POLICY PERSPECTIVE

The invasion of the freshwater diatom *Didymosphenia geminata* in Patagonia: prospects, strategies, and implications for biosecurity of invasive microorganisms in continental waters

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Keywords
Biosecurity; conservation planning; freshwater invasion; invasion model; river network; Tierra del Fuego; transmission vector.

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Received
20 March 2012
Accepted
15 June 2012

Editor
David Strayer

doi: 10.1111/j.1755-263X.2012.00264.x

Abstract

The diatom *Didymosphenia geminata*, which forms nuisance blooms in low nutrient streams worldwide, was documented as an aggressive invader in South America in 2010 from the Futaleufú basin (43.2°S), in Chilean and Argentinean Patagonia. Within 1 year it was confirmed from 20 rivers distributed over 800 km. Driven by perceived economic impacts to tourism and recreation, a strong response ensued, with education, monitoring and nascent biosecurity efforts based on similar measures in New Zealand. Considering the difficulty in containment (potential range on New Zealand's South Island was occupied by *D. geminata* within 3 years), the much larger potential range, and limited resources or previous experience in managing invaders in continental waters in South America, it is unlikely that current biosecurity measures will produce significant results. Lacking a coordinated strategic approach or conservation priorities, existing efforts may divert resources from alternatives with greater potential for success, while potentially feeding the public perception that the problem is being addressed. We propose a conservation strategy based on best available but incomplete information on habitat requirements, and a conceptual model of invasion vectors to identify defensible conservation zones (islands and hydrographically isolated areas) with greater potential for being maintained invasion-free.

Introduction

Didymosphenia geminata (Lyngbye) M. Schmidt, a diatom native to mountain and boreal streams in the Northern Hemisphere, has recently attracted considerable attention as an aggressive invader (Whitton *et al*. 2009; Spaulding *et al*. 2010). Following the first Southern Hemisphere introduction to the South Island of New Zealand in 2004, Biosecurity New Zealand recognized *D. geminata* (DG) as a top priority due to its propensity for developing unusually high biomass in rivers despite low nutrient concentrations (Kilroy *et al*. 2009), and potential economic impacts to fly-fishing and tourism (Kilroy & Unwin 2011). DG proliferation is also characterized by novel biogeochemical processes, physical structure and microbial communities (Sundareshwar *et al*. 2011), may alter stream hydraulic properties (Larned *et al*. 2011) and benthic invertebrate abundance and community composition (Kilroy *et al*. 2009). Significant investment in monitoring, education/outreach and research, an existing biosecurity program, and application of tools such as River Environment Classification (REC, Snelder & Biggs 2002) did not prevent the subsequent spread of DG throughout the South Island within 3 years (Kilroy & Unwin 2011).

The first South American occurrence of DG nuisance blooms was confirmed in April 2010 from Rio Espolón in the Los Lagos Region, Palena Province in Chile (det. Sarah Spaulding, CIEP 2010a), subsequently appearing upstream in Chubut Province, Argentina, in September 2010 (Sastre *et al*. 2010). Despite limitations such as a lack of a biosecurity framework for aquatic invaders, initial doubts regarding institutional responsibility, early stage of river classification tools (e.g., Universidad de Chile 2010), limited baseline data on aquatic systems (Pascual *et al*. 2007), and significantly less funding, Chile and Argentina followed the New Zealand example of an aggressive response (plague declaration, Chile Subsecretaría de Pesca 2010, Res. 3064 and 3078), largely because of potential economic impacts to tourism (Branson 2006; Spaulding & Elwell 2007). In Chile alone well over a half million US$ has been dedicated to monitoring, in addition to education campaigns and materials, workshops, signage, and biosecurity measures (decontamination stations and checkpoints). However by the end of 2011, less than 18 months after the first occurrence, DG had spread to nearly 20 rivers distributed over 800 km in the Los Lagos and Aysén Regions of Chile, and four rivers in Chubut and Neuquén Provinces in Argentina (Figure 1).

The affected areas in New Zealand and Patagonia are roughly equivalent in size (~150,000 km^2). DG is probably close to its maximum range on the South Island of New Zealand, although it has still not been documented from several medium-sized river basins and Fiordland National Park within the South Island or from the North Island (Kilroy & Unwin 2011). The DG invasion is still in its early stages in South America, and has the potential to expand throughout extensive potential habitat predicted for much of the Andean cordillera (Figure 1). A substantial body of gray literature and published scientific work has accumulated from the efforts at managing DG in New Zealand. However the responses in South America have been based more on imitation than a critical or strategic approach, or a lack of distinction between strategy and tactics (sensu Doppelt *et al*. 1993). If any success is to be expected in Latin America, or any developing region with limited resources, a new strategy is needed.

A clear understanding of the factors that confer resistance to DG invasion is still lacking: "apparent" invasion resistance may be just a delay in introduction, depending on transmission vectors and their associated probabilities accumulated over time (Johnson *et al*. 2001). Lack of invasion on the North Island of New Zealand, after 8 years of presence on the South Island and despite high rates of inter-island travel, may be a consequence of aggressive biosecurity policies and management, and/or less suitable environmental conditions. Nevertheless, where the environment is suitable for a potential invader, islands or other hydrographically isolated systems may confer a strategic advantage in implementing imperfect biosecurity policies.

It may already be too late to prevent the spread of DG across its potential range in South America. But positive results may still be achieved at smaller scales in hydrographically isolated areas, such as New Zealand's Fiordland National Park. A strategic approach may also help prevent future introductions, spread of other potential aquatic invaders, and lead to better defined management and conservation priorities for freshwater ecosystems, especially in regions where freshwater conservation is not well developed.

Strategic approach to biosecurity and management of freshwater invasive species

We propose a conservation strategy for DG based on best available but still incomplete information on habitat requirements, a conceptual model of invasion vectors, combined with identification of defensible conservation zones (islands and hydrographically isolated reaches) with greater potential for being maintained invasion-free. Our proposal represents a specific application of conservation planning (modified from Margules & Pressy 2000) implemented in the larger context of national-level invasive species management/biosecurity and on-the-ground natural areas management (Figure 2).

Prevention of initial introduction as first line of defense (Johnson *et al*. 2001; Jeschke & Strayer 2005), and an early warning system essential for eradication (Simberloff 2009), are obvious elements of national coordination (objective one, Figure 2). We note only briefly that national coordination is still lacking in the region. Given the already advanced stage of DG invasion in South America, our focus here is on conservation planning (objectives two to six, Figure 2) as the foundation for defining basic conservation units. A conceptual model of introduction and dispersal vectors (objective two, described in detail in the following section) is an essential complement to the prediction of potential distribution (objective three). Several examples exist for independent modeling of potential DG habitat (objective three) at the regional (Kilroy *et al*. 2008), continental (Kumar *et al*. 2008) or global scales (e.g., Spaulding & Elwell 2007), and a first attempt

Figure 1 Current and potential distribution of *D. geminata* in South America (potential distribution redrawn from Spaulding and Elwell 2007).

at river classification in Chile (Universidad de Chile 2010) might be adapted toward this end. Modeling of potential habitat together with dynamics of transmission vectors is more typical of epidemiology; the potential synthesis between disease forecasting and invasion ecology was recognized in a recent review (Crowl *et al*. 2008). Habitat estimation and the baseline survey (objective four, Biosecurity New Zealand's basic response for newly arrived

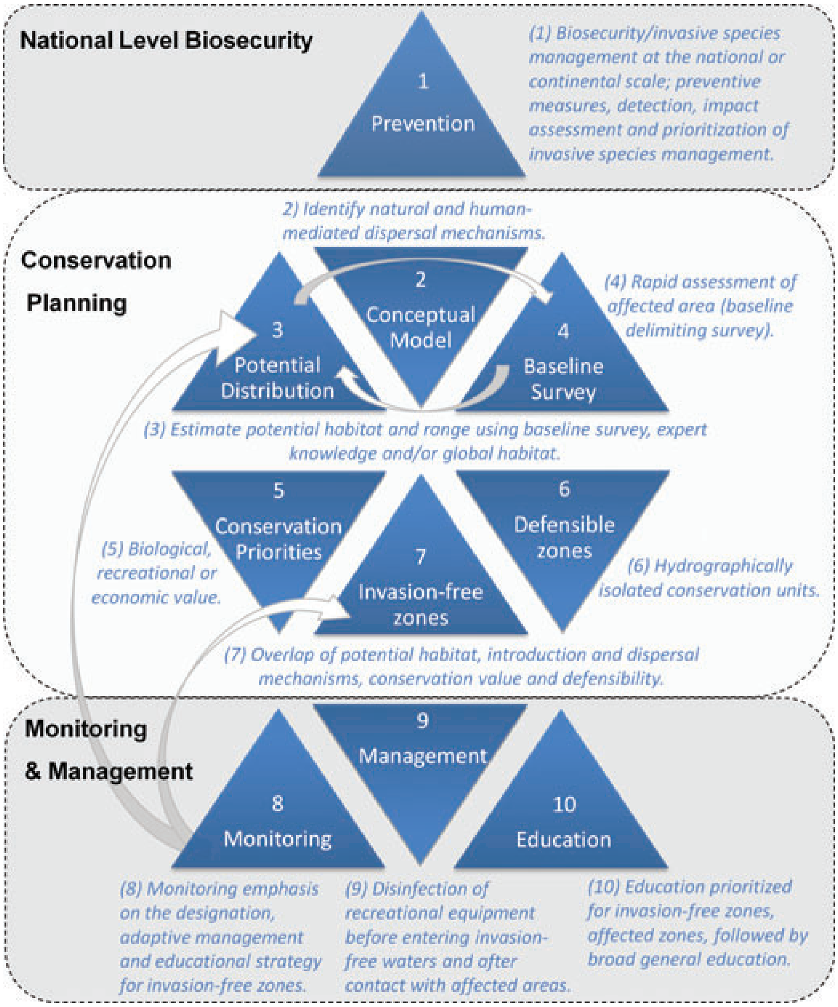

Figure 2 Flow diagram of proposed strategic response to DG invasion, a coordinated effort integrating groups focused on national biosecurity, conservation planning, and implementation, respectively.

unwanted organisms) is also an interactive and iterative process.

The key to conservation planning is that the desire for more information (scientific studies, general observations, number of environmental parameters) must be weighed against the need for rapid assessment and thorough coverage. For example, linking physico-chemical characteristics to presence/absence data (model calibration) may be severely limited during the early stages of invasion, since suitable habitat may be unoccupied due to dispersal limitation. Lack of knowledge of at-risk ecosystems may also be an impediment toward determining conservation priorities (objective five), validating specific invasion vectors (objective two), and hence identifying respective hydrographic isolation (objective six, see the following section). Alternatives based on expert-driven approaches (Poiani *et al*. 1998; Salafsky & Margoluis 1999), public participation or a combination (e.g., mental models, Biggs *et al*. 2011) may be necessary. The outcomes (prediction of potential distribution or prioritization of areas worthy of protection) will always be imperfect and subject to change, and management actions may be based on incomplete information. But once priorities are established, among the tens of thousands of kilometers of stream network, implementation (monitoring, management, and education, objectives seven through nine respectively, Figure 2) may be focused on a more reasonable scale, with greater impact and probability of success (e.g., designated invasion-free zones).

Conceptual model for DG invasion and transmission vectors

A conceptual model for DG secondary spread (sensu Johnson *et al*. 2001, see supplementary material) is the basis for the conservation planning case studies illustrated below. The model considers human, wildlife and natural physical dispersal vectors, and their respective interaction within the fluvial network and the landscape (Poole 2010). The conceptual model (together with associated transmission probabilities, where possible) is important in determining the possibility for eradication or control, the potential for spread, estimating distribution over time, and ultimately defining the scale of monitoring and management. Initial introduction of DG by recreational users (i.e., anglers or kayakers, Kilroy & Unwin 2011) is followed by rapid downstream colonization by drift, and slower expansion upstream depending on suitable habitat and competing algae (i.e., the traditional model for stream algae, Lutscher *et al*. 2006). Upstream DG populations may increase propagule pressure downstream (Flöder & Kilroy 2009, Eschtruth & Battles 2011), potentially explaining a high frequency of DG downstream (Kilroy & Unwin 2011), and overcoming physical habitat constraints (colonization of submerged macrophytes, moss, sandy substrates and shoreline herbaceous vegetation, CIEP 2010b, 2011; Sastre *et al.* 2010).

Fish-borne dispersal of DG remains an untested possibility, but may explain a significant percentage of new introductions upstream (Kilroy & Unwin 2011). Natural or artificial barriers to upstream passage such as waterfalls or dams might therefore inhibit the upstream dispersal of DG, while lakes could limit (or at least delay) downstream physical dispersal. Avian vectors are far better documented in the dispersal of aquatic organisms (Kristiansen 1996), and translocation across watersheds is possible depending on migration routes and the survival capacity of the organism (>60 days in a humid environment for DG). Since DG dominates more than 50 km of the Río Baker (CIEP 2011), a major route for migrating waterfowl (B. Reid unpublished data), continental-scale eradication may no longer be possible.

We illustrate the application of this model using two case studies: (1) small-scale conservation planning within the invasion epicenter; (2) islands such as Tierra del Fuego as conservation units and defensible invasion-free zones. Both examples represent first iterations that could benefit from future refinement, especially if conducted in a participatory stakeholders setting (Poiani *et al*. 1998; Salafsky & Margoluis 1999; Biggs *et al*. 2011).

Case Study 1 (Aysén Region of Chile): conservation planning within the invasion zone

A first iteration of DG invasion conservation planning conducted for the Aysén Region in Chile addressed the possibility of maintaining invasion-free zones directly within the affected area (CIEP 2011). Based on limited understanding of habitat requirements, and lacking river typology for predicting potential habitat across the region, we applied a coarse filter in identifying glacial rivers and dystrophic systems (pH << 7, Kilroy *et al*. 2008) as less suitable habitat (estimated from forest cover maps as drainages with significant headwater rainforest or bogs, data source: Corporación Nacional Forestal, Gobierno de Chile). As the inverse of potential habitat, this allowed us to eliminate a significant portion of the western part of the region from consideration. The distribution of DG positive sites and sites where DG was not detected was based on several independent surveys (CIEP 2010a, b, 2011; CIEN Austral 2011; POCH Ambiental 2011). Data sets for river access, fishing lodges and recreational areas were compiled during monitoring campaigns (CIEP 2011). Hydrographic barriers (lakes and waterfalls) were determined from existing hydrographic data (data source: Dirección General de Aguas, Gobierno de Chile), digital elevation models and field surveys. Identification of conservation priorities was severely limited by lack of systematic habitat classification or preexisting assessments of species richness or endemism. Instead we focused on areas where fishing lodges were concentrated, as these represented high-risk sites for introduction of DG, an economic priority in terms of tourism and recreational value, and an opportunity for local collaboration in implementing biosecurity measures.

Six priority DG-free areas were identified in a first iteration of analysis (Figure 3), based on the overlap between conservation priority (concentration of lodges), threat (potential DG habitat and points of access) and hydrographic isolation (upstream and downstream dispersal barriers). The smallest site is a 10-km lake outlet system on the upper Río Baker, with many fishing lodges and bounded by waterfalls downstream (inset, Figure 3). Two medium sized watersheds were also identified: Río Cisnes, located between major zones of invasion, and Río Bravo: the latter lacks any determination of DG presence/absence, but forms the southern boundary of the currently known DG distribution. These sites represent a range of feasibility and defensibility in terms of preventing the spread of DG. The large watersheds (Río Cisnes and Río Bravo) are more challenging; rivers closer to populated areas and known DG blooms have higher threat (Río de la Paloma, Río Ñirehuao); and one binational watershed requires cooperation with Argentina (Río Figueroa). Of these six sites, two were recently confirmed for the presence of DG (Río Figueroa and Río Ñirehuao, B. Reid unpublished data), less than 5 months after the first iteration of this analysis, and before biosecurity stations could be established.

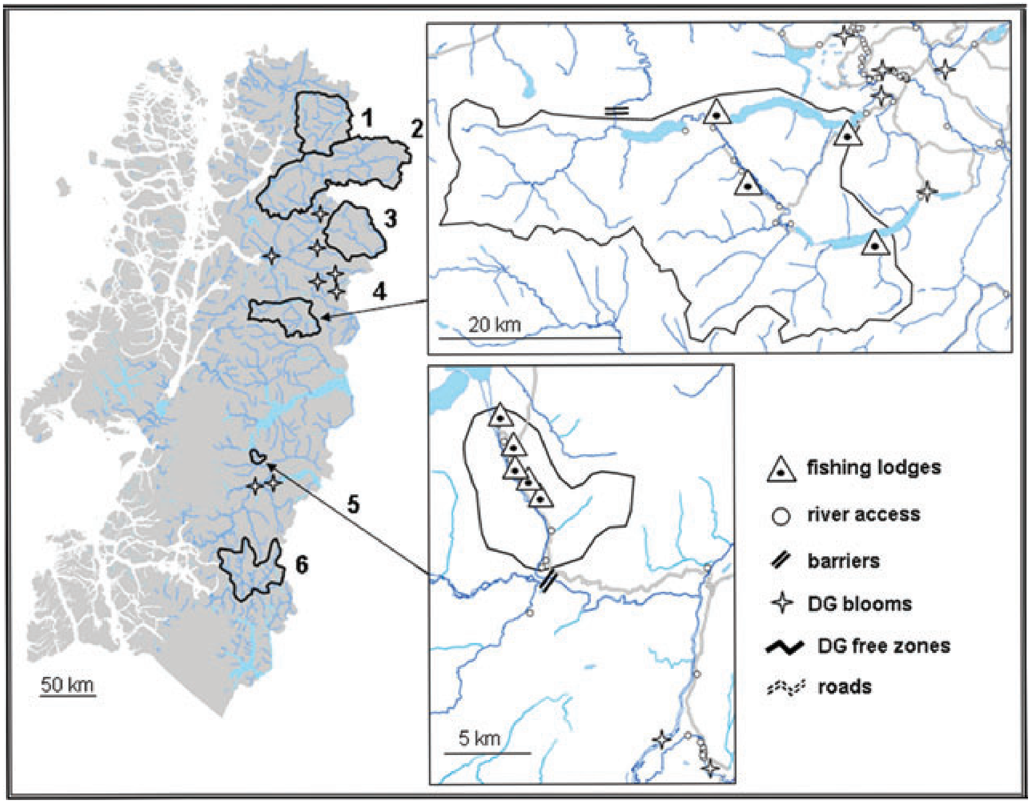

Figure 3 Map of biosecurity priorities, proposed *D. geminata* invasion-free zones and major blooms, case study 1, Aysén Region of Chile: 1 Río Figueroa; 2 Río Cisnes; 3 Río Ñirehuao; 4 Río de la Paloma; 5 Río Baker; 6 Río Bravo. This first iteration was based on the overlap of potential habitat east of the cordillera, hydrographic isolation from natural barriers (falls and lakes), and economic value and potential management resources (clusters of fishing lodges).

Conservation units identified from this analysis may not necessarily correspond with current administrative units of watersheds or sub-watersheds (Subsecretaría de Pesca 2011). Hence currently designated "plague" zones may include hydrologically distinct and defensible DG-free reaches. Invasion-free zones may be difficult to maintain within heavily affected areas compared to outside the invasion front. However the scope of management efforts is significantly reduced from that of the entire region. By selecting areas where natural vectors are minimized, the success or failure of biosecurity efforts will depend more on local support and political will. A second iteration of this effort will focus on the extensive system of national parks and reserves and private parks (over 50% of the Aysén Region). Although many of these protected areas fall within the temperate rainforest to the west, and the convoluted park boundaries usually exclude medium or large river corridors, some reserves may include potential DG habitat, and the logistic support and infrastructure may be more available for proactive management of invasion-free zones.

Case Study 2 (Tierra del Fuego): islands as priorities for invasion free zones

We propose that offshore islands present an opportunity for conservation of DG-free zones, due to: (1) relative simplicity of implementing biosecurity measures at fewer points of entry; (2) elimination of introduction by leading edge and corridor effects, with less frequent lower probability jump or long-distance dispersal (Wilson *et al*. 2008); and (3) synergism with other conservation priorities (e.g., diatom endemism in isolated Southern Hemisphere lakes, Vyerman *et al*. 2007) in islands and isolated regions. Within the range of potential DG distribution in South America (Figure 1), three large islands are noteworthy: Tierra del Fuego, Chiloé, and the Falklands (Malvinas).

A rapid assessment was conducted in Chilean Tierra del Fuego in November 2011, including a general characterization of river habitat, conservation units, and baseline sampling. Initial observations suggest widespread suitable DG habitat, dominated by tundra (i.e., DG's native range, Whitton *et al*. 2009), possibly more favorable than in affected areas to the north. Ultra-oligotrophic conditions (soluble reactive phosphorous <2 μg/L for 12 of 20 sites, M. Frangópulos, unpublished data), and circumneutral pH (Moorman *et al*. 2006; M. Frangópulos, unpublished data) are not limiting factors for most drainages; "the world's cleanest freshwater" is both a conservation value and an imminent risk given DG habitat preference. Baseline visual assessments in 20 rivers with fishing access indicated the absence of DG blooms. Hydrographically isolated units were not significant except at the scale of entire islands. The Magellanic sub-Antarctic rainforest forest region (including the Cape Horn Biosphere Reserve) is one of the world's most pristine areas based on low human population, intact native vegetation and extensive size (Mittermeier *et al*. 2003). The recreational value is clearly important, especially the angling contribution to the tourism economy in Argentine Río Grande (not included in the survey). High angling activity also suggests high threat of future DG introduction. In summary, the island of Tierra del Fuego is a clearly defined conservation unit, threatened by potential DG invasion, may still be free of DG (pending similar assessment in Argentina), and has other overlapping conservation value. We note that conservation and biosecurity on the island presents a distinct challenge, cooperation and coordination between Chile and Argentina being essential (Jaksic *et al*. 2002).

Coordinated management of invasive species impacts to continental waters in Patagonia

DG is only one among many invaders threatening Patagonian ecosystems: how should we prioritize DG among the ranks of potential invaders? Can invasive microbes be contained? In developing countries with limited resources is it reasonable to invest in management actions with expected high failure rates? And are there any long-term benefits to investing in biosecurity of aquatic invaders in the region? Simberloff (2009) argues for more optimism with respect to control and eradication. We assume here that the window for general eradication of DG in South America has passed, with an already extensive distribution, potential for long-distance transport by waterfowl, and lack of precedent for eradicating aquatic microbial invaders from dynamic fluvial networks.

Regardless of whether control or eradication of DG is possible, the same biosecurity measures are applicable to slowing the spread or preventing initial introduction of other future aquatic invaders. Whirling disease (*Myxobolus cerebralis*) to date confirmed only for Columbia (Hoffman 1990), could have clear direct impacts to trout in Patagonia, Asian clam (*Corbicula fluminea*) is established in Patagonian Argentina (Rumi *et al*. 2008), and many potentially overlooked algal and microbial invaders (Kilroy *et al*. 2009) could be addressed by the same biosecurity protocols. Secondly, the identification of zones of high defensibility due to hydrographic isolation could also enhance the protection of native fish and native ecosystems. Introduced trout and salmon (Pascual *et al*. 2007) are some of the most significant global invaders (Cambrey 2003), and one of the largest remaining lakes in Patagonia that still supports only native fish is isolated by a steep coastal drainage (Correa & Hendry 2012).

In essence we argue, in the context of DG, that decentralized biosecurity and education, and emphasis on short-term, strategically implemented management focused on well-defined priorities (such as invasion-free zones), may be a necessary step toward developing a more comprehensive invasive species biosecurity program (e.g., Comisión Nacional de Medioambiente 2003). The previously noted shortfall in centralized coordination (objective one, Figure 2), is indeed a major obstacle in terms of prevention. Broad-brush campaigns, general circulation of pamphlets, classroom education, and roadside billboards organized regionally or nationally may produce results in the long term, but are too abstract to contribute to rapid short-term responses needed for managing areas of conservation or economic importance. A framework for decentralized implementation, based on iterative or adaptive conservation planning, is equally important. In regions where management resources are limited, decentralized implementation focused on well-defined objectives may more effectively incorporate local stakeholders (residents, public agencies, tourism guides), whom in turn may contribute valuable observations to citizen-based science (Crall *et al*. 2011). Monitoring is most effective when directly linked to management actions. Implementation without planning, monitoring without well-defined objectives, and centralized general education run the risk of draining limited resources while maintaining the false appearance that something is being done.

Conclusions

Invasions by nonindigenous organisms receive disproportionate public attention when they threaten economic sectors, and the recent establishment of DG in Patagonia may prove to be a stimulus for enhancing local and regional biosecurity and invasive species management by Chile, Argentina and potentially other Latin American nations. However, once established, invasive species are very difficult to control or contain, and probably impossible to eliminate, especially in the case of microorganisms. While the prospects for preventing the spread of DG across much of its predicted range in South America are somewhat limited, some success might be possible at smaller scales. Where a lack of previously defined conservation priorities presents a significant obstacle to management response, we recommend prioritizing areas based on potential defensibility due to hydrographic isolation, and general conservation or economic values. Even in the worst-case scenario of limited success in containing the DG (which is the current scenario), a strategic response would strengthen the capacity of public agencies to respond to future invasive species, short-term successes being a necessary step toward developing broader competence. We view the response to DG invasion in Patagonia as a test for public agencies charged with managing continental waters, and also for private sectors that benefit from unique ecosystems in Patagonia.

Acknowledgments

A series of workshops organized by Georgina Lembeye and Viviana Montecino were the impetus for developing the strategic approach. Leonardo Nuñez, Paola Castillo and the X, XI, and XII regional offices of Servicio Nacional de Pesca, Chile, provided commentary on the concepts outlined here. The case studies in Aysén and Tierra del Fuego were supported in part by Sernapesca licitación 701–9-LE11 and FIC-r 2010 N°30106934–0 Region XII, respectively.

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