ESSAY

Invasion Ecology:
An International Perspective Centered in the Holarctic

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The Fourth International Symposium on "Alien Species in the Holarctic" was convened September 22–28, 2013, by the Russian Academy of Sciences at the I.D. Papanin Institute for the Biology of Inland Waters (IBIW) on the Volga River in Borok (~355 km north of Moscow). The Organizing Committee spanned five countries (France, People's Republic of China, Poland, Russian Federation, and the United States), with participants (n=150) across the breadth and depth of the Russian Federation, from countries in proximity to it (i.e., Armenia, Lithuania, Kazakhstan, Kyrgyzstan, Ukraine, Siberia, and The Republic of China), and more globally from the United States to Tasmania and Norway to South Africa. This report provides a synopsis of invasive species issues that were discussed at the symposium and, as such, provides an international window for the evaluation of fisheries-related topics in this part of the globe.

The human-mediated introduction of organisms into areas outside of their potential ranges (as defined by natural dispersal and biogeographic barriers) is a distinct branch of science termed "invasion ecology" (Davis 2009; Lockwood et al. 2009). It was first developed by Elton (1958) as a means to imbed life histories and population ecologies of invasive species within the context of conservation and management. Additional early efforts (Laycock 1966) established to the lay public the extensive economic and conservation harm that can be produced by such introductions. However, as a discipline, invasion ecology is not without controversy. Much of it is due to a clock that has oscillated between slower and faster manifestations. For example, invasion ecology clearly has historic roots long associated with human dispersal, particularly within regions such as the Holarctic, where continental landmasses are interconnected and biodiversity can be easily transported. Such a perspective lends credence to contrarian arguments that biological invasions are not unique or contemporaneous, and thus to develop a specialized discipline for its study may be a bit abstruse (Davis 2009; Valéry et al. 2013). Other disagreements (Davis et al. 2011) focus not on invasives as one pole in the "indigenous-alien" spectrum, but rather in the context of "damages wrought," with a rejoinder (Simberloff 2011a) that impacts may not be manifested ecosystem-wide until decades following innocuous introductions (Crooks 2005; see below Amur Sleeper *Perccottus glenii*). In this sense, counter-arguments suggest that invasives should be considered "guilty until proven innocent" (Ricciardi and Simberloff 2009; Simberloff 2011b).

A more contemporary aspect of invasion ecology, and hence its potential timeliness as a discipline, has been the enormous increase in species now considered invasive. Numbers have increased exponentially since 1975 (Richardson and Pyšek 2008) due largely to globalization of trade (Meyerson and Mooney 2007) and a concomitant laxity with regard to the dissemination of biodiversity (Hulme 2009). The end result is that already-established invasives have become even more mobile (see below Rainbow Trout *Oncorhynchus mykiss*), whereas those that lack a history of invasiveness (Amur Sleeper and Pumpkinseed *Lepomis gibbosus*) are establishing the rudiments of a global network. This process has become so provocative that invasive species are now viewed as a major threat to national security (Richardson et al. 2011), due largely to the substantial economic and ecological damages they produce (Ricciardi et al. 2011). Furthermore, the severity of the situation is rapidly accelerating due to the effects of global climate change (Rahel and Olden 2008), an aspect that magnifies the invasive threat. In this sense, and importantly for the Holarctic, climate change has altered its topography by reducing and mobilizing perennial sea ice so as to generate different economic and environmental opportunities, such as new navigational routes (e.g., Northwest and Northeast passages), resource extraction, oceanic productivity, tourism, and wildlife management.

Interestingly, the upsurge in numbers of invasive species has occurred in lockstep with increasing human life expectancy and per capita gross domestic product (GDP) (Lotz and Allen 2013). This means that while countries modernize with regard to their social structures, they also become excruciatingly more vulnerable to the establishment and proliferation of invasive species, and those with higher percentages of invasive and endangered species also reflect lower ecosystem resilience (i.e., disturbance that can be absorbed before changes in structure and control of a system are altered). And as the populace extends its life expectancy, disproportionately larger (and more negative) ecological and carbon footprints are produced and more natural resources concomitantly mobilized. The admonition "live long and prosper" does have its downsides. These aspects are discussed below in the context of an economic infrastructure that supports and sustains invasive species.

The release of ballast water from large oceanic tankers was repeatedly recognized as an issue promoting the transportation and dissemination of marine invasives.

Dire as the increasing extent and complexity of invasive species issues seemingly are, one could still pose the question, "How damaging has the impact of invasive species been to native biodiversity?" Preliminary statistics are startling. The Invasive Species Specialist Group (ISSG) of the International Union for the Conservation of Nature (IUCN) reports that some 1,159 species have potentially gone extinct since tracking began, while an additional 22% of vertebrates, 41% of invertebrates, and 70% of plant species propelled into "endangered" status (Vié et al. 2009). The rank of an invasive within the predator-prey hierarchy is the causative agent for provocative environmental and economic damages, particularly when compared to native predators (Paolucci et al. 2013). In this sense, invaders that insert within higher trophic levels clearly have more severe impacts, deemed as a top-down consumer control of ecosystem regulation (Sax and Gaines 2008). These data underscore the fact that invasive species, and their historic and contemporary repercussions, form a burgeoning scientific discipline with roots in conservation and management.

In recognition of these aspects, the Fourth International Symposium on "Invasion of Alien Species in Holarctic" was

Figure 1. Motif of the Fourth International Symposium on "Invasion of Alien Species in Holarctic," Russian Academy of Sciences, I.D. Papanin Institute for the Biology of Inland Waters, Borok, Russian Federation.

convened by the Russian Academy of Sciences, from September 22–28, 2013, at the I.D. Papanin Institute for the Biology of Inland Waters (IBIW) on the Volga River in Borok, 355 km north of Moscow (Figure 1). The institute is renowned as a research center for freshwater ecology and, with the A. N. Severtsov Institute of Ecology and Evolution (Moscow), served as intellectual focus for the symposium. Presenters underscored the fact that the enormous growth of trade and the advancement of technologies that facilitate travel have clearly promoted invasive species translocations (Minchin and Gollasch 2002), not only across large oceans but into freshwater rivers as well (Slynko et al. 2002). The release of ballast water from large oceanic tankers was repeatedly recognized as an issue promoting the transportation and dissemination of marine invasives (Gollasch et al. 2002; Rothlisberger et al. 2012), yet proposed solutions vary globally. An initial approach has been to require either ballast water exchange or saltwater flushing (i.e., replacing ballast water with open ocean water), but both have obvious limitations. Thus, the iterative take-home message heard at the symposium was a request to agree on new legislation so as to better regulate the dumping of ballast (see also 2013 articles in the section "Managing Ballast Water Discharges" Ecological Applications 23(2):287-351; esajournals.org/toc/ecap/23/2).

Others in the symposium stressed the extraordinary development of invasion ecology in the past 20 years by demonstrating its breadth and depth as well as its involvement in the environmental and political milieu. In addition, comprehensive ecological data sets coupled with hardware and software innovations have opened new avenues of data amalgamation and analyses (Figure 2) that, in turn, have broadened and extended the field (e.g., Olenin et al. 2013). Yet, invasion ecology is largely recognized as an applied discipline that still struggles to develop successful conservation and management policies as a mechanism to quell unregulated invasions. Numerous case studies in the symposium indeed reported on the invasive problem "after the fact" (i.e., from a reactive stance), with monitoring programs serving as early warning systems and with subsequent management actions emphasizing control and eradication (Figure 3).

However, the opportunity to conduct natural experiments that yield data on real-time ecological and evolutionary phenomena (per Sax et al. 2007) was an aspect other practitioners acknowledged. For example, predicting and thus preventing invasions by *a priori* deciphering their dynamics, particularly in a changing climate, would be proactive approaches that utilize ecological theory as a basis for research. Similarly, a focus on the manner by which anthropogenic modifications of aquatic ecosystems have facilitated the invasion process would also be proactive, but from a management stance. These, in turn, could transform invasion ecology from a "crisis discipline" similar to that of "conservation biology," to one that both predicts and adaptively manages alien species and their impacts (Ricciardi et al. 2013). These approaches could be employed, for example, to model the occurrence and extent of a predicted North American invasion by Amur Sleeper, a fish currently invasive to Eurasia (Reshetnikov and Ficetola 2011; USFWS 2012).

Many at the conference argued that molecular methods are but one of the more promising approaches that could advance the discipline. Hybridization (Simberloff 2006) and habitat ho-

Figure 2. Front page of an integrated information system on aquatic non-indigenous and cryptogenic species, AquaNIS (corpi.ku.lt/databases/aquanis). Although developed to store biological invasion data from European and neighboring regional seas, AquaNIS has the capacity to accommodate information from other global marine and freshwaters.

Figure 3. Left: Russian fisheries biologists setting a net on the Tsimljansky Reservoir; Right: Dmitry A. Vekhov with invasive Silver Carp *Hypophthalmichthys molitrix* caught in Tsimljansky Reservoir. Photo credits: Dmitry A. Vekho.

mogenization (Olden et al. 2007), for example, promote genetic swamping via introgression (Echelle and Conner 1989), with species extinction an end result. Despite the success of molecular methods in elucidating evolutionary and ecological mechanisms, only a few tests can be effectively employed in invasive ecology. This is largely due to the short and contemporary timescales over which invasions have most often occurred, and which in turn limit the numbers and types of applicable tests. These might include: (a) identifying the geographic origin of an invasive, (b) evaluating potential bottlenecks, and (c) assaying for potential hybridization with native species (Fitzpatrick et al. 2012). However, molecular approaches are rapidly expanding, and new tests are now being devised and revised. For example, the population structure of an invasive species in its native range has been found to correlate negatively with geographic spread in its introduced range (Gaither et al. 2013). This offers a mechanism to quantify which invasive is likely to become widespread once established. It can also provide a firm scientific basis from which policy makers can establish management priorities.

An interesting intellectual twist for North American participants was a focus on Nearctic species that have now become serious aquatic invasives elsewhere in the globe, specifically the Palearctic. A classic but largely unappreciated example is Rainbow Trout, a native of the North American Pacific Rim that subsequently dispersed during Late Pleistocene to the Kamchatka Peninsula of the Russian Federation (Behnke 1992). It is now globally invasive and seriously problematic (Halvorsen 2010), with a long history of deliberate recreational stocking, accidental aquaculture escapes, and/or illegal introduction (Leprieur et al. 2008). The end results are strong impacts on endemic freshwater systems.

A Global Invasive Species Database (issg.org) maintained by the Invasive Species Specialist Group (ISSG) of the World Conservation Union (IUCN) highlights eight fishes among the "World's Worst 100 Invasive Alien Species" (Lowe et al. 2004). Three of these are introduced solely for sport, with the poster child being Rainbow Trout, now found in more than 90 countries (Casal 2006). As a successful invader, it has precipitated two distinct but parallel effects. First, it disturbs ecological interactions among indigenous species, with displacement through competition and predation (Simberloff et al. 2013; Table 1). It concomitantly alters a shared aquatic invertebrate community as well (Joseph et al. 2011). These impacts are greatest in places where other salmonids have not been distributed historically (e.g., Australia and New Zealand). In the Southern Hemisphere, exotic salmonids are the most abundant freshwater fish and have caused widespread ecological damage (Consuegra et al. 2011). In Germany, Rainbow Trout is also the most widespread of introduced fishes with 5,872 records in open waters, and it represents the largest commercial inland fishery with >21,000 tons annual yield (Wolter and Röhr 2010).

The second negative aspect for Rainbow Trout is that it is a component of a global consumer society (Olden et al. 2005) within which recreation is deemed more important than conservation (Cambray 2003). This rings especially true given associated expenses relating to fishing gear, specialty magazines, and the infrastructure of food and accommodations, all of which can promote economic growth and GDP (as previously noted), yet to the detriment of the environment. The question then be-

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Figure 4. Some endemic fishes of European Russia are relatively immune to non-anthropogenic predation when at adult size. One of these is the Wels Catfish *Siluris glanis*, as netted in the Tsimljansky Reservoir. It is primarily found in deeper waters of larger rivers, but grows to very large size near dams in reservoirs, yet is harvested as food. Photo credits: Dmitry A. Vekhov.

Figure 5. Left: Fishes caught by Russian fishery biologists documenting the first case of the alien species Amur Sleeper *Perccottus glenii* in Tsimljansky Reservoir (on the River Don in the Volgograd region). The Amur Sleeper is the dark predator in the center of the pail. The three fish immediately above are Gibel Carp *Carassius auratus*, another alien species; the curved fish immediately below is Northern Pike *Esox lucius*, a native predator, while the three fish with red eyes below the Pike are Roach *Rutilus rutilus*; Right: Amur Sleeper (top) with Northern Pike (3 individuals below) along with aquatic vegetation at site of capture. Photo credits: Dmitry A. Vekhov.

comes whether a country can divest itself of a positive economic component despite its negative effects on endemic biodiversity. While an answer is not immediately apparent, its formulation is not favorably disposed towards biodiversity conservation (see Figure 4).

A second Nearctic invasive, a warm-water centrarchid (the Pumpkinseed), was first introduced into Europe circa 1885 (Holčík 1991) and is now established in at least 28 European countries (Cucherousset et al. 2009). It is one (of two) aquatic species considered "very invasive" in Europe (García-Berthou et al. 2005) with greatest impacts within the Iberian Peninsula, whereas those in more northern European ecosystems are still being evaluated (Fobert et al. 2011). One aspect of its natural history, and the Centrarchidae in general, is an elevated phenotypic polymorphism in both native and introduced ranges. For example, considerable morphological variance is found among littoral versus pelagic and lake versus stream dwelling sunfish (Yonekura et al. 2007; Bhagat et al. 2011). This provides considerable ecological latitude when freshwater niches somewhat novel to their life histories become occupied. Another important aspect that seemingly has manifested itself with Pumpkinseed is the capacity for introduced forms to remain relatively inconspicuous for extended periods within novel habitats before they quickly spread and become invasive (Simberloff 2011b).

North American participants in the symposium were also made aware of the dangers stemming from an invasive fish (the Amus Sleeper [Odontobutidae], also termed the Rotan or Chinese Sleeper), that has spread westward into Europe from far eastern Asia (Figure 5, left). It is a relatively small (25 cm TL) voracious predator of ponds, oxbow lakes, temporally isolated flood plains, and other low-oxygenated lentic water bodies of the Amur River basin (the border between the Russian Far East and northeastern China). Its large gape and broad dietary proclivities, coupled with high reproductive output, are natural history attributes that in tandem have operated to severely depress densities of fishes, macroinvertebrates, and amphibians within its introduced range. During high water levels, the Amur Sleeper is often transported from adjacent oxbows and flood plains into the dispersal corridors of larger rivers (Reshetnikov 2013). It has become widely distributed in European Russia since 1916 (Reshetnikov 2004) and has now spread westward as far as Bavaria (Reshetnikov and Schliewen 2013). One concern is that global climate change will promote the long-term range dynamics of this invasive (Reshetnikov 2013) with the probability that in the coming decades it will substantially transform freshwater ecosystems of Western Europe (Figure 5, right). The most troubling aspect for conservation biologists in the Nearctic is that bioclimatic suitability analyses underscore suitable habitat for the Amur Sleeper within North American aquatic systems, particularly those in Great Lakes but also the Mountain West (Reshetnikov and Ficetola 2011: Figure 4).

The symposium concluded with a wide-ranging roundtable discussion that touched upon many of the points articulated above (see Richardson and Ricciardi 2013). For example, several participants pointed to the similarities that exist between restoring ecosystems to historic conditions, a common conservation theme, and one that seeks their maintenance free of invasive species. At odds with each is the practical recognition that nature no longer remains untouched by anthropogenic activities, particularly given changes in the global climate. Another prominent aspect of this discussion involved the accelerated spread of invasives in manifestly greater numbers than recorded historically, and via invasion pathways fundamentally distinct from those deemed non-anthropogenic and thus natural. A recurring theme was not only "how to accommodate" but more appropriately, "should we?" (Simberloff 2013).

Symposium participants with a managerial background acknowledged that a more applied stance may be a potential handicap for the discipline, but also that the methodical process of monitoring has provided the baseline data necessary to fully grasp the impacts of invasives. For example, we now know that invasives unequivocally impact ecosystem functioning, both singly as well as in synergy with other anthropogenic impacts (Strayer 2012). Thus, the trenchant differences between opposing positions (as previously noted) are clearly philosophical rather than data-driven and will not be easily adjudicated, either with regards to conservation biology or invasion ecology (per Simberloff 2012). For sure, modified ecosystems are more the norm rather than the exception, and agencies and NGOs must react accordingly. Yet relinquishing a protocol that promotes the control and potential removal of invasives will do little to sustain natural ecosystems and the indigenous biodiversity that promotes their functioning (Strayer et al. 2006). A baseline for managing and thus predicting invasions will require carefully controlled, empirical data, and these fall within the bailiwick of methodical and regimented monitoring. Given this, the two arguments may not be as distant as their written rhetoric would depict. It will be interesting to gauge whether philosophical distances expand or contract as the region moves towards the Fifth International Symposium on "Alien Species in the Holarctic."

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