).

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