MOLECULAR ECOLOGY

Molecular Ecology (2017) **26**, 413–419 doi: 10.1111/mec.13941

Recipient of the 2016 *Molecular Ecology* Prize: Louis Bernatchez – advancing the conservation of aquatic resources with his contributions on the ecological genomics of adaptation and speciation

Louis Bernatchez, professor and holder of Canadian Research Chair in Genomics and Conservation of Aquatic Resources at Université Laval, Québec City, Québec, Canada, is the Molecular Ecology Prize winner of 2016. As long-standing collaborators, friends and, in the case of one of us (SMR), student of Louis Bernatchez, we can only applaud this as an exceptionally good choice. For three decades, Louis has represented a Herculean scientific force influencing and shaping the field of molecular ecology and there are definitely no signs that this should not continue. He was a pioneer in the early days of phylogeography, a pioneer in applying functional genomics to the study of nonmodel organisms and is currently a pioneer in population genomics and its integration into a holistic framework, encompassing physiological, life history and population historical components of adaptation. His study organisms cover a wide taxonomic span from marine invertebrates, birds and mammals to fishes, but with the latter being the most important in his research. Louis runs a big research group and is immensely productive, with more than 375 published papers at the time of writing and a continuing trend of strong growth. This staggering productivity is matched by an impressive flow of talented graduate students, postdocs and research professionals who have worked in his laboratory. Louis clearly inspires his students to continue in the field, with the majority of his graduates pursuing successful careers in related science fields. In fact, well over 100 highly qualified personnel have moved on from the Bernatchez Lab, with over 20% now working as professors/instructors worldwide in eight different countries. The field of molecular ecology is in good hands considering this extensive and impressive training.

It is simply impossible to do justice to all the excellent contributions that have come out of Louis' laboratory, so in addition to a more formal biographical sketch, we decided to focus on three main themes: his early contributions to our understanding of the phylogeography of freshwater fishes, his long-standing research programme in understanding the mechanisms of adaptive divergence in dwarf and normal-sized lake whitefish *(Coregonus clupeaformis)* and his research into

genetic structure and adaptive responses in panmictic Atlantic eels (*Anguilla rostrata* and *A. anguilla*). This has been a hard choice and for instance leaves out highly substantial contributions towards understanding adaptive divergence and genetic structure of such important species as Atlantic salmon (*Salmo salar*) and brook char (*Salvelinus fontinalis*) (Castric & Bernatchez 2003; Fraser *et al.* 2004; Fraser & Bernatchez 2005a,b; Garant *et al.* 2005; Roberge *et al.* 2007; Dionne *et al.* 2008, 2009; Gauthier-Ouellet *et al.* 2009; Bougas *et al.* 2013; Bourret *et al.* 2013, 2014; Moore *et al.* 2014; Ferchaud *et al.* 2016) and several important contributions to conservation biology (Fraser & Bernatchez 2001, 2005a; Fraser *et al.* 2004; Lippé *et al.* 2006; Roberge *et al.* 2006, 2008; Milot *et al.* 2007; Marie *et al.* 2010, 2012; April *et al.* 2011; Lamaze *et al.* 2012, 2013; Valiquette *et al.* 2014; Bernatchez 2016). Overall, Louis' passion and dedication to the genetic conservation of aquatic resources has significantly advanced these fields, such that the notions of genetic health and evolutionary adaptive potential are synonymous with his achievements in all of these areas.

Curriculum

Louis Bernatchez obtained his PhD in 1990 at Université Laval, Québec City, Quebec, Canada, in 1990 with Prof. Julian Dodson as supervisor. Whereas most of his Ph.D. work concerned the phylogeography of salmonid fishes,

it is interesting to note that his very first paper focused on the bioenergetics of fishes (Bernatchez & Dodson 1985), a theme he has later revisited in his pursuit of understanding adaptive divergence of sympatric lake whitefish species pairs (Dalziel *et al.* 2015). From 1990 to 1991, he was a postdoc at Université Montpellier II, France, in the laboratory of Prof. Francois Bonhomme and from 1991 to 1992 a postdoc at the University of Guelph, Canada, collaborating with Profs. Moira Ferguson and Roy Danzmann. From 1992 to 1995, he was first a research associate and subsequently assistant professor at the Université du Québec (INRS). Finally, in 1995 he returned to Université Laval to continue his curriculum and became full professor in 2004 and since 2006 holder of a Canadian Research Chair in Genomics and Conservation of Aquatic Resources. In between he has been a visiting scientist at the University of Brisbane, Queensland, Australia (2000–2001), and the University of Konstanz, Germany (2002). He has received numerous awards; in addition to his Canadian Research Chair, some highlights include the E.W.R. Steacie Award from NSERC (2002), elected member of the Royal Society of Canada (2011), elected Fellow of the American Association for the Advancement of Science (2011), the Prix du Québec, Marie-Victorin (2012) and invited membership of FacultyRow's Super Professors (2013). This year he has also been elected into the Hall of Excellence, Genetics Section, American Fisheries Society

Louis has done extensive services to the scientific community, and many readers will have been in contact with him in his editorial capacities. Among others, he has previously been Associate Editor of Evolution and Journal of Evolutionary Biology. He currently serves as Reviews Editor of Molecular Ecology and Editor-in-Chief of Evolutionary Applications and is a key force behind the success of both journals. It is characteristic for Louis' editorial work that he maintains a deep respect for the submissions he handles, understanding that behind many manuscripts lie a motivated student who may be experiencing the peer review process for the first time. His capacity to foresee the future of the field has resulted in *Molecular Ecology* reviews having extremely high citations for the journal.

Phylogeography of salmonid fishes

Louis Bernatchez' early research career coincided with the rise of phylogeography as a research field (Avise *et al.* 1987). It was an obvious question to ask whether the remarkable phenotypic and ecological diversity observed in salmonid fishes and freshwater fishes in general could reflect circumstances of phylogeographical history. Some of the first papers focused on lake whitefish, where phylogeography seems to play an important – but not sole – role in the occurrence of sympatric morphs (Bernatchez & Dodson 1990), and where intriguing patterns of postglacial recolonization were revealed, encompassing four distinct lineages from different refugia and a contact zone between a local lineage and a Eurasian lineage in Beringia (Bernatchez & Dodson 1991, 1994).

In 1992, as a result of his postdoc at Université Montpellier II, he published a paper that remains a milestone in phylogeographical research (Bernatchez *et al.* 1992). It was one of the first papers that employed sequencing, as opposed to restriction fragment length polymorphism analysis of mitochondrial DNA, and it demonstrated the presence of five distinct phylogeographical lineages within the brown trout (*Salmo trutta*) that made perfect sense in the light of glaciation history and geography. Along with follow-up papers (Giuffra *et al.* 1994; Bernatchez & Osinov 1995; Bernatchez 2001), it became a virtual paradigm for more than a decade of phylogeographical studies of freshwater biota in Europe and elsewhere.

His subsequent phylogeographical studies have focused on other both salmonid and nonsalmonid species, such as brook trout and rainbow smelt (*Osmerus mordax*) (Bernatchez & Danzmann 1993; Bernatchez 1997), including fascinating cases of hybridization between species leading to fixation of exogenous mitogenomes within populations (Bernatchez *et al.* 1995; Wilson & Bernatchez 1998). Wilson and Bernatchez (1998) have written an excellent review on the phylogeography of freshwater fishes of the Northern Hemisphere that summarizes the findings from the Bernatchez and many other laboratories. Even two decades after its publication, it still serves as a refreshing and excellent introduction to the topic and it continues to be a highly cited paper.

The adaptive evolution of dwarfism and ecological speciation in the lake whitefish species complex

The study of adaptation and speciation and the engines of biological diversity have been a primary focus of Louis' research programme. Louis has addressed many fundamental evolutionary questions with his work on the lake whitefish species complex, a widespread group of fishes in the Northern Hemisphere that exhibit extraordinary variation (Lindsey & Woods 1970). Their broad distribution and successful colonization of lake and river environments following the retreat of glacial ice has contributed to the repeated evolution of a small, derived 'dwarf' ecotype that persists in sympatry with a 'normal' benthic ecotype (Bernatchez *et al.* 2010;

Renaut *et al.* 2012; Rogers *et al.* 2013; Mee *et al.* 2015). I (SMR) shared Louis' fascination for the evolution of dwarfism following my first field trip to the Allagash Basin in Maine, USA, with fellow student Bob St-Laurant and Maine Fish and Wildlife biologist, Dave Basely at the outset of my PhD. Dwarf salmonids exhibit remarkable behavioural, physiological and morphological adaptations, namely slower growth and earlier maturation in association with their limnetic environment. Louis has published >60 contributions on Lake Whitefish that have significantly advanced the field of ecological speciation by teaching us: (i) the role of history and historical contingency. Louis' phylogeographic studies on allopatric divergence and demographic history among glacial races have demonstrated that secondary contact has significantly influenced adaptation and reproductive isolation in lake whitefish (Bernatchez *et al.* 1996; Lu *et al.* 2001; Rogers *et al.* 2001). (ii) Ecological opportunity during ecological speciation. In new postglacial environments, trophic niche availability (Pigeon *et al.* 1997) and limnological features of lakes (Landry *et al.* 2007; Landry & Bernatchez 2010) promote parallel population divergence in whitefish, with trophic specialization correlating strongly with genetic divergence in sympatric lake whitefish ecotypes (Lu & Bernatchez 1999; Renaut *et al.* 2011; Gagnaire *et al.* 2013). (iii) Adaptation is extremely multifaceted in lake whitefish (Rogers & Bernatchez 2007; Whiteley *et al.* 2009; Dalziel *et al.* 2015; Laporte *et al.* 2015, 2016a), with the genetic architecture of ecological speciation associated with several genes of variable effect size that underlie adaptation (Rogers & Bernatchez 2007; Gagnaire *et al.* 2013; Laporte *et al.* 2015) and contribute to both intrinsic (Lu & Bernatchez 1998; Rogers & Bernatchez 2006; Renaut *et al.* 2009; Dion-Côté *et al.* 2014, 2015) and extrinsic (Chouinard & Bernatchez 1998; Rogers & Bernatchez 2007) postzygotic reproductive isolation. (iv) The evolutionary significance of regulatory genes, as revealed by extensive sequencing and gene expression analyses (St-Cyr *et al.* 2008; Nolte *et al.* 2009; Jeukens *et al.* 2010; Filteau *et al.* 2013; Hebert *et al.* 2013), provides a genomic basis for the observed tradeoffs in life history traits distinguishing dwarf and normal whitefish species pairs, wherein enhanced survival via increased activity in feeding and predator avoidance is associated with higher energetic costs that translate into slower growth rate and reduced fecundity in dwarf relative to normal whitefish (v) Evolution is rapid. These studies have reinforced that rapid evolutionary processes contribute to the generation of this important biodiversity in Canada, with up to 20 species pairs from five distinct glacial races that deserve protection under federal guidelines. Louis' work extends the importance of maintaining genetic diversity to preserve the evolutionary potential of species (Mee *et al.* 2015) and that human disturbance of such evolutionary processes can lead to extinction (Smith & Bernatchez 2008; Mee *et al.* 2015) or unintended evolutionary consequences such as fisheries-induced evolution (Chebib *et al.* 2016). (vi) Collectively, these results reinforce the importance of nonmodel organisms studied in their ecological context towards understanding adaptation and its role in the speciation process. Perhaps of equal importance, Louis' enthusiasm has clearly achieved his personal goal of stimulating the interest of evolutionary ecologists for molecular genetics, but also that of molecular biologists for ecology (Bernatchez & Wilson 1998; Bernatchez *et al.* 1999). His extensive research on lake whitefish speciation has promoted the fusion of what were once remote fields of research and represents one of his most important achievements in molecular ecology as a discipline. Louis continues to push the envelope here. This is exemplified by recent contributions of cytogenic and other complementary approaches to study evolution in lake whitefish (Dion-Côté *et al.* 2016) and ongoing efforts to sequence the lake whitefish genome, as well as a return to a more holistic view of the mechanistic roles that these associated genes have on phenotypic variation during the speciation process.

Elusive eels

Atlantic eels remain some of the most enigmatic animals. From an evolutionary perspective, they represent extreme life histories, encompassing spawning migrations over thousands of kilometres to the remote Sargasso Sea, labile sex determination and panmictic population structure.

Louis has provided numerous important contributions towards understanding the biology of eels and has in general developed Atlantic eels into models for understanding how geographically varying adaptive responses can occur in cases where panmixia precludes local adaptation. The work conducted by him and his collaborators includes testing the panmixia hypothesis in both species (Wirth & Bernatchez 2001; Als *et al.* 2011; Côté *et al.* 2013), demonstrating that transient patterns of geographically varying selection occur despite panmixia (Gagnaire *et al.* 2012b; Pujolar *et al.* 2014) and demonstrating a complex but nevertheless genetic basis of different ecotypes and adaptive responses to human stressors (Pavey *et al.* 2015; Laporte *et al.* 2016b). Some results are really mind-boggling, such as differences in reaction norms and growth patterns between eels from different localities (Côté *et al.* 2014, 2015); this is not to be expected in panmictic species but could perhaps indicate a role of epigenetics, not exclusive to the

consequences of spatially varying selection. Other important contributions include studying the dynamics behind the strange phenomenon of hybrid eels that occur almost exclusively in Iceland (Albert *et al.* 2006; Gagnaire *et al.* 2009) and showing that cytonuclear incompatibility may be an important factor underlying postzygotic reproductive isolation between European and American eel (Gagnaire *et al.* 2012a).

Atlantic eels are probably as far from being classical model organisms as one can imagine. Adult eels have never been caught nor observed in the Sargasso Sea, and identification of the spawning area is based exclusively on catches of eel larvae. It is also still not possible to rear the species in captivity through a full life cycle. Nevertheless, Louis and coworkers have recently sequenced and assembled a draft genome of the American eel (Pavey *et al.* 2016). This tells something about the increasingly blurred boundaries between model and nonmodel organisms, but also about Louis' high levels of ambition.

Louis Bernatchez as a supervisor and colleague

We are sure that everybody who has interacted with Louis can subscribe him as being a friendly, generous and easy-going person with a very well developed sense of humour. Louis is a dedicated, energetic supervisor who fosters an inspirational laboratory dynamic. He has always maintained a large, active group. Yet, somehow he has the time to be equally supportive of every single student. I (SMR) can still recall the manner in which Louis would introduce us to visiting speakers or his colleagues during a conference. He is clearly very proud of his students, their accomplishments and achievements. He also challenges us to challenge ourselves, encouraging his students to be collaborative and seek solutions to problems together. Whether it was a one on one meeting with Louis or during a laboratory meeting, Louis was always on point when it came to the data or topic at hand. I learned a great deal about evolution from Louis, but I learned even more about the importance of communication and collaboration. The laboratory dynamic has always been incredibly social. My very first trip to Quebec involved a laboratory party that the police eventually asked us to take down a notch. Louis would almost certainly attribute this dynamic environment and success to the incredible research professionals that have been part of his group. Lucie Papillon has worked with Louis for almost 20 years and has been an unbelievable resource for the group. Bob St-Laurant, Guillaume Côté, Eric Normandeau, Serge Higgins and the dedicated staff of the aquatic facility at Université Laval (Laboratoire de Recherche en Sciences Aquatiques, LARSA), among many others, have been an integral part of the success of Louis and his students.

As a collaborator Louis has always been dedicated, enthusiastic and generous with good ideas and suggestions. One of us (MMH) has particularly fond memories of research expeditions to remote places. In 2007, Louis joined the Danish Galathea 3 marine expedition on a trip to the Sargasso Sea, with the intention to sample larvae and adult European and American eels on their spawning grounds. Whereas the latter purpose was unsuccessful (and remains so to this day), substantial numbers of larvae were collected that formed the backbone of subsequent studies. The expedition involved, among other things, a bone-breaking transfer by zodiac in 4 metre waves from a trawler to the main expedition vessel, identifying eel larvae in plankton samples at midnight on a rolling ship while at the same time attempting to control one's stomach, but also numerous thoughtful scientific discussions and countless moments of fun and excitement when hauling in sampling nets from deep in the ocean in the middle of the night. In 2014, Louis and another good colleague, Dylan Fraser, participated in an expedition to Greenland in order to sample Arctic char and three-spined sticklebacks. Due to the inaccessibility of many of the sampling locations, it is often the easiest option to sample Arctic char by angling. However, this involves the inherent problem that anglers tend to go for the biggest fish. It was a concern if all sizes and cohorts would be sufficiently represented, but knowing Louis' reputation as an angler, he was enrolled to solve the problem. He did not let us down and as a result the representation of small fish in the samples was substantially increased.

In total, there are numerous reasons for celebrating Louis Bernatchez as recipient of the Molecular Ecology Prize. The best, however, relates to the fact that he is at the stage of mid-career. We can therefore expect even more exciting scientific contributions in the years to come.

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doi: 10.1111/mec.13941