REVIEW

Physiological and genetic basis for variation in migratory behavior in the three-spined stickleback, *Gasterosteus aculeatus*

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Abstract Closely related species of fish often exhibit different migration patterns. Even within species, anadromous and resident populations can be found in a diverse number of taxa. Although several environmental factors that regulate behavioral and physiological changes associated with fish migration have been identified, the genetic mechanisms underlying the variation in the ability to respond to these environmental cues in fishes that show different migratory behaviors are not well known. The three-spined stickleback *Gasterosteus aculeatus* (Linnaeus 1758) is a good model system for elucidation of the genetic basis for variation in migratory behaviors and other physiological changes associated with migration. First, the three-spined stickleback exhibits great inter-population variation in migration patterns. Second, genetic and genomic tools are now available for studying this species. In the present study, variation in the migration patterns among *G. aculeatus* populations and the recent progress in our understanding of the genetic and physiological basis for variation in traits important for *G. aculeatus* migration are reviewed.

Keywords *Gasterosteus aculeatus* · Anadromy · Partial migration · Genomics · Hormone

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Introduction

Fishes exhibit great diversity in their migration patterns (McKeown 1984; McDowall 1988; Dodson 1997; Hendry and Stearns 2004). Migration has both advantages and disadvantages. Advantages include optimal foraging, avoidance of unfavorable environments, and increased reproductive output, while disadvantages include energetic costs, osmoregulatory shocks, and increased predation (McKeown 1984; McDowall 1988; Dodson 1997; Hendry and Stearns 2004). Optimal trade-offs between benefits and costs may differ between environments and can lead to diversity in migratory behaviors. For example, anadromy is more common in temperate regions, while catadromy is more common in tropical regions (Gross et al. 1988). This pattern can be explained by the difference in productivity between freshwater and marine environments, with oceans being more productive than freshwater environments in temperate regions and vice versa in tropical regions. When there are two or more optimal strategies, alternative life histories with different migration patterns can evolve within populations (Gross 1985; Chapman et al. 2011). Compared to the theoretical and ecological studies on the driving forces of diverse migratory behaviors (Gross 1985, 1997; Dodson 1997; Hendry and Stearns 2004), surprisingly little is known about the genetic mechanisms underlying variation in migratory behaviors.

Diadromous migration comprises multiple behavioral traits (Hoar 1958, 1976; McKeown 1984; Quinn 2005), including salinity preference (Baggerman 1957; Houston 1957; McInerney 1964; Iwata et al. 1986), response to water current (rheotaxis) (Hensleigh and Hendry 1998), response to light (Hoar et al. 1957), response to overhead cover (Kemp et al. 2005), and magnetoreception (Quinn 2005). Divergence in some of these behavioral traits has

been observed among closely related species of several taxa, including *Oncorhynchus* (Hoar et al. 1957; Houston 1957; Hoar 1958; Taylor and McPhail 1985; Hutchinson and Iwata 1997) and Gasterosteidae (Audet et al. 1985). These behavioral traits are usually regulated by environmental factors, such as photoperiod and temperature, internal factors, such as hormones, and their interactions (McKeown 1984; Iwata 1995; McCormick 2001; Ramenofsky and Wingfield 2007). Therefore, elucidation of the genetic mechanisms by which the endocrine system of migratory and non-migratory species responds differently to environmental cues is indispensable for a better understanding of the genetic and molecular mechanisms underlying the variation in diadromous migration.

The three-spined sticklebacks *Gasterosteus aculeatus* (Linnaeus 1758) provides a good model system for understanding the genetic mechanisms underlying variation in migratory behaviors (Fig. 1). First, tremendous diversification of *G. aculeatus* in the last few million years has resulted in the evolution of phenotypically and ecologically divergent forms, which can often exhibit different migration patterns (Wootton 1976, 1984; Bell and Foster 1994; McKinnon and Rundle 2002; Östlund-Nilsson et al. 2007). Second, genetic and genomic tools, such as linkage maps, whole-genome sequencing, microarrays, single-nucleotide polymorphism (SNP) arrays, restriction-site-associated DNA sequencing (sequenced RAD), and transgenics are available for studying *G. aculeatus* (Hosemann et al. 2004; Peichel 2005; Cresko et al. 2006; Kingsley and Peichel 2007; Geoghegan et al. 2008; Kitano et al. 2009, 2010; Leder et al. 2009; Chan et al. 2010; Hohenlohe et al. 2010; Jones et al. 2012a, b). Recent genetic studies have elucidated molecular mechanisms underlying morphological divergence between anadromous and freshwater-resident forms of *G. aculeatus* (Shapiro et al. 2004; Colosimo et al. 2005; Miller et al. 2007; Chan et al. 2010). However, little is known about the genetic and molecular mechanisms underlying variation in behavioral and physiological traits involved in fish migration or the photoperiodic response of the endocrinological system in *G. aculeatus*. This study reviews variation in migratory behaviors among and within *G. aculeatus* populations and recent progress in the genetic and genomic studies on the physiological divergence between anadromous and freshwater-resident *G. aculeatus*.

Diversity of migration in *Gasterosteus aculeatus*

Substantial variation in migration patterns exist among *Gasterosteus aculeatus* populations. First, the *G. aculeatus* species complex includes both anadromous and freshwater-resident forms of *G. aculeatus* (Bell and Foster 1994; McKinnon and Rundle 2002). The ancestral forms of

Fig. 1 Pictures of anadromous (*upper panel*) and stream-resident forms (*lower panel*) of *Gasterosteus aculeatus*

G. aculeatus are considered anadromous, whereas freshwater-resident forms have evolved independently from the anadromous forms in multiple lineages (Haglund et al. 1992; Orti et al. 1994; Taylor and McPhail 1999, 2000; McKinnon et al. 2004; Colosimo et al. 2005). The anadromous forms of *G. aculeatus* usually migrate to freshwater or estuaries in spring (Table 1), while juveniles migrate to the sea in fall (Table 2), although there are substantial variation in the timing of migration (Tables 1, 2). Interestingly, the timing of spawning migration tends to be earlier in populations at lower latitudes than in populations at higher latitudes (Table 1). Although we did not see any clear latitudinal trends of the timing of juvenile migration, the Japan Sea forms likely descend earlier than the Pacific Ocean forms in Japan (Kume and Kitamura 2003; Table 2). Variation also exists in the offshore distance during migration among anadromous *G. aculeatus* populations (Table 3), but the precise migratory routes in marine environments have not been systematically investigated.

Freshwater-resident forms are sometimes completely landlocked and never come in contact with the anadromous forms (Fig. 2a). In other cases, habitats of freshwater-resident forms are connected to the sea; when anadromous

Table 1 Variation in the timing of upstream migration between anadromous populations

Population	Month	Latitude	References
Japan Sea form from Nagata River, Japan	Apr.	34	Amaoka and Haruta (1972)
Japan Sea form from Mimi River, Japan	Mar.–Apr.	35.6	Mori, pers. obs.
Japan Sea form from Kuriyama River, Japan	Feb.–Apr.	36	Kume (2008)
Japan Sea form from Kahoku Lagoon, Japan	Mar.–Apr.	36.6	Mori (1987)
Japan Sea form from Niigata, Japan	Feb.–Mar.	38	Ikeda (1937)
Japan Sea form from Mogami River, Japan	Mar.–May	39	Mori, pers. obs.
Japan Sea form from Oga Peninsula, Japan	Apr.–May	40	Mori, pers. obs.
Japan Sea form from Lake Ogawara, Japan	Apr.–May	40.8	Katayama et al. (2000)
Pacific Ocean form from Akkeshi, Japan	Apr.–May	43	Kume and Kitamura (2003), Kume et al. (2005)
Japan Sea form from Akkeshi, Japan	Apr.–May	43	Kume and Kitamura (2003), Kume et al. (2005)
Little Campbell River in British Columbia, Canada	June–July	49	Hagen (1967)
Långskär and Vindskär Bays in Baltic Sea, Finland	May–July	60	Candolin and Voigt (2003)

Table 2 Variation in the timing of seaward migration between anadromous populations

Population	Month	Latitude	References
Japan Sea form from Lake Shibayama, Japan	June–July	36.3	Mori, pers. obs.
Japan Sea form from Lake Kahoku, Japan	June–July	36.6	Mori, pers. obs.
Navarro River in California, USA	Sep.	39	Snyder and Dingle (1989)
Japan Sea form from Lake Ogawara, Japan	July	40.8	Katayama et al. (2000)
Japan Sea form from Akkeshi, Japan	July–Aug.	43	Kume and Kitamura (2003)
Japan Sea form from Biwase, Japan	July–Aug.	43	Kume and Mori (2009)
Pacific Ocean form from Akkeshi, Japan	Nov.–Dec.	43	Kume and Kitamura (2003), Kitamura et al. (2006)
Duwamish estuary, Washington, USA	Sep.	47.5	Kitano, pers. obs.
Shilshole Bay, Washington, USA	Sep.	47.6	Kitano, pers. obs.
Island of Tholen and Yerseke, The Netherlands	July	51.5	van Mullen and van der Vlugt (1964)
England	Oct.	52	Craig-Bennett (1931)
Northern Germany	Sep.	53.5	Leiner (1930)

Table 3 Records of *Gasterosteus aculeatus* caught at sea

Collection site	Distance from the nearest land (km)	Season	Depth (m)	References
North Atlantic Ocean	145–160	Dec.–Jan.	221–232	Jones and John (1978)
North Pacific Ocean	<945	May–Oct.	36–127	Quinn and Light (1989)
Bay of Fundy	<100	Winter	<0.18	Williams and Delbeek (1989)
New York Bright	<110	May–July	<2	Cowen and Chiarella (1991)
North Pacific Ocean, Bering Sea, Okhotsk Sea	>22	ND	ND	Morita et al. (2009)

ND not described

forms migrate to spawning sites in the coastal regions, their spawning sites overlap with those of the resident forms (Fig. 2b). Although the extent of gene flow between anadromous and resident forms varies according to the geography of the location, anadromous and resident forms are often reproductively isolated and genetically differentiated because of multiple isolating barriers, including ecogeographical isolation (Hagen 1967), temporal isolation (Hagen 1967), sexual isolation (Hay and McPhail 1975; McKinnon et al. 2004), and postzygotic isolation against hybrids (Jones et al. 2006, 2008).

Partial anadromous migration (i.e., part of a population migrates, while the other part does not) is also found in Japanese lakes. At least two lake populations, Lake
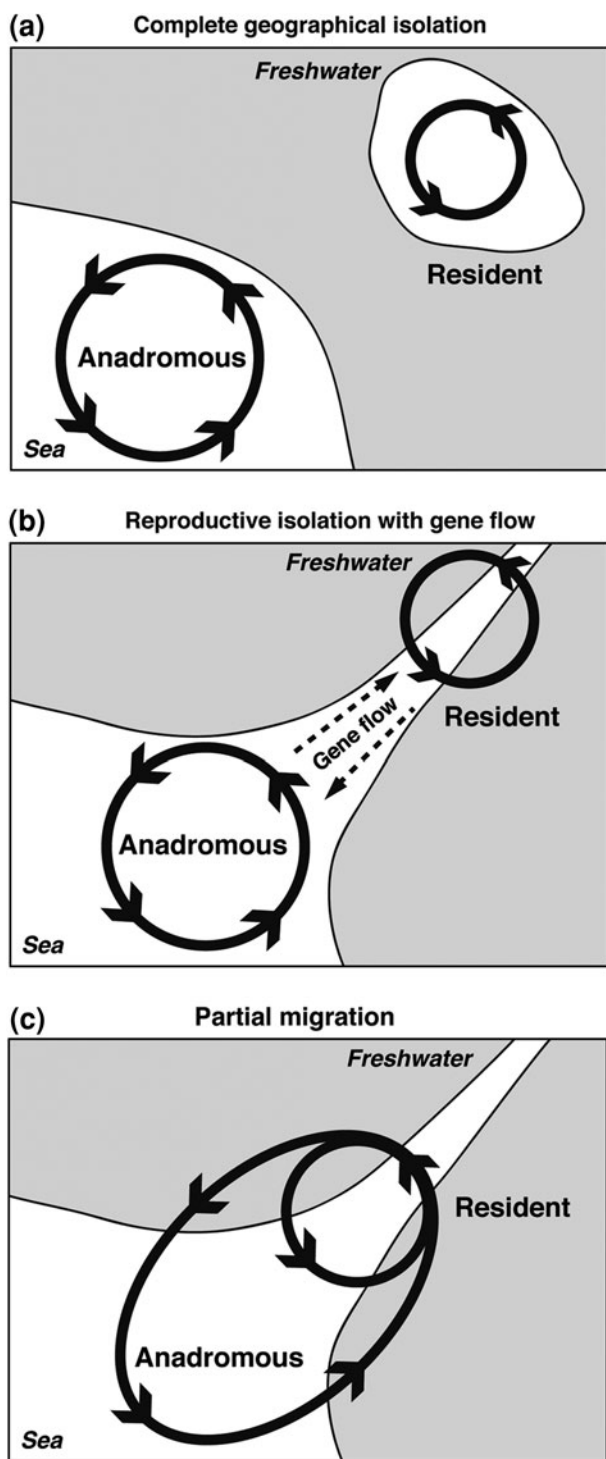
Fig. 2 **a** Complete geographical isolation between anadromous and resident forms. **b** Reproductive isolation with various levels of gene flow between anadromous and resident forms. **c** Polymorphism of anadromy and residency within a population

Harutori, and Lake Hyotan populations, exhibit polymorphism of anadromy and residency (Fig. 2c) (Mori 1990; Kitamura et al. 2006). No significant genetic differentiation in nuclear markers has been observed between the

anadromous and resident forms in these two lakes (Higuchi et al. 1996; Kitano et al. 2007; Ishikawa and Kitano, unpublished data). Early growth rate may determine the migratory fate of each fish, as in the Atlantic salmon (Jones 1959; Hutchings and Myers 1994), because juvenile *G. aculeatus* descending a river are smaller than the juvenile *G. aculeatus* that remain in a pond (Kitamura et al. 2006). Populations that show partial migration are particularly suitable for investigating the genetic basis of migratory behavior, because such polymorphic populations maintain genetic variation in traits important for both migration and residency (Berthold 1993; Pulido 2011).

Physiological basis for stickleback migration

Several physiological and behavioral traits important for anadromous migration diverge between anadromous and resident forms (Table 4). Divergence in salinity preference may contribute to the divergence in migratory behaviors. Other traits related to migration, such as metabolic rate, swimming endurance, and osmoregulation, also diverge between anadromous and resident forms. The expression of these traits is regulated by hormones (Table 5). Thyroid hormone signaling pathways are one of the most extensively characterized systems that have been compared between anadromous and resident forms (Fig. 3). Anadromous forms have higher plasma thyroxine and triiodothyronine levels than resident forms (Kitano et al. 2010). Thyroid hormone increases the metabolic rate and swimming activity in *Gasterosteus aculeatus* (Gutz 1970; Kitano et al. 2010). Therefore, higher thyroid hormone levels may be adaptive for longer distance migration in anadromous forms; such migrations require more energy than that required by resident forms. Importantly, thyroid hormone not only regulates swimming activity (Kitano et al. 2010), but also salinity preference behavior (Baggerman 1957). Although thyroid hormones do not exhibit photoperiodic changes in either anadromous or resident forms, mRNA expression levels of the thyroid stimulating hormone-$\beta2$ (*TSH$\beta2$*) in the pituitary gland exhibit striking photoperiodic changes only in anadromous forms (Kitano et al. 2010). Because TSH regulates the synthesis and release of thyroid hormones in thyroid gland, and the sensitivity of thyroid hormones in peripheral tissues (Wu et al. 1985), thyroid hormone signaling pathways may be an important regulator of migratory behavior in *G. aculeatus*.

The genetic basis for divergence in thyroid hormone signaling pathways between anadromous and resident forms has also been investigated. Pyrosequencing of *TSH$\beta2$* transcripts in hybrids between anadromous and resident forms revealed that divergence in the *cis*-regulatory regions of the *TSH$\beta2$* gene can partially explain the

Table 4 Physiological and behavioral divergence between migratory and resident ecotypes

Trait	Divergence	Environmental regulator	Genetic basis	References
Physiology				
Seawater tolerance	High in migratory	Season, temperature	ND	Koch and Heuts (1943), Heuts (1946, 1947), Gutz (1970)
Freshwater tolerance	High in resident	Photoperiod	ND	Koch and Heuts (1943), Heuts (1947), Lam and Hoar (1967), Lam and Leatherland (1969a, 1970), Honma (1975)
Oxygen consumption rate	High in migratory	Photoperiod	Yes	Gutz (1970), Tudorache et al. (2007), Kitano et al. (2010)
Behavior				
Salinity preference	ND	Photoperiod, temperature	ND	Baggerman (1957), Audet et al. (1986a, b)
Swimming endurance	High in migratory	ND	ND	Taylor and McPhail (1986), Schaarschmidt and Jürss (2003), Tudorache et al. (2007)

Table 5 Hormones that can regulate traits important for stickleback migration

| Hormone	Function	Environmental regulator	Divergence	References
Thyroid hormone	Salinity preference Salinity tolerance Metabolic rate Swimming activity Reproduction	Photoperiod, season, salinity	High plasma levels in migratory form	Koch and Heuts (1942), Baggerman (1957), Ahsan and Hoar (1963), Gutz (1970), Leatherland (1970b), Honma (1975), Honma et al. (1976, 1977), Bernhardt and von Hippel (2008), Kitano et al. (2010)
Prolactin	Freshwater adaptation Salinity preference	Season, photoperiod, plasma Ca^{2+} levels, plasma Mg^{2+} levels	Slower and smaller response to changes in salinity and season in resident form	Lam and Hoar (1967), Lam (1968, 1969a, b), Lam and Leatherland (1969a, b, 1970), Leatherland and Lam (1969), Leatherland (1970a), Benjamin and Ireland (1974), Wendelaar Bonga and Veenhuis (1974), Honma et al. (1976), Wendelaar Bonga (1976, 1978, 1980), Wendelaar Bonga and Greven (1978), Benjamin (1980), Audet et al. (1985)
Cortisol	Salinity preference	Photoperiod	ND	Audet et al. (1985, 1986b)
Growth hormone	ND	Season	ND	Leatherland (1970b), Benjamin (1980)
ACTH	Freshwater tolerance	Season, salinity	ND	Lam and Leatherland (1970), Leatherland (1970a), Benjamin and Ireland (1974), Honma et al. (1976), Benjamin (1980)

ND not determined
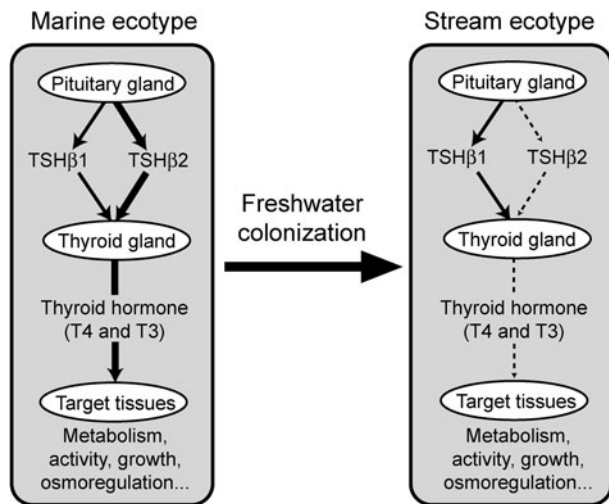
Fig. 3 Schema of thyroid hormone signaling pathways in anadromous and resident forms of three-spined sticklebacks

differential expression of *TSHβ2* (Kitano et al. 2010). In addition, a signature of divergent selection was also observed at the *TSHβ2* locus: most anadromous forms from multiple geographical regions have one type of allele, whereas most stream-resident forms have another type of allele (Kitano et al. 2010). A similar signature of divergent selection was observed at the ectodysplasin (*Eda*) and the kit ligand (*kitlg*) genes, which are responsible for repeated evolution of the low-armored phenotype (Colosimo et al. 2005) and reduced pigmentation (Miller et al. 2007), respectively, in freshwater-resident forms of *G. aculeatus*. The *TSHβ2*, *Eda*, and *kitlg* genes are located on different chromosomes. Therefore, divergent natural selection acted on various chromosomal regions leading to parallel evolution of multiple phenotypic traits.

The signaling pathways of other hormones may also diverge between migratory and resident forms. For example, prolactin is important for freshwater adaptation; injections of prolactin increase the survival rate of anadromous forms in fresh water (Lam 1968; Lam and Leatherland 1969a, 1970). Prolactin regulates the osmotic influx of water in isolated gills (Lam 1969a) and structural changes in the kidney (Lam and Leatherland 1969b; Wendelaar Bonga and Veenhuis 1974; Wendelaar Bonga 1976) in anadromous forms. Other hormones, such as gonadal steroids, also play important roles in migration, such as in the migration of eels (Lokman et al. 1998; Lokman and Young 1998; Sudo et al. 2011) and salmonids (Munakata et al. 2001, 2002). However, divergence in the signalling pathways of prolactin or gonadal steroids between anadromous and freshwater-resident forms has not yet been characterized, but it should be investigated in the future.

The future of physiological genomics of fish migration

Studies on *TSHβ2* demonstrate that the search for a genomic signature of divergent selection between different migratory forms will be useful for identifying the candidate genes important for divergence in migratory behaviors (Fig. 4a). By using microsatellite markers, divergent loci between anadromous and freshwater forms, including genes potentially important for physiological adaptation, have been identified (Mäkinen et al. 2008; DeFaveri et al. 2011; Shimada et al. 2011). Recent progress in next-generation sequencers is making it possible to find an increasing number of genetic markers at relatively low costs (Hudson 2008; Stapley et al. 2010; Davey et al. 2011; Elmer and Meyer 2011). For example, SNP analysis with sequenced RAD is a powerful method to identify a signature of divergent selection (Baird et al. 2008; Hohenlohe et al. 2010; Roesti et al. 2012). Because the genome sequences of *Gasterosteus aculeatus* are relatively small (<450 Mb) and the reference genome sequence is available (Kingsley and Peichel 2007; Jones et al. 2012b), whole-genome re-sequencing of *G. aculeatus* is relatively easy by using next-generation sequencers (Jones et al. 2012b). The presence of multiple phylogenetically independent pairs of anadromous and freshwater-resident sticklebacks provide us great opportunities to scan the genome for regions that contribute to the repeated evolution of adaptive traits importance for freshwater residency (Jones et al. 2012a, b; Elmer and Meyer 2011).

Studies on *TSHβ2* also demonstrate that transcriptome analysis will be useful in identifying genes potentially involved in the initial switch to migration (Fig. 4b). Transcriptomic studies of salmon migration have been extensively conducted (Aubin-Horth et al. 2005, 2009; Giger et al. 2006; Bernier et al. 2008; Miller et al. 2009, 2011; Seear et al. 2010). Microarrays of *G. aculeatus*, which have been used to investigate the effects of endocrine disruptors (Geoghegan et al. 2008; Williams et al. 2009; Katsiadakia et al. 2010), sex-biased gene expression (Leder et al. 2010), the transcriptomic response to predators (Sanogo et al. 2011), comparison of gill transcripts between anadromous and stream-resident forms (Kitano et al. 2010), and comparison of testis transcripts between incipient species (Kitano et al. 2011), are also useful for transcriptome analyses of divergent migratory forms of *G. aculeatus* at various migratory stages.

Quantitative trait loci (QTL) mapping, performed for *Oncorhynchus mykiss* (Walbaum 1792) (Nichols et al. 2008), is also useful in identifying the genomic regions responsible for divergence in behavioral traits and photoperiodic response between migratory and resident forms of *G. aculeatus* (Fig. 4c). *Gasterosteus aculeatus* is a suitable model system for QTL mapping because its body size,
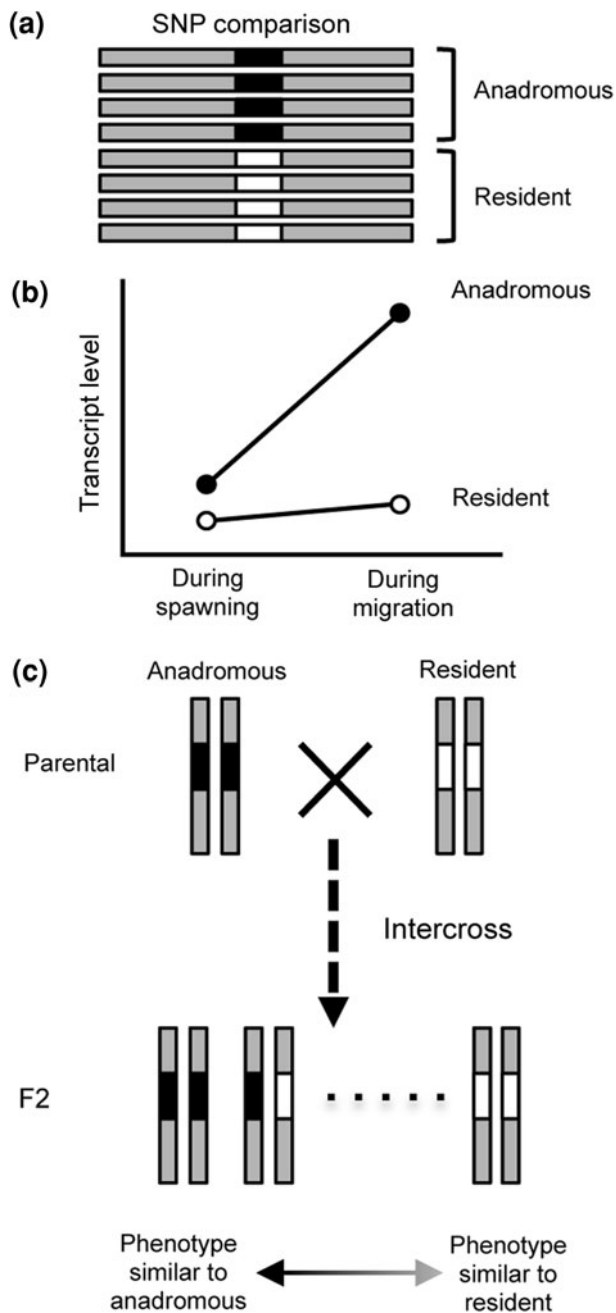
Fig. 4 Genomic studies of divergence in migratory behaviors. a Genome scan analysis can reveal chromosomal regions that repeatedly diverge between multiple anadromous and resident populations. b Transcriptome analysis can reveal genes that exhibit expression difference in accordance with seasonal migration in anadromous forms, but not in resident forms. c QTL mapping using an intercross between an anadromous form and a resident form can reveal chromosomal regions that explain phenotypic variation in traits important for seasonal migration

genome size, and generation time are smaller than those of salmonids. QTL mapping of several morphological and behavioral traits has been successfully performed for *G. aculeatus* (Peichel et al. 2001; Colosimo et al. 2004,

2005; Cresko et al. 2004; Shapiro et al. 2004; Albert et al. 2008; Kitano et al. 2009; Greenwood et al. 2011).

Finally, it should be noted that rapid advances in next-generation sequencers are making it possible to obtain a large amount of sequence data, even for non-model organisms (Hudson 2008; Stapley et al. 2010; Davey et al. 2011; Elmer and Meyer 2011). Therefore, the gap between model and non-model organisms is becoming increasingly blurred. Next-generation sequencers would facilitate genome scan analyses by using sequenced RAD (Baird et al. 2008; Hohenlohe et al. 2010; Rowe et al. 2011; Roesti et al. 2012) and transcriptome analyses by RNA-sequencing in non-model organisms (Vera et al. 2008). Applications of such genomic tools to non-model organisms that exhibit diverse migratory behaviors will enable us to elucidate whether the same sets of genes are important in the divergence of migratory behaviors across diverse taxa.

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