Advancing aquatic vegetation management for fish in north temperate lakes

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ABSTRACT

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Despite the known linkage between aquatic plants and fish communities, research that quantifies the relationship between aquatic habitat and fisheries management is lacking, particularly for lakes. Lake management is often driven by recreational interests and fails to evaluate outcomes or identify conservation benefits. Effective management of vegetation to benefit fisheries will require information on how fish utilize aquatic plant stands, as well as how they are affected by changes in vegetation coverage or richness. Management strategies will need to account for both local and large-scale effects on aquatic plant habitat. Studies that assess the economic benefits of aquatic plants to fisheries will provide support for sustainable aquatic vegetation management approaches. Finally, natural resources managers (including both aquatic botanists and fisheries biologists) will have to collaborate to identify priorities to implement and evaluate vegetation management activities. Marine seagrass and fisheries research is presented as a means to provide guidance on aquatic plant inventory and monitoring, as well as potential research opportunities to better understand aquatic plant and fish relationships and the implications for lake management.

KEYWORDS

Aquatic plants; fish; lake management; seagrass

The close linkage between aquatic plant communities and fish communities is well recognized (Jeppesen et al. 1998). Aquatic plants provide food and oxygen, shelter and spawning areas, and improved water quality for fish. Despite this knowledge, however, efforts to manage aquatic plants for fisheries benefits are still limited (Olson et al. 1998). Research that quantifies the relationship between aquatic plants and fish is particularly plentiful in the marine environment (Hemminga and Duarte 2000, Larkum et al. 2006, Olafsson 2016). Exploring some of the various seagrass inventory and monitoring programs may allow fisheries managers, through analogous thinking, to apply the lessons learned in the marine environment to lake ecosystems. The objective of this article is to provide a short synthesis of the scientific studies and management of vegetation in the marine environment to serve as a template for future lake vegetation work and to encourage lake managers to explore several potential research opportunities and various lake vegetation management actions that may provide fisheries benefits.

Seagrass as fish habitat

Within the marine environment, research on seagrass systems provides background and guidance that may be relevant to lake environments. Seagrasses are a unique group of flowering plants with adaptations that allow them to occupy shallow (intertidal to a few meters deep) temperate or tropical coastal waters, where they typically cover extensive areas (Les et al. 1997). These seagrass meadows provide critical ecosystem services including fish habitat, food for invertebrates and waterfowl, nutrient recycling, carbon sequestration, and formation and stabilization of coastal soil and sediments (Nordlund et al. 2016, Sunny 2017, Namba et al. 2018). Seagrasses come from four families (Posidoniaceae, Zosteraceae, Hydrocharitaceae, and Cymodoceaceae); however, seagrass meadows are often made up of a single species. Zostera marina (eelgrass) is widespread within the shallow waters along the coastlines of North America, Europe, and Asia, and is the dominant seagrass in the coastal and estuarine areas of North America (Larkum et al. 2006).

One-third to one-half of seagrass meadows have been lost globally (Waycott et al. 2009, Short et al. 2016), with losses mainly near developed areas due to decreased water clarity and increases in sedimentation and nutrient loading.

The importance of seagrass in coastal ecosystems has been studied through a vegetation-centric approach, as well as an approach that links fish community attributes with vegetation dynamics to develop predictive models of fisheries attributes with seagrass changes. One vegetation-centric study was conducted by Schubert et al. (2015), who extensively mapped Zostera marina in the western Baltic Sea and produced models using depth, wave exposure, and slope to predict occurrence of the plant. Lefcheck et al. (2017) used 31 years of mapped Zostera marina stands in Chesapeake Bay to determine that spatial and temporal variables as well as water clarity and water temperature were significant predictors of eelgrass cover. Thom et al. (2014) assessed potential effects of climate change on eelgrass, concluding that climate-linked factors such as variation in water temperature and mean sea level may affect the abundance and temporal distribution of eelgrass.

Fish-centric studies on how fish use eelgrass stands are also common. Kwak et al. (2014) explored fish composition in Zostera marina stands across seasons and found that seasonal changes in the abundance of fish corresponded with eelgrass biomass. Stavely et al. (2017) found that Zostera marina meadows were the preferred habitat for juvenile fish as predator refuges and feeding areas, and Hovel et al. (2016) and Kennedy et al. (2018) reiterated the importance of eelgrass for providing foraging areas for juvenile fish. Henderson et al. (2017) investigated fish community composition in seagrass meadows dominated by Zostera muelleri and found differences in composition related to harvest limits (abundance of exploited species was higher within marine reserves) and seagrass meadow locations (abundance was higher in meadows closer to the open ocean).

In addition to vegetation-centric and fish-centric studies, a third type of study links fish community attributes with vegetated habitat to develop predictive models. Two recent studies illustrate the value of understanding the importance of seagrass to fish and quantifying the ecosystem services of this habitat. Blandon and zu Ermgassen (2014) completed a meta-analysis of juvenile fish abundance in seagrass habitat along Australia's southern coast and found that 13 fish species of commercial value had recruitment enhanced by seagrass meadow presence. They also applied population dynamic models to quantify the contribution of seagrass to commercial fish biomass and landings and estimated that each hectare of seagrass restored may enhance commercial harvest by 9.8 tonnes per year. Jackson et al. (2015) estimated that seagrass (Posidonia oceanica) habitat had a direct annual economic contribution of about 4% of the Mediterranean commercial fisheries landing value and 6% of all recreational fishing expenditures, despite this habitat only covering about 2% of the area. They noted that seagrass-associated fish species (mostly during their juvenile stage) account for 35% of the commercial landing value and 29% of the recreational fishing expenditure.

The guidance suggested by these studies is plentiful. The vegetation-centric studies demonstrate the importance of species distribution monitoring and modeling. Such studies lead to greater understanding of the factors that affect aquatic plants and build a foundation for understanding aquatic plant distributions and dynamics. The fish-centric research provides a reminder that interactions between fish and aquatic plants are rarely simple. Stavely et al. (2017) found that increased habitat complexity was not always a benefit; they found no association between seascape structure and mean species richness, and concluded that less complex seascapes were, in fact, more suitable for juvenile fish. This suggests a rethinking of the assumption, common in lake management, that monotypic stands of vegetation equal poor quality habitat. Kennedy et al. (2018) stress the importance of monitoring critical habitat, particularly as it relates to availability for fish species. Presence of aquatic vegetation may not equate to utilizable habitat, and managers must consider other factors (including water temperature, oxygen levels, etc.) when developing management plans. In addition, mapping and monitoring may provide information on how aquatic vegetation responds to anthropogenic pressure (Kennedy et al. 2018). As many lakes are subject to increased development

pressure, the ability to assess changes or predict in-lake habitat will be crucial in developing effective plans. Henderson et al. (2017) found that habitat context (i.e., the spatial arrangement of ecosystems) played a role in the distribution of several fish species. Although they did not find a relationship between the effectiveness of reserve areas and habitat context, this may not always be the case. In lake ecosystems, there is little information on how the spatial context of aquatic vegetaeffectiveness of harvest tion impacts the regulations. Effective fisheries management will require empirical data on both how and where aquatic vegetation interacts with the surrounding landscape to affect fish distribution and harvestregulated areas. Jackson et al. (2015) discuss the importance of aquatic plants from not only an ecological perspective but an economic one as well. They note that seagrass contributed meaningful market value to both commercial and recreational fisheries. In north temperate lakes, where recreational fisheries may be abundant, studies such as this present a strong argument for fisheries managers to evaluate aquatic plant protection strategies.

Other lessons may be found in the marine literature as well. Unsworth et al. (2018) advocated for an interdisciplinary approach to tackle seagrass conservation challenges. They note the need for basic inventories of status and conditions of seagrass meadows, understanding the linkages between the ecological and sociological elements of these ecosystems, and research targeted to support management actions. Applying their advice to lake submerged vegetation and fisheries is necessary. Vegetation in northern lakes constitutes an important ecosystem that provides valuable ecosystem services. Obtaining information on lake vegetation and the role it plays in fisheries production, as done for seagrass meadows, is a recipe for how we might advance lake vegetation management for fisheries benefits.

Lake macrophytes as fish habitat in north temperate lakes

It is well recognized that aquatic plant communities provide important ecosystem services (e.g., food, oxygen, substrate stabilization, nutrient uptake, and fish and wildlife habitat) and that these communities are under substantial and sustained threats from eutrophication and development of shorelines (Radomski et al. 2010, Radomski and Perleberg 2012, Dustin and Vondracek 2017, Nohner et al. 2018). There is considerable research on the consequences of eutrophication on lake plant communities. Carpenter and Lodge (1986) summarized and cited the research on submerged macrophytes, noting substantial changes in macrophyte abundance and species composition due to eutrophication. The dynamics of macrophyte-dominated versus phytoplankton-dominated systems have been particularly well studied in shallow lakes that shift between clear and turbid phases (Scheffer 1990, Phillips et al. 2016). The consequences of eutrophication on aquatic plants depend on the lake's initial trophic status and morphology. Wetzel (2001) described relative changes in aquatic macrophytes along a gradient of nutrient loading: With low nutrient loads submersed plant coverage is low due to nutrient limitations; at modest nutrient loads submersed macrophytes and epiphytic growth on plants increase; and at high loads with resulting reduced light submersed macrophytes are reduced or eliminated. In addition, the capacity of aquatic macrophytes to suppress nutrient recycling was reduced at high nutrient input levels (Genkai-Kato and Carpenter 2005). In deep-water lakes, Valley and Drake (2007) found that as eutrophication or productivity increased, variability in macrophyte biovolume increased.

Building on the work of Moyle (1945), recent northern lake studies provide additional understanding of the factors influencing aquatic macrophyte community structure. Borman et al. (2009) found that elodeid and characid species increased in abundance while isoetid cover and species richness declined on lakes with increased shoreland use compared to historical data from the 1930s. Mikulyuk et al. (2011) found that environmental factors (e.g., alkalinity and land-use disturbance) explained much of the variation in aquatic macrophyte composition from lake to lake. Radomski and Perleberg (2012) found that macrophyte richness was a function of total phosphorus, alkalinity, lake size, maximum depth, and ecoregion. They identified typical aquatic macrophyte communities, and found that lakes with high total phosphorus, watershed disturbance, and shoreland disturbance often had lower aquatic macrophyte richness and floristic quality (as stated, however, caution should be used when using aquatic plant richness indices to determine habitat quality, as the two are not necessarily synonymous). Lastly, development along northern lake shorelines has reduced emergent and floatvegetation ing-leaf (Jennings et al. 2003, Radomski 2006, Beck et al. 2013).

Through technological advances, greater quantification of dynamic lake plant communities is now possible, and natural resource management agencies are beginning to inventory and monitor lake vegetation habitat at fine spatial scales and high spatial accuracy on high-priority waterbodies. For example, the Minnesota Department of Natural Resources provides standard protocols for lake plant assessments that have led to repeatable surveys, including extensive mapping of emergent and floating leaf vegetation (Perleberg et al. 2019). Advances in hydroacoustic data processing and remote-sensing techniques now allow managers to collect information on spatial distributions of aquatic macrophytes at low cost (Radomski and Holbrook 2015, Dörnhöfer and Oppelt 2016). Using these inventory techniques in combination with plot-based sampling can provide a more complete understanding of a lake's vegetation (Valley et al. 2015, Valley 2016). As more lakes are mapped and surveyed within an ecoregion and across time, reliable predictive models may be developed that estimate aquatic plant occurrence and abundance both within and among lakes.

As with marine seagrass investigations, there have been many freshwater fish-centric studies exploring vegetation-fish associations, distribution of fish in lake macrophyte communities, and foraging success in lake plant stands (Smokorowski and Pratt 2007). For example, Pratt and Smokorowski (2003) observed that the dominant factor in the habitat selection of fishes in a northern lake appeared to be the presence or absence of aquatic vegetation. Weaver et al. (1997) investigated how the distribution of submerged macrophytes affected the distribution of littoral fishes within a lake. They found spatial heterogeneity of macrophytes varied widely within a lake, and the patchiness of macrophytes was an important factor in fish composition. In addition, dense vegetation supported large numbers of fishes of many species, with more abundant yellow perch and yearlingand-older bluegill in dense, species-rich vegetation than elsewhere. Freshwater fisheries biologists, like marine fisheries biologists, have also determined specific vegetated habitat preferences for recreationally important fish species (e.g. Reed and Pereira 2009, Kapuscinski and Farrell 2014), and many freshwater studies have noted that the complexity and density of aquatic macrophytes affects fish foraging behavior (e.g. for largemouth bass: Savino and Stein 1982, Valley and Bremigan 2002). Cross and McInerny (2006) note that protecting and enhancing lake vegetation stands, at both the site-specific and broad scales, are effective fish population protection strategies.

Despite the clear need, there are few freshwater studies that attempt to predict fish community response to changes in aquatic vegetation. For the Great Lakes coastal freshwater fisheries, Kovalenko et al. (2018) illustrate the importance of basinwide models to predict fish probability of occurrence and community metrics, and note how these models could be improved with high-resolution submerged macrophyte complexity data. In freshwater lakes, Valley et al. (2010) conducted markrecapture experiments on three vegetation-dependent fish species and developed three-dimensional models to predict fish probability of occurrence. They found that fish species occurrences were positively associated with macrophyte biovolume greater than 20% and with a high probability of occurrence of the macroalgae Chara. These studies had clear management implications for habitat protection for fish species that are declining in north temperate lakes.

Potential research and management opportunities for lake fisheries habitat

The intersection between in-lake habitat and fisheries management needs additional work (Cheruvelil et al. 2005; Sass et al. 2017). In particular, the inability to predict the consequences of changing aquatic macrophyte communities in north temperate lakes on a range of fish species points to likely avenues of research. First, studies are needed that assess the amount, morphotype, and heterogeneity of vegetation use by perceived vegetation-dependent fish species (Kovalenko et al. 2018). In some critical habitats, such as fish nursery areas, marine researchers have hypothesized that habitat structure may be more important than the habitat type itself (Heck et al. 2003). Answering this question in a lake ecosystem may provide managers valuable guidance on how to manage aquatic vegetation for fish. For example, if a nonnative plant species provides the necessary habitat characteristics to a community of fish, managers should consider the implications of removal versus perpetuation.

Surveys that provide high-precision spatial accuracy for both fish and vegetation distribution and abundance in lakes will be necessary. Cross and McInerny (2006) point out that existing data are insufficient for some vegetation-dependent fish species, as they may not be vulnerable to some fish sampling gear. Hydroacoustic surveys for lake plants combined with acoustically tagged fish data may provide one option in obtaining affordable fine-scale habitat associations. Sonoki et al. (2016), in assessing seasonal seagrass variability, stress the importance of long-term, continuous monitoring of habitat to effectively manage vegetation and fishery resources into the future. They found acoustic monitoring to be a viable method for data collection that was efficient, sustainable, and repeatable, all qualities that will be valuable to lake managers as well. Huijbers et al. (2015) assessed fish movement across marine habitats using acoustic telemetry. They determined this methodology was highly useful to detect variable or occasional movement patterns but that it did not come without challenges. It will be important for lake fishery managers to assess the trade-offs between the technical capabilities of different equipment, and then match this to the life history characteristics of the fish species of interest (Huijbers et al. 2015).

In addition, predictive models could also be developed to quantify and rate available habitat or to provide fisheries managers with a better understanding of habitat preferences and resource limitations on fisheries production. Elliot et al. (2017) developed predictive seabed models and assessed them in relation to distribution of several fish species. Their suggestions for developing an accurate predictive model included utilizing a range of environmental variables, such as extent and heterogeneity of habitat. Lake managers will likely find this guidance useful. In addition, they note that such models can be applied to various scales.

Second, given the destruction of aquatic plant stands along developed shorelines of north temperate lakes, understanding the consequences of these habitat losses would be helpful to those agencies tasked with regulating, enhancing, and educating about the importance of nearshore habitat. Marine researchers note that fish communities associated with seagrass are influenced strongly by both natural and anthropogenic variables, and these variables operate at different scales (Aller et al. 2014), a finding that is relevant to lakes as well. Therefore, effective lake fisheries management strategies need to acknowledge the role of both local and large-scale changes to aquatic plant habitat, as well as the sources of change. Other questions include whether the habitat loss consequences are expressed on a continuum, and if there are loss thresholds, then what is the disturbance-response threshold pattern (e.g., dose response, phase shift, breakpoint, etc.)? Seagrass has been found to demonstrate a threshold response to nutrient enrichment (Connell et al. 2017). Aquatic vegetation within deep-water lakes appears to respond similarly (Valley and Drake 2007), and the effects on fish could be substantial. In addition to the direct implications of habitat loss, a system unable to compensate for the major loss of vegetation may transition to another trophic state. Research that quantifies the type of response aquatic plants have to ecological or anthropogenic change will enable managers to implement adaptive management approaches that avoid approaching or crossing critical tipping points.

Third, quantifying the ecosystem services generated from these vegetated communities would provide valuable information to those who manage nearshore habitat. Apportioning fisheries biomass or economic value of fisheries production to aquatic plant habitat would likely be beneficial. In the marine environment, there has been found to be a clear economic cost to fisheries of seagrass degradation associated with ineffective habitat management (Jackson et al. 2015). In many north-temperate areas, fishing is a widespread form of recreation and provides a substantial contribution to the economy; in Minnesota alone, angler expenditures contributed nearly \$2.4 billion to the state's economy (USFWS 2011). Assigning a value to the relationship between fisheries and aquatic plants will help provide an economic justification for sustainable aquatic vegetation management strategies.

Most federal and state natural resource agencies originated out of a need for better management of fish and wildlife species after unregulated harvests resulted in economic and environmental disasters. In recent decades the public and agencies have also recognized the need to manage natural resources holistically, including nongame species, prairies, wetlands, and seagrass ecosystems. Formal management planning efforts for these resources typically include written management plans that outline objectives and measurable outcomes; they consider multiple uses of resources; they include a review and comment process and follow-up evaluations; and individual site plans are typically part of a larger regional planning effort. Lake plant communities often remain the exception. Management of lakes is often focused on recreational use interests, and ranges from eradication of nuisance aquatic plants, to managing vegetation that interferes with water access and boating ability, to stocking of fish species and regulation of harvest, often without quantified outcomes or identifiable conservation benefits. For example, in the last 20 years, nonnative aquatic plant management has been a specific focus with more than \$100 million annually spent on nonnative aquatic plant control (Pimentel et al. 2005).

In developing management plans, natural resource managers should be aware that stakeholders may have a different viewpoint on what effective vegetation management means for a particular lake. Both must understand the importance of maintaining a healthy lake ecosystem, while acknowledging that social and recreational pursuits are also part of system management. Identifying various perspectives and sharing information and goals will be valuable in enabling managers to implement sustainable lake management strategies. For example, lakeshore residents are more likely to protect nearshore plant stands if they recognize the erosion control benefits of rooted macrophytes, and lake managers are better able to prioritize sites for nuisance plant control if they understand the recreational boating use patterns on the lake. An informed and engaged community will be more likely to support lake management goals, leading to the sustainable management of both lake vegetation and fish communities.

In order for combined vegetation and fish dynamic studies to guide management, natural resources managers will have to collaborate on ecosystem studies and work together in evaluating vegetation management activities. This will take aquatic botanists and fisheries biologists working on the ridges between these two highly specialized ecological fields. First, managers will have to clearly identify current priorities. Approaches to vegetation management may vary depending on specific goals, such as increasing/ maintaining abundance of a particular fish species or managing for a diversity of species. If there are nonnative vegetation taxa present within the lake, managers need to weigh calls for removal against the habitat benefits provided (Engel 1995) and the potential impacts of the proposed control activity (Evans 2008). This may require forgoing some current activities, such as the current emphasis on managing non-indigenous plant taxa simply because they are non-indigenous (Radomski and Perleberg 2019). Managers will also need to consider fisheries goals at a wider scale than previously, as climate change results in shifts in the geographical ranges and dominance of both aquatic plants and fish species. This will likely require evaluating current work and funding priorities. These points reiterate the need for additional studies that link fish communities with vegetation changes; results of these studies may provide rationale for advanced regulatory controls to protect and enhance or restore aquatic habitat and provide management goals for aquatic vegetation that are too often lacking today.

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