# The Science of Invasive Species in a Dynamic Delta

Draft Report (May 23, 2020)
Delta Independent Science Board

If you need assistance interpreting the content of this document, please e-mail disb@deltacouncil.ca.gov.

## Table of Contents



## Preamble

The Sacramento-San Joaquin Delta Reform Act of 2009 stipulates that the Delta Independent Science Board "shall provide oversight of the scientific research, monitoring, and assessment programs that support adaptive management of the Delta through periodic reviews."[1] Management of the Delta to realize the coequal goals stated in the Delta Reform Act is directed by the Delta Plan. The Act also stipulates that the Delta Plan should restore a healthy ecosystem by promoting "self-sustaining, diverse populations of native and valued species by reducing the risk of take and harm from invasive species."[2] Box 1 describes how invasive species are considered in the Delta Plan and throughout the State of California.

[1] California Water Code Section 85280.
[2] California Water Code Section 85302(e)(3).

## Box 1. How are Non-native Species Considered in the Delta Plan?

Reducing the impact of non-native species and protecting native species is one of the five core strategies discussed in the Delta Plan's Chapter 4 amendment ("Protect, Restore and Enhance the Delta Ecosystem"). Within this strategy, the Plan recommends that state and federal agencies should prioritize and implement actions to control non-native species (ER R7), including communication and funding for a rapid response to invasive species (Delta Stewardship Council 2020). The Plan classifies non-native species into four categories: naturalized species, widespread and unmanaged species, widespread and managed species, and emerging species of concern. Invasive species are described as non-natives whose introduction may cause harm to the economy, environment, or human health. The Plan addresses the specific threats posed by several invasive species, including aquatic weeds (water hyacinth, Brazilian waterweed, water pennywort, Eurasian water milfoil, and parrot feather), overbite clams, and zooplankton. In addition, it explains the potential threat of invasions by zebra mussels, quagga mussels, and nutria.

The Plan also discusses measures and entities that have been established to prevent introduction of non-native species. California law requires that ships entering from outside the United States Exclusive Economic Zone either retain, properly exchange, or discharge ballast water to a treatment facility to reduce the chances of introduction. In addition, the California State Lands Commission limits the allowable concentration of living organisms in discharged ballast water. Several interagency programs have also been formed to prevent, detect, and manage invasive species, including the Delta Interagency Invasive Species Coordination Team, which is organized by the Sacramento-San Joaquin Delta Conservancy and aims to strengthen coordination among agencies to detect, prevent, and manage invasive species. The California Invasive Species Plant Council is a non-profit organization that catalogs invasive plants present in California, and the California Department of Food and Agriculture leads the control of toxic weeds in California. In addition, the Delta Region Areawide Aquatic Weed Project is a collaboration among academic and governmental agencies tasked with sustainably managing aquatic weeds in the Delta. The Delta Plan recommends increasing funding and communication among agencies for invasive species management through similar organizations. More broadly, the Invasive Species Council of California (ISCC website, http://www.iscc.ca.gov/) was formed to coordinate and strengthen the various organizations that address invasive species in the state of California.

The purpose of this review is to assess the state, quality, and potential usefulness of scientific information that helps agencies understand and manage the consequences of shifts of non-native invasive species (plants and animals) into Delta lands and waters. This review included an extensive literature review and two panels each comprised of five experts who explored the status of science relative to invasive species in the Sacramento-San Joaquin Delta. Additionally, Delta Independent Science Board members participated in several workshops, presentations, and discussions with managers.

We begin the review with a brief discussion of what is meant by the term "invasive species." We follow with an overview of how invasion fits into the broader picture of changes in species composition in a dynamic and rapidly changing ecosystem and how science can inform management at different invasion stages. We then review how science has been used to deal with several species invasions in the Delta. We follow by considering how ecological restoration may affect and be affected by invasive species, and how invasive species affect and are affected by the practice of adaptive management. Following a commentary on how invasive species may relate to ecosystem functioning, we conclude by highlighting areas in which scientific knowledge or its application in the Delta relative to invasions could be expanded and better coordinated and offering recommendations to strengthen the use of science dealing with invasive species in the Delta.

Although invasive species occur throughout the Delta, they have received by far the greatest attention in aquatic environments; wetlands, riparian habitats, and upland ecosystems are less well researched and should receive greater attention. In agricultural systems, various "pests" and "weeds" (which are also invasive species) have been the focus of intensive prevention and control efforts. While many of our comments apply to invasive species in any ecosystem, our focus in this report is primarily on invasive species in aquatic ecosystems.

## Defining Terms

The emergence of invasion ecology as an area of broad scientific and public concern dates from the publication of Charles Elton's book, *The Ecology of Invasions by Animals and Plants* (1958). Elton cast the challenge of invasive species using a military metaphor:

> *"I have described some of the successful invaders establishing themselves in a new land or sea, as a war correspondent might write a series of dispatches recounting the quiet infiltration of commando forces, the surprise attacks, the successive waves of later reinforcements after the first spearhead fails to get a foothold, attack and counter attack, and the eventual expansion and occupation of territory from which they are unlikely to be ousted again"* (Elton 1958: 109).

Although this militaristic metaphor may no longer be appropriate (Davis et al. 2011, Janovsky and Larson 2019), it does capture many of the features of the battle against invasive species. Yet it does not define what is or is not an invasive species. For that, we can turn to the National Invasive Species Management Plan (Beck et al. 2006), which defined an invasive species as "*a species that is non-native to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm to human health*." The National Invasive Species Council added that invasive species are those introduced to an area as a result of intentional or unintentional human actions.

By this definition, all invasive species are non-native, but not all non-native species are invasive. The two essential elements in the definition of an invader are that the species is non-native and that it causes harm. However, these elements are not as clear-cut as might first appear. First consider "non-native." How long must a species have been in a place to be considered "native"? In practice, species present in an area when Europeans first arrived and described what they found are considered to be native. Pysek and Richardson (2010) suggest that native species "evolved in a given area without human involvement or … arrived there by natural means … from an area in which they are native." Thus, species such as cattle egrets (*Bubulcus ibis*), which emigrated from their native Africa on their own and colonized much of the Americas, are not generally considered invasive. By this measure, a human vector must be involved for a species to be called invasive.

As more species expand their ranges from areas in which they are native into new areas in response to climate changes, however, determining whether a species is or is not native may be less important than determining whether it meets the second defining element: causing harm. For example, barred owls (*Strix varia*), native to eastern North America, have expanded into forests of the Pacific Northwest where they were historically not present. They compete with federally threatened northern spotted owls (*Strix occidentalis caurina*), displacing them from many areas and hastening their decline (J.D. Wiens et al. 2014). Should barred owls be considered an invasive species?

Whether a non-native species entering an ecosystem causes harm is a matter of human values, which can change or differ among groups of people. In the Delta, for example, sport fishers currently value non-native striped bass (*Morone saxatilis*) that were introduced over a century ago and have become "naturalized," whereas others emphasize the harm they now may cause by preying on native fishes. Striped bass are now managed as a recreational resource in the Delta. Therefore, determining whether a species should be labeled "invasive" can depend on how people perceive the economic and environmental benefits and costs of the species and how these are balanced (Beck et al. 2006), and different people do it differently. In general, managers have favored native over non-native species to conserve biodiversity, ecosystem services, and historical Native American cultural functions.

# I. SPECIES INVASIONS: AN OVERVIEW

## Setting the Stage for the Sacramento-San Joaquin Delta

Globally, invasive species are one of the greatest threats to the ecological integrity of ecosystems (IPBES 2019). Locally, the San Francisco Estuary (including the Delta) has been described as one of the most invaded estuaries in the world (Cohen and Carlton 1998). Because the Delta and San Francisco Bay Area is one of 25 global biodiversity hotspots of highest priority for conservation, the threat of invasive species is a major environmental concern. More than 200 non-native species have invaded the Delta's aquatic and terrestrial habitats. The high introduction rate is largely due to the many transport vectors that bring non-native species into San Francisco Bay—international shipping, recreational boating and fishing, horticulture and pet industries, agriculture, and deliberate introduction (Luoma et al. 2015). These vectors, combined with the Delta's highly altered landscape, have facilitated the establishment of many non-native species (Ruiz et al. 2011). About one quarter of non-native species introduced to the estuary are arthropods, followed by mollusks, fish, and vascular plants (Cohen and Carlton 1998).

Historically, invasions likely began to accelerate as ships started entering San Francisco Bay in 1775. As global shipping into the Bay increased around 1850, propagule pressure intensified (Cohen and Carlton 1995, Ruiz et al. 2000). Invasion rates have increased since the mid-1900s; about half of non-native species recorded in 1995 were introduced after 1960 (Cohen and Carlton 1998). This increase coincides with a time of growing international commerce from East Asia, the opening of new ports in the 1970s, faster ships, and increasing anthropogenic disturbance (Carlton et al. 1990, Carlton 1996). In particular, habitats were altered by increasing hydrological management through freshwater diversions beginning in the 1920s and major dam construction on the Sacramento River and its tributaries between 1945 and 1968 (Arthur et al. 1996, Winder and Jassby 2011). Conditions will continue to change into the future (Lund et al. 2010). Salinity will change in different parts of the Delta with changes in hydrological regimes (Fleenor et al. 2008), with cascading effects on Delta ecosystems and fish (Moyle and Bennett 2008). These transformations of the Delta facilitate the establishment and persistence of new species.

The vulnerability of disturbed environments to invasion is well documented in other ecosystems and has been substantiated by studies in the Delta (Leidy and Fiedler 1985, Feyrer and Healey 2003, Conrad et al. 2016). Hydrologic alterations—especially water diversions, altered flows, and increased water temperatures—have exacerbated drought-like conditions, which are linked to increasing invasions by non-native zooplankton that have in turn created conditions more favorable to non-native fish (Feyrer and Healey 2003, Winder et al. 2011).

Non-native species can often outcompete, prey upon, and exclude native species. The continuous arrival and spread of non-natives have displaced native vegetation, decimated native fish populations, contributed to the decline of native biodiversity, altered food webs and ecosystems, structurally damaged both natural and constructed habitats, and affected ecosystem services such as the provision of clean water (Simberloff and Rejmanek 2011). As in other estuaries, the Delta ecosystem also is vulnerable to invasion because brackish waters generally have fewer indigenous animal species than other habitats, facilitating the establishment of non-native species (Cohen and Carlton 1998, Wolff 1998, Cloern and Jassby 2012). The range of salinity conditions exposes the Delta to potential invasion by non-native species through a multitude of vectors and creates conditions favoring establishment once they arrive.

## The Invasion Process

Once a new non-native species has become established in an ecosystem, the structure, composition, and functioning of the ecosystem are changed. Science is often challenged to define the magnitude and even direction of these changes. To evaluate the science underpinning efforts to address invasive species problems in the Delta, invasion can be considered as one aspect of the broader dynamics of the community of species occurring in the Delta (the “species pool”; Figure 1).

Several forces drive changes in the species pool. These drivers—climate change, sea-level rise, land-use change, habitat alteration, hydrological changes, resource use, pollution and nutrient loading, droughts, and a host of other human actions—all affect species and their habitats directly or indirectly. As a consequence, the species pool in an area of interest is in a continual state of flux, with changing population levels of species already present, additions of new species from elsewhere, and loss of species previously present in the pool. Additions come from immigration of species moving of their own accord and from human introductions of new species, which may be intentional (e.g., assisted migration or stocking) or inadvertent (e.g., unintended release of bait fish, clams hitchhiking on recreational boats). Whether a newly arriving species becomes established depends on abiotic conditions, the characteristics of species that moved into the area earlier, and how they assembled themselves into ecosystems. Once established, an immigrant may affect the persistence or decline of species already present and those that arrive subsequently. Losses of species from the pool occur when a species becomes extinct or is extirpated from the area of interest or when a species disappears because individuals and population centers have moved elsewhere (e.g., as a result of climate change). Some species that vary in abundance may seem to disappear at times simply because they have become rare, only to reappear as numbers increase; Chinese mitten crabs (*Eriocheir sinensis*) are an example.

There are also transients such as migratory birds and fishes. The species pool of any location therefore contains a mixture of native and non-native species that changes over time, which creates an ever-changing mosaic of ecosystems over a broader area as species move among locations.

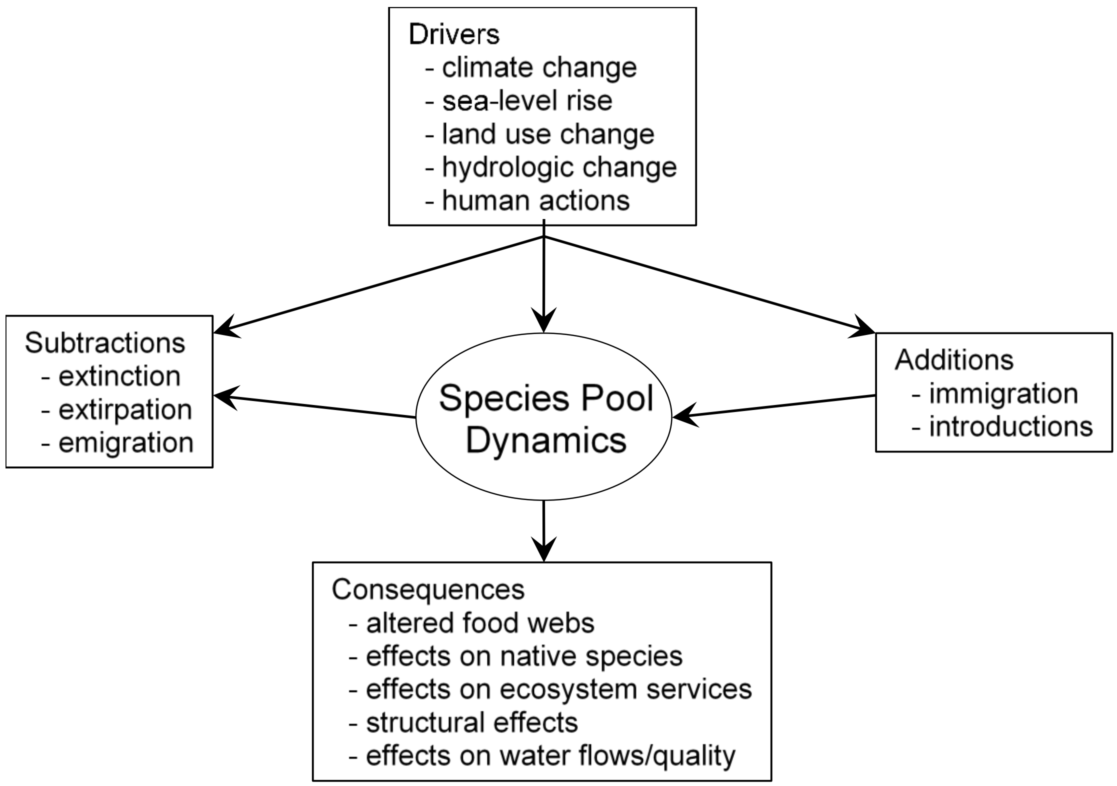


*Figure 1. A conceptual model of changes in the species composition (the "species pool") of an ecosystem, leading to multiple consequences.*

Changes in the species pool present in an area are not a recent phenomenon, of course. The species pool changed naturally for millennia before any people were around to change it either for their purposes or as an unintended consequence of their actions. Well before the arrival of European settlers in the Delta, Native Americans altered the mosaic of species by tending local plant species that bore acorns, fruits, and construction materials and by moving them into new locations (Zedler and Stevens 2018). Hunting reduced or eliminated populations of several species, particularly large mammals. Subsequent people domesticated species that grazed, introduced grasses that enhanced grazing, and used fire to favor grasslands. Beginning with European colonization of the Americas, people mixed species between the eastern and western hemispheres (Mann 2011), continuing on through to the economic globalization of today. The massive alterations that began in the mid-nineteenth century and the subsequent engineering of the Delta to encourage farming accelerated invasions by non-native species.

Compositional changes in the species pool can have a variety of ecological, economic, or sociological consequences (Figure 1). Ecologically, altered competitive or predator-prey relationships among species may disrupt food webs. The effects on native species that are rare or declining in abundance may be especially great, leading some to be extirpated. If these species are legally recognized as threatened or endangered, there will be political and economic as well as ecological consequences.

Other consequences of changes in the species pool may affect human interests more directly. Ecosystem services provided by existing species and biological communities may change. For example, new species may alter the biological, hydrological, or physical structure of the ecosystem (e.g., nutria, *Myocastor coypus*, burrow into levees). Changes in the composition of aquatic vegetation can alter water flows, temperature, and chemistry and can affect other elements of aquatic ecosystems as well as the quality and quantity of water available to people.

Changes in the composition of a species pool and their consequences, of course, are just changes. It is *people* who determine whether the changes are good, bad, or benign, depending on how they affect something about the system that people value, for whatever reasons. In some instances, the introduction of a new species into an area may have little observed effect on other species, ecosystem processes, or how humans use or manage the system. In other situations, a new species may be valuable to people (e.g., striped bass) or increase the productivity of food webs. When new species have harmful consequences they are labeled invasive species.

## Focusing Management on Individual Species

All invasive species are native somewhere, and they often exist there without causing any specific, recognized harm to human interests. They become targets for management when they enter and change an ecosystem to which they are not native. One way to eliminate the threat of invasive species, therefore, is to control or eradicate them at the source, before they spread into places where they are not natives. This is the approach taken, for example, in dealing with highly communicable diseases such as smallpox or Ebola (which fit the definition of invasive species, although they are not usually considered as such). For invasive plants and animals that come from other countries, however, such measures are usually impractical for a host of legal, political, cultural, and economic reasons. Consequently, most management is directed at eliminating the potential corridors of entry and at the invasive species in the locations they have invaded, where they can have negative effects such as those shown in Figure 1.

The general management protocol for dealing with invasive species is well established. The focus is largely on prevention, early detection, and rapid response to individual species. Management of invaders follows a sequence of stages from the initial detection of an invasion threat to the eventual adaptation to dealing with a well-established invader if all else fails (Figure 2).

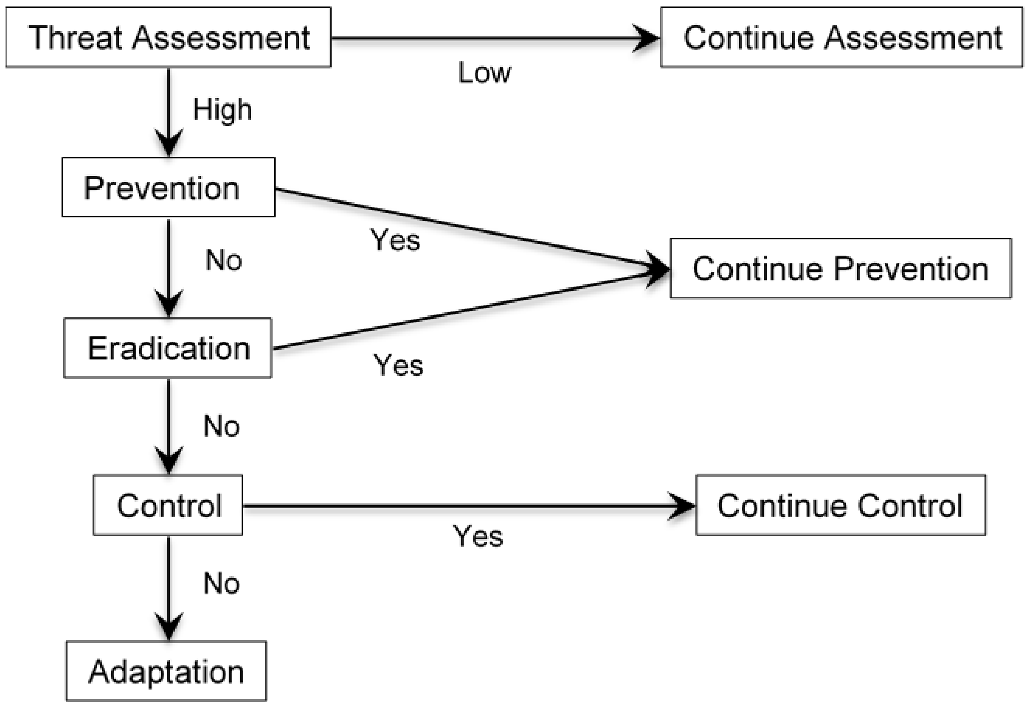


*Figure 2. Stages of management and responses in dealing with a potential invasive species. All of the stages and responses are informed by science and require monitoring to determine the course of action.*

The primary goal of management action is to reduce the chances of introducing a potential invader to the ecosystem in the first place. Effort is usually targeted at primary corridors for invasions and at particular species that might become invasive, often on the basis of effects they have had elsewhere and an evaluation of potential vectors. A first step is to conduct a threat assessment for the species (Figure 2). Science can be used to assess risks and identify species that have a high probability of entering the ecosystem of interest, becoming established, and doing harm. Elements of a scientific risk assessment would include; 1) an evaluation of the habitat requirements of the potential invader (including growth and reproduction, food resources and predators) relative to the habitat characteristics of the ecosystem, 2) a probabilistic evaluation of the potential corridors of entry; and 3) a measure of the degree of harm of a successful invasion. In essence; What are potential corridors of transport from one ecosystem to another? Will the species find suitable habitat and be able to survive, reproduce, and spread? And what harm will it do, to whom?

One of the best examples of prevention involves zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*). These mussels entered the Great Lakes via ballast water and have had ecosystem-level impacts on water quality, fisheries production, and even water supply and power intakes. The economic cost has been large (ref). The species have spread throughout much of the country (refs.). Studies have focused on predicting the potential for invasions into ecosystem by comparing the habitat requirements and restriction of zebra mussels (based on temperature, salinity, PH, flow rates, and calcium concentrations) to potential receiving waters (e.g. Whittier et al. 2008). Other studies have developed risk-based decision models focused on potential food-web disruption and other impacts (e.g. Wu et al. 2010). Corridor control has ranged from boat inspections for overland transport to extensive education programs and outreach, such as the nationwide 100th Meridian Initiative.[3]

Gauging the potential ecological and economic impacts of an invading species is a judgment that can draw on a variety of quantitative and qualitative tools. These can range from expert opinion and ratings (used by the ISCC), to observations of the species in nearby or similar habitats (e.g., zebra and quagga mussels, nutria), to a comparison of the species' habitat requirements to habitat availability in the ecosystem of interest, to risked-based decision models (e.g. Wu et al. 2010). For example, the ISCC assessed the threat of 200 species to California based on expert opinion of their potential impact and managers' ability to control the species.

If a species is identified as a threat, the next management step is prevention (Figure 2). Prevention is usually targeted at eliminating the primary paths for the species to enter the ecosystem. In some cases, this might be done through an approach targeted on specific species, such as inspecting boats traveling into a region or a particular ecosystem for zebra and quagga mussels. Often prevention is targeted more broadly at minimizing or eliminating general pathways of potential introductions, such as ship ballast water discharged into estuaries. The Border Protection Stations at entry points into California are intended to intercept the flow of potential invasive species on well-travelled transportation corridors. Monitoring targeted toward individual species or as part of a more general sampling program can provide the data needed to map and assess new invasions.

If prevention fails, rapid response and eradication may be the next management steps. Eradication means that no individuals remain of the invading species. Few invaders have actually been eradicated, and then only where invaders were detected at an early stage and in a small region. An example is the macro-alga. *Caulerpa taxifolia,* which is highly invasive in the Mediterranean Sea but was being controlled within 17 days of its discovery in the Delta (Anderson 2002). Once an invader has become established, controls can limit the spread, reduce the abundance, or lessen the impact of the invader. Various techniques have been used, ranging from harvest to poison (e.g. vegetation in the Delta), as described later in this review.

[3] The 100th Meridian Initiative:
https://www.fws.gov/fisheries/ANS/pdf_files/100thMeridian.pdf

Science is needed to assess the impact of the invader and the most effective ways to map, assess, control, or limit the impact of a successful invasion. Often an invading species may be resistant to control efforts or the efforts may come too late. The invader becomes established in the ecosystem. . Often an invader is not even detected until it becomes well established, like Corbicula in the Delta (refs). Management must then adapt to the presence of the invader in the ecosystem (Figure 2). In some instances, the invader may fit into an ecosystem with minimal observable effects on other species or little disruption of ecosystem functions—it has become integrated into the ecosystem ("naturalized") and no longer meets the definition of an invasive species (i.e., causing harm).

Sometimes we do not know about a new invader until it becomes well established in an ecosystem. This can happen, for example, if the invading species is small or cryptic or otherwise escapes notice until it has reached a level that allows it to persist and grow. It may take some time before a new species becomes established, its population expands, and it can be linked to a change in ecosystem services that we value. Such time lags complicate management responses and require ongoing monitoring.

Implementing any of the management responses shown in Figure 2 also requires that efforts be effectively organized and managers are prepared for action. This entails mobilizing the relevant scientific expertise and legal authorities and ensuring that financial and logistical support is sufficient. Lines of authority and responsibility must be clearly defined.

# II. DEALING WITH INVASIVE SPECIES IN THE DELTA

## Invasive species in the Delta[4]

To respond to and manage invasive species in the Delta, it is important to understand their specific and combined impacts. Some introduced species have had more substantial environmental and economic impacts than others due to their capacity to reshape their environment, with cascading effects on habitat, nutrient and contaminant cycling, and trophic structure (Kimmerer at al. 1994, Crooks 2002, Sousa et al. 2009). Significant habitat-altering invasive species include several species of aquatic plants that alter flows and create novel habitat for non-native fish (Brown and Michniuk 2007, Loomis 2019). Filter-feeding bivalves have altered benthic and pelagic food-web structure and nutrient cycling.

The following examples highlight several significant non-native species and their impacts on the Delta ecosystem.

[4] Drawn from a literature review by Madison Thomas while a Fellow of the Delta Science Program

### ***Bivalves and their effects on the pelagic food web***

The Delta has been invaded by several bivalve species that have significantly altered food webs through competition with native filter- and deposit-feeding invertebrates and through altering phytoplankton concentrations. The most notable and well documented of these invaders is *Corbula amurensis*, which was first sighted in the San Francisco Estuary in Grizzly Bay in 1986 (Carlton et al. 1990). The species was likely brought to California as larvae in the ballast of cargo ships. Benthic communities in invaded areas were significantly disrupted and species richness in these habitats gradually decreased during the late 1980s as *C. amurensis* came to dominate the community (Nichols et al. 1990). The combination of the high population growth rate of *C. amurensis* with its filter-feeding efficiency led to a nearly five-fold decrease in average phytoplankton biomass within 2 years of invasion, limiting food availability to zooplankton (Jassby et al. 2002, Thompson 2005). This reduction in phytoplankton biomass shifted food-web dynamics by directing primary production toward benthic consumers (clams) instead of zooplankton (Kimmerer at al. 1994). By depleting native zooplankton, *C. amurensis* facilitated the growth of non-native species in the Delta and shifted the system from a zooplankton community dominated by herbivores and omnivores to one dominated by predatory species. The decreasing food availability for pelagic fish is thought to have contributed to the decline of many fish populations (Nobriga 2002, Cloern and Jassby 2012, Brown et al. 2016). The decrease in productivity of pelagic species stemming from declining phytoplankton was likely due to the combined effects of diversions of freshwater from the Delta, drought conditions that altered salinity and favored non-native zooplankton species, and the *C. amurensis* invasion (Hammock et al. 2019). Thus, the increase in non-native zooplankton in the Delta and associated decline of native pelagic organisms followed multiple human alterations, including water diversions in the Delta (Winder and Jassby 2011, Winder et al. 2011).

### ***Aquatic plants***

Several species of non-native aquatic plants reduce native plant diversity and clog waterways, threatening water quality, altering nutrient cycles, and diminishing recreational values in the Delta (Borgnis and Boyer 2016). Of the 19 submerged and floating aquatic plants that occur in the Delta, at least half are non-native. Two of the most widespread non-native species are *Egeria densa* (Brazilian waterweed) and *Eichornia crassipes* (water hyacinth). *Egeria densa* is an example of Submerged Aquatic Vegetation (SAV). It was introduced to the Delta in 1946 from aquarium release and became a species of concern in the 1990s. It forms thick-rooted mats that alter water flow and habitat while impairing recreational activities such as boating and fishing. These hydraulic alterations create a positive feedback loop in which the presence of *E. densa* facilitates its further growth and dispersal (Hestir et al. 2015). The species' low salinity tolerance limits its growth into the western Delta relative to native aquatic vegetation (Borgnis and Boyer 2016). *Egeria densa* cover increased 50%

between 2007 and 2014 to about 2900 ha. It is now the dominant submersed aquatic plant, covering 11% of Delta waters.

*Eichornia crassipes* is an example of a Floating Aquatic Vegetation (FAV) species. It was introduced to California in 1907. It has invaded slow-moving waterways, where its growth changes water quality, displaces native vegetation, clogs channels and marinas, and increases water loss due to its high transpiration rate (Underwood et al. 2006). *Eichornia crassipes* cover increased four-fold between 2004 and 2014 to about 800 ha (Santos et al. 2011a, Dahm et al. 2016).

In addition to *E. densa* and *E. crassipes*, several other non-native plant species pose a threat to Delta waterways. *Ludwigia* spp. (water primrose) is a FAV species that increased 4-fold in cover between 2004 and 2016 and encroached into both open water and emergent marsh habitat (Khanna et al. 2018). *Ludwigia* has been recognized as an emerging problem only in the past decade; coverage in 2014 was similar to that of *E. crassipes* (800 ha) (Boyer and Sutula 2015, Dahm et al. 2016). An additional common non-native FAV species of emerging concern, *Limnobium laevigatum* (South American sponge plant), somewhat resembles water hyacinth and is often found alongside it. Common non-native SAV species include *Myriophyllum aquaticum* (parrot feather), *Myriophyllum spicatum* (Eurasian watermilfoil), *Potamogeton crispus* (curlyleaf pondweed), and *Cabomba caroliniana* (Carolina fanwort) (Ta et al. 2017). *Hydrilla verticillata* (hydrilla) is not yet present in the Delta but occurs elsewhere in California and could migrate into the Delta during high water periods (Ta et al 2017). Many non-native plant species in the Delta pose major threats to native plant biodiversity and habitat; species richness of non-native vegetation has been correlated with a decrease in native vegetation species richness and biomass (Santos et al. 2011a).

Despite decades of research and policy directed at managing invasive aquatic plant species, monitoring and controlling their spread remains difficult due to insufficient funding, the absence of consistent monitoring programs, and complex regulations that restrict treatment (Ta et al. 2017). However, remote sensing and chemical, mechanical, and biological controls have been somewhat effective with managing invasive vegetation. For example, several studies have identified and mapped invasive vegetation with high accuracy using hyperspectral remote sensing (Underwood et al. 2006, Hestir et al. 2008, Khanna et al. 2018). However, this method is subject to error due to spectral variation associated with plant phenology. Nonetheless, remote sensing may be an alternative to costly and time-consuming methods that require direct monitoring of vegetation in remote locations. Drones offer some potential to deliver herbicide to specific patches of invaders (Huang et al. Project: https://www.ars.usda.gov/research/project/?accnNo=427340).

Efforts to control vegetation may have unintended consequences. For example, mechanical shredding of *E. crassipes* may increase overall carbon, nitrogen, and phosphorous levels in the water column up to 10% (Greenfield et al. 2007). Mechanical shredding may also facilitate the spread of many invasive aquatic species, as fragmented plants may re-propagate. Over half of the cut fragments of *E. crassipes* may survive mechanical control and reach a habitat suitable to produce new plants, suggesting that mechanical control may have limited effectiveness in the Delta (Spencer et al. 2006). Alternative uses for the shredded plant material (e.g., feed for livestock) may not be cost effective.

Non-native SAV species also differ functionally from native species. Their greater leaf area, denser canopies, and greater light-use efficiency give them a competitive advantage over native species (Santos et al. 2011b). Thus, the removal of one non-native species may result in colonization by another non-native species instead of the intended native vegetation. Inadvertent effects of control methods must be considered in management of invasive species in the Delta.

Non-native aquatic plants have substantial economic impacts in the Delta, affecting water quality, turbidity (and thus habitat suitability for species such as Delta smelt), recreational and commercial boating and fishing, water exports, and virtually all human uses of water. Consequently, there are major ongoing efforts to control invasive plant species in the Delta, spearheaded by a variety of agencies and programs (Box 2). From 2013 to 2017, combined state and federal efforts in chemical control of invasive SAV and FAV averaged approximately $12.5 million per year (Conrad et al. 2020). Because of regulatory restrictions, control could not be applied everywhere it was needed, and even this level of expenditure was insufficient to achieve effective control of invasive aquatic plants (Conrad et al. 2020).

**Box 2. Controlling Aquatic Plants**

Management of invasive aquatic vegetation in the Delta is controlled by several agencies, including the California Department of Food and Agriculture (CDFA), the California Department of Fish and Wildlife (CDFW), and the California Department of Parks and Recreation, Division of Boating and Waterways (DBW). Because these are independent agencies, coordinating management strategies is often difficult. Several aquatic invasive species, including *E. crassipes* and *E. densa,* are frequently targeted by the DBW Aquatic Invasive Species Program, which is the principal state agency with the authority to treat invasive aquatic species in the Delta (Ta et al. 2017). Treatment typically consists of herbicide application between March and November. Mechanical and biological control measures are also taken to reduce coverage. Biological controls involve alien insects or mites that are introduced to lower the density of non-native vegetation (Ta et al. 2017). Three insect species have been introduced to target *E. crassipes* and two to target *Arundo donax* (giant reed), although only one of these, *Neochetina bruchi* (water hyacinth weevil), has become established in the Delta (Akers et al. 2017, Hopper at al. 2017). There are plans to release other species of weevils and planthoppers in the Delta to selectively feed on invasive vegetation (Ta et al. 2017).

Because managing invasive vegetation is an interagency effort, there are also several collaborative organizations in the Delta that aim to control and manage invasive aquatic species. The Delta Interagency Invasive Species Coordination Team (DIISC) is an interagency group of individuals from agencies focused on preventing, detecting, controlling, and managing invasive species in the Delta (Ta et al. 2017). They aim to increase collaboration among agencies through meeting and facilitating symposia focused on invasive species. USDA sponsors the Delta Region Areawide Aquatic Weed Project (DRAAWP), which focuses on management strategies, control agents, mapping of weeds, and documenting their effects on ecosystem services. DRAAWP centers its efforts on *E. densa*, *E. crassipes*, and *A. donax* and how to best prioritize management practices and provide agencies with essential information.

### *Wetland vegetation*

Wetlands such as tidal or freshwater marshes are a major component of ecological restoration programs in the Delta (e.g. California EcoRestore). Once disturbed, wetlands are vulnerable to invasion by non-native plant species; once established, the invaders are often difficult to control or eradicate. Box 3 describes the difficulty in dealing with invasive *Phragmites*.

Because wetlands have been a major focus of restoration for a long time, there is considerable knowledge available about several widespread, aggressive invasive plants such as cattails, reed canary grass, and common reed (Zedler and Kercher 2005). Such species are characterized by rapid clonal growth and resistance to control. Their tall leaves and stems enable them to outcompete native species. Wetland restoration provides opportunities for field experiments that can enhance our understanding of invader biocontrol methods, herbicide resistance, or the use of heterogeneous topography to facilitate diverse plantings that resist invasions.

**Box 3. A model invader: *Phragmites* in wetlands**

A tall grass called common reed (*Phragmites australis*) is highly invasive in global wetlands and in the Delta and, where it crowds out competitors and forms monotypes. Mapping and tracking distributions are difficult in the Delta because native genotypes (not usually invasive) and European strains (highly invasive) both occur and look alike from the air and on the ground (Hickson and Keeler-Wolf 2007). As it does elsewhere, *P. australis* inhabits multiple habitats: palustrine emergent wetlands, freshwater drainage ditches, intertidal bay islands, muted tidal marshes, and wetlands with saline soils (Galatowitsch et al. 1999). Another aggressive grass, giant reed (*Arundo donax),* is also a major invader (Ta et al. 2017). Both invaders resist chemical and biocontrol efforts (*Arundo donax* website: https://www.cal-ipc.org/plants/profile/arundo-donax-profile/).

***Fish***

Many non-native species of fish have been introduced to the Delta through stocking to improve local food and sportfishing opportunities and diversify fish communities. One of the first species introduced was *Alosa sapidissima* (American shad), which was brought to the Sacramento River in 1871 and supported a commercial fishery until the 1950s (Dill and Cordone 1997). *Ameiurus nebulosus* (brown bullhead catfish) were introduced to the San Joaquin River in 1874, followed by several other species of catfish. Striped bass were then introduced to the Carquinez Strait in 1879, leading to a successful commercial fishery that recorded over one million pounds of catch within 20 years. Although large-scale stocking of hatchery-raised striped bass ended in 1992 due to threats to native fish, stocking continued at lower levels in later years.[5]

[5] In February 2020 the California Fish and Game Commission adopted a policy of striving “to maintain a healthy, self-sustaining striped bass population in support of a robust recreational fishery” while eliminating the policy of supporting artificial propagation.

Several other bass species were introduced to California prior to 1900, with records indicating that smallmouth bass (*Micropterus dolomieu*) were first stocked in 1874 and largemouth bass (*Micropterus salmoides*) as early as 1891. Stocking continued for many years. Other bass, including the spotted and redeye bass (*Micropterus punctulatus* and *Micropterus coosae*), were introduced on a lesser scale during the 1930s to 1960s. The establishment of several species of bass in the Delta has resulted in a world-class bass fishery, leading to conflicting goals among individuals managing non-native fish in the Delta: many people wish to recover populations of native species, while others aim to maintain healthy populations of harvestable non-native species. Many of these species, like largemouth and striped bass, prey on or compete with native species like Chinook salmon (*Oncorhynchus tshawytscha*) (Brown and Michniuk 2007). Consequently, management of fish in the Delta involves balancing conflicting interests and ecological goals.

Some other fish species have been introduced into California but not the Delta as biocontrol agents. *Gambusia affinis* (western mosquitofish) and *Menidia beryllina* (inland silverside) were introduced for biological control of mosquitoes in the 1920s and 1960s, respectively, and became established soon thereafter. *Menidia audens* (Mississippi silverside) were also introduced in the 1960s as a biological control agent; they became widely established by 1975 and are now one of the most widespread and abundant fish species in the Delta (Mahardja et al. 2016).

Other fish species have been introduced unintentionally. One of the most abundant demersal fish in the Delta, *Acanthogobius flavimanus* (yellowfin goby), was first observed in 1963 and was likely introduced through ballast-water transport (Dill and Cordone 1997; Workman and Merz 2007). Their abundance is likely due to their generalist diet, but their inability to reproduce in freshwater has likely limited their expansion. More recent introductions through ballast water include *Tridentiger bifasciatus* (shimofuri goby) and *Tridentiger barbatus* (shokihaze goby), which were first recorded in 1985 and 1997, respectively. Collectively, non-native species introduced since the 1800s have established populations exceeding the abundance of native species, resulting in major reductions in native fish biodiversity.

Several studies have substantiated that more non-native than native fish species are present in the Delta. In one study that analyzed fish-catch data throughout the Delta between 1994 and 2002, 62% of the species caught and 59% of the overall catch were non-native (Brown and May 2006). Feyrer and Healey (2003) reported that only eight of the 33 species sampled in the southern Delta between 1992 and 1999 were native; no native species accounted for more than 0.5% of the total catch. Higher abundance of native species was correlated with high river flow and turbidity, whereas more non-native fish were associated with warmer water temperatures and low river flow—characteristics of the highly modified south Delta. Similarly, a majority of the overall catch of fish larvae collected between 1990 and 1995 was non-native species associated with low flow and high temperature conditions during the late season; native species were more abundant during early-season conditions (Feyrer 2004). Marchetti et al. (2004) suggested that restoring natural hydrologic processes could mitigate the invasion of non-native fish species while favoring native fish populations.

### *Non-native fish and submerged aquatic vegetation (SAV)*

Although both non-native fish and plants have significantly increased in recent decades, it is not entirely clear that these trends are causally related. Several studies have linked the proliferation of invasive vegetation to the growth of non-native fish populations. One study found that *Egeria densa* is important habitat for juvenile largemouth bass, and the proliferation of this plant likely supported the growth of the largemouth bass fishery in the Delta (Conrad et al. 2016). *Egeria densa* habitat is very productive and several studies have correlated its presence with fish assemblages dominated by non-native species, some of which are predators of native fish such as juvenile salmonids (Brown 2003, Grimaldo et al. 2003, Nobriga et al. 2005, Brown and May 2006, Brown and Michniuk 2007, Loomis 2019). Nobriga et al. (2005) found that native special-status fish species were less abundant in SAV (primarily *E. densa*) habitat than in turbid open water. In contrast, Young et al. (2018) reported that *E. densa* was not correlated with increased macroinvertebrate food for non-native largemouth bass when compared with other SAV species. Although it has been proposed that restoring tidal-wetland habitat would provide important habitat for native fish species, this may only be true where invasive SAV (*E. densa*) is not well established and therefore would not invade the restored habitat (Brown and Michniuk 2007). As a result, restoration for native fish communities may be more successful in the northern Delta where *E. densa* and non-native fish are less well established. The possibility that the proliferation of non-native fish may have been facilitated by a concurrent increase in non-native SAV should be considered when planning future management of both SAV and non-native fish.

### *Aquatic mammals*

Nutria are non-native aquatic rodents that are a major threat in the Delta. Although nutria were first introduced to California from South America in 1899 for fur farming, this attempt was commercially unsuccessful (Evans 1970, Carter and Leonard 2002). Subsequent introductions led to a small feral population by the 1940s (Schitoskey 1972), but nutria numbers remained low and the species was eradicated from the state by 1978 (Deems and Pursley 1978). However, a reproducing population was found in the San Joaquin Valley in 2017, and nutria are currently found in the Delta in San Joaquin and neighboring counties (CDFW 2019).

Nutria can be vectors for parasites and pathogens and their burrowing and herbivory damage habitats and infrastructure. This is especially a concern in the Delta where burrowing in levee systems can lead to breaches, erosion, and widespread structural damage. Nutria also can consume up to a quarter of their body weight in vegetation a day, posing a major threat to native plant communities and agriculture. The state began an eradication program in 2018 and had caught over 410 nutria by March 2019. Establishment of nutria in the Delta could extensively damage both natural habitat and water infrastructure, ultimately threatening native species, agriculture, flooding, and water conveyance.

## Invasions in a changing environment

The Delta is a dynamic place and will become more so in the future. Rapid and accelerating changes in the Delta—the effects of climate change, sea-level rise, changes in water management, salinity intrusion, and so on—will affect virtually all of the factors driving changes in species pools shown in Figure 1. For aquatic invasive species, the changes will affect the vectors and dispersal patterns, characteristics of the receiving habitats, water flows, salinity, seasonal pulses of floods and food-web dynamics, water temperature, and human activities. These will all influence the probability of entry and establishment of invasive species, as well as their impacts, creating complex management challenges (Rahel and Olden 2008).

Changing habitats will alter the suitability of the Delta to different species and therefore change risk assessment. Corridors may also change. Vulnerability to invasions may differ among habitats and broad taxonomic groups. For example, in a broad metananlysis, Sorte et al. (2013) found that non-native invaders were more likely to benefit from the effects of climate change than native species in aquatic ecosystems, but not in terrestrial ones. Non-native fish are generally able to tolerate warmer temperatures, giving them an advantage over native species as the climate warms. Moyle et al. (2013) found that 82% of native fish are vulnerable to the effects of climate change, versus 19% of non-native species.

Consideration of the consequences of predicted climate change in the Delta will be important in forecasting future invasions. Sea-level rise will increase salinity intrusion and inundation in the Delta. Maximum tidal inundation should be mapped to evaluate changes in habitats that will favor the establishment of new species. Climate warming also will change habitat availability. Some species will likely be extirpated from the Delta as their temperature limits are exceeded, while other species may invade or encroach as higher temperatures or disruptions benefit them (i.e., the subtractions and additions of species to the species pool shown in Figure 1). Part of this process will involve range expansions of species occurring elsewhere in California.

Warming climate, especially warmer surface water, is expected to shift species distributions and allow non-native species to invade new areas (Walther et al. 2009). Of arguably greater concern are extreme events (e.g., floods, droughts, storms) that will disturb aquatic and wetland ecosystems and facilitate non-native species at every invasion step (Diez et al. 2014). Cloern et al. (2011) modeled how the Delta might change in both average conditions and extreme events. They advised Delta managers to strategize how to adapt to warmer temperatures, higher sea levels, and salinity intrusion and to plan for more runoff in winter and less in spring-summer. They viewed their projections as a starting point, warning “Today's extremes could become tomorrow's norms.”

Changes in temperature and precipitation are expected to affect all aspects of invasion: dispersal pathways (as trade and transport change), establishment (as species ranges shift), impacts (more insect pests, greater food requirements as animals experience stressful conditions, lower streamflows as trees increase evapotranspiration rates), and efforts to manage and control (e.g., shifts in biocontrol-prey interactions, shifts in herbicide tolerance, and more fire-tolerant weeds as drought and fire increase) (Dukes 2011). Along the coast of southern California, invasive non-native plants expand their distributions in years with greater rainfall and lowered soil salinity, which trigger seed germination of upland weedy species as well as native plants (Noe and Zedler 2001a, 2001b; Noe 2002).

Assisting the migration of natives to keep up with climate change and rising sea levels could keep them from going extinct and deter non-native invaders. Sea levels and climate are expected to change faster than native plants and associated animals can migrate to escape changing conditions. Even a single storm can bring saltwater well inland of the normal high tides, killing salt-intolerant species and opening space for invasions. As Callaway and Parker (2012) noted, management of invasive species is already extremely difficult, but “shifting climates will create additional challenges to consider, as changing conditions could create opportunities for a different group of nonnative species, and the future spread of existing invasives will be even more difficult to predict.” The value of assisted migration of native species, however, is debatable. Proponents expect the benefits of translocations to outweigh the risks; opponents argue that the impacts of introduced species are not understood well enough to make informed decisions about species translocations (Ricciardi and Simberloff 2009).

Some invasive species seem pre-adapted to thrive with changing climate. For example, common reed (Box 3*,* is well adapted to varied climatic conditions where it is native: each lineage has multiple genotypes and grows in diverse habitats and its plastic traits respond to changes related to global warming (temperature, $CO_2$). Responses to co-occurring environmental changes (drought, salinity, flooding) vary by genotypes within lineages (Eller, Skálová et al. 2014; Eller, Lambertini et al. 2014).

## Invasive species, ecological restoration, and adaptive management

The connection of invasions to restoration is two-fold. First, restorations can create opportunities for non-native species to invade a site, so restorations often include targeted efforts to control or reduce the abundance of invasive species (e.g., by harvesting vegetation). Second, habitat restoration provides the opportunity to use adaptive management approaches to test and select effective methods that favor native species over non-natives.

Restoration actions are often accompanied by disturbances that allow invaders to become established. Once non-native plant species become dominant, they often form monotypes that resist eradication. Most attempts to eradicate species covering >1 ha have not achieved their goal (Rejmanek and Pitcairn 2002). The multimillion-dollar attempt to eradicate hybrid cordgrass (*Spartina foliosa X S. alterniflora*) along the shores of San Francisco Bay (San Francisco Estuary Invasive Spartina Project: http://www.spartina.org/) sparked debates over costs vs. benefits (such as restored habitat for shorebirds, endangered species of rails, or salt marsh harvest mice).

Combinations of co-occurring events and sequences of extreme events may also create opportunities for non-natives to invade restoration sites. Such “sequence events” may have different outcomes when the sequence is reversed (e.g., flood-then-drought effects differ from drought-then-flood effects; Zedler 2010a). Coinciding extremes, such as the co-occurrence of high river discharge and high coastal water levels, must be considered in risk assessments (Khanna et al. 2019). It is important to include such worst-case scenarios in restoration planning, as there will be surprises and decision protocols will be needed throughout implementation and monitoring.

Restoration often involves transplanting plants into newly restored sites. This may create opportunities for the spread of disease. For example, native plants in northern California nurseries were infected with the non-native fungus, *Phytophthora tentaculata*, which caused root and stem rot. When planted to restoration sites, the disease spread. While there are now effective guidelines for nurseries to follow, future non-native pathogens await detection (Hunter et al. 2018).

Substantial knowledge is available for replacing non-native plants with former natives. Researchers know where invaders do and do not dominate (Hickson and Keeler-Wolf 2007). Local ecologists often know where there are opportunities to effect control, how to attempt eradication, and what to expect as outcomes. Although preventive programs are envisioned for new invaders, these have not yet been developed or implemented for aquatic invasive plants and wetlands. Inspections, education, and training of people who use Delta waters are essential ingredients of early detection (Ta et al. 2017).

Many researchers with experience in upland vegetation assume that restoring diverse vegetation will resist invasion. Reviews by Guo et al. (2018) and D'Antonio et al. (2016) suggest that aiming for high biodiversity, biomass, and productivity will reduce invasions. However, this is not necessarily true everywhere. Stohlgren et al. (2003) reported the opposite, finding that some diversity hotspots have also been hotspots for invasion.

Restoration projects can be designed as adaptive-management experiments (Zedler 2017). Large adaptive-management experiments can reveal best methods for restoring habitats and managing invaders. Because new invaders will likely appear during restorations, an experimental approach may reveal reasons for their expansions, helping to inform effective management. Adaptive-management experiments may also be the most practical way to determine the effectiveness of new methods to control invasive species, although Conrad et al. (2020) caution that such experimentation may not be possible in some restoration sites because of regulatory restrictions (e.g., protections of endangered species).

Ecological restoration is always a long-term process and adaptive management requires monitoring to determine whether and when adaptation of management practices may be necessary. Norton (2009) offered cogent advice: "Restoration outcomes in the face of biological invasions are likely to be novel and will require long-term resource commitment, as any letup in invasive species management will result in the loss of the conservation gains achieved."

**The status of invasive-species science in the Delta**

The science dealing with invasive species in the Delta has largely emphasized: 1) prevention, early detection, eradication, assessment and monitoring, and control of individual species (e.g., nutria) or groups of similar invaders (e.g., emergent aquatic vegetation); 2) retrospective impact assessment (e.g., the effects of invasive clams); and 3) development of new technologies for monitoring (e.g., remote sensing and eDNA).

We can consider the state of the state from two perspectives. First is the science associated with individual invaders. Second is the ecosystem-level science that address ecosystem services and function relative to management needs in the context of a continually invaded and changing ecosystem.

The science of dealing with individual invaders in the Delta seems well established, of excellent quality, and coordinated across the Delta and the State. Examples include work on invasive plants and recent efforts on nutria. At the same time, quantitative assessment of the risk of invasion or the impacts of specific invaders is often difficult. Of necessity, most research has focused on correlations (e.g., invasive clams and the decline of pelagic fish species); carefully designed experiments to establish causal relationships are difficult. There does not seem to be an operational food web model of the Delta whereby the impacts of established or potential invaders can be assessed. Assessments of invader impacts are also confounded by other ongoing changes in environment drivers, so management must be undertaken in the context of a continually changing ecosystem and species pool.

Ecosystem sustainability is one of the coequal goals for the Delta. But "sustainability" does not mean unchanging stasis. As the species pool changes, managers need to assess species' functions and determine the benefits and costs of changes in dynamic ecosystems. New tools are becoming available for predicting, tracking, and controlling invaders. Dick et al. (2017) created a Relative Impact Potential metric to predict the likelihood and magnitude of ecological impacts of invasive species, using data on the numerical responses and functions derived from other populations elsewhere. Foxcraft (2009) established "thresholds of potential concern" as triggers to begin controlling non-native species in the adaptive management of South Africa's Kruger National Park. Such approaches may help to shift the management of invasive species from response to prevention.

Godoy (2019) challenged researchers to uncover "emergent properties" of ecosystems being invaded by considering multispecies assemblages and learning how communities change once invaded. Efforts focused on just two competing species at a time (e.g., a native and non-native) miss the emergent properties of ecological communities. Researchers and modelers need to understand the risks of invasion impacts at species, multispecies, and ecosystem levels (Vila et al. 2011). That is the context in which invasions occur.

That said, many of the critical questions about invasive species and their management still boil down to specific situations. Box 4 provides several examples.

**Box 4. Examples of science needs for invasive species management in the Delta.**

The American bullfrog, red-eared slider turtle, and Mississippi silverside have caused irreversible damage to the Delta ecosystem. More needs to be known about persistent non-natives, including invasive alien clams (early studies in Carlton et al. 1990; Nichols et al. 1990), Chinese mitten crabs, and eastern softshell clam (*Mya arenaria).*

Despite studies of non-native burrowing invertebrates in San Francisco Bay, information on the specific effects of burrowing invertebrates appears to be lacking for the Delta. Talley et al. (2001) reviewed invertebrates (such as annelid worms, molluscs, echinoderms, cnidarians, echiurans and sipunculans) that burrow into coastal sediments, wetland soils, and stream banks. Their burrows bring oxygen below the surface and alter substrate chemistry, water content, and shear strength. The invasive shipworm *Sphaeroma quoyanum* can become dense enough in intertidal habitats to weaken and collapse substrates, leading to erosion of the edges of salt marshes by waves and creek flows.

Four of the Delta's invasive FAV species disperse with tides and winds (Ta et al. 2017). Many are easily grown in micro- or mesocosms to test factors that influence invader survival, help predict native vs. non-native competition, and identify further research needs. Some researchers use simulated tidal inundation regimes to predict plant growth with varying salinity, as will accompany rising sea level (Woo and Takekawa 2012, Charles et al. 2019).

Research on chemical treatment of invasive species is needed. Ta et al. (2011) listed research needs for eradicating *Hydrilla* as follows: "[A] replacement for fumigation, DNA tracing of populations and introductions, management strategies that prevent development of herbicide resistance, and studies on how to maintain herbicide contact time with water flow and tidal influence." Herbicide resistance is a general issue. Boyer and Burdick (2010) called for more assessment of non-target effects and native-plant recovery following the use of herbicides to control invasive plants.

Effective alternatives to herbicide are needed to control exotic annual grasses. Holl et al. (2014) compared non-chemical exotic management strategies (mulching, tarping, and topsoil removal) and found reductions in invasive plant cover in years 1-2 but not lasting control.

## Invasive species in an ecosystem context

Figure 2 describes the stages of an invasion that prompt various responses. Research and management actions in the initial stages of the invasion process—threat assessment, prevention, eradication, and control—are usually directed toward individual invasive species. However, invasions occur in a broader ecosystem context. If an invasive species becomes established, it becomes a participant in the functional processes of the ecosystem—as a competitor or predator of other species, a node in the ecosystem food web, a contributor to biogeochemical cycles, as habitat for other species, or other functional roles. Functionally, the line between a native species and an established non-native species begins to blur. It may then be less important for managers to focus on the degree of nativeness of a species than on the functional role it plays in the ecosystem.

As many of the examples we have previously mentioned illustrate, the roles of invasive species are often disruptive. They alter aspects of the structure, composition, and function of ecosystems that we wish to maintain. In some situations, however, the impacts of the invader are benign from a human perspective or do not warrant the costs of eradication, control, or ongoing management. Consequently, we must adapt to the presence of the non-native species. Determining an appropriate course of action should include an assessment of the functional role the invading species has come to play in the ecosystem. This requires that we not only know the ecology and habitat requirements of the invader, but that we understand the strengths of its interactions with other species, its food-web relationships, how it affects water quality or hydrological flows, and how it fits into a myriad of ecosystem processes. Unfortunately, our knowledge of the details of how Delta ecosystems function is generally inadequate to support such assessments.

Invasive species become established in an ecosystem because conditions there fulfill their ecological niche requirements, either because the invader excludes some native species that previously occupied that niche or because there was no species present that had the same ecological niche requirements (an “empty niche”). Absence of controlling predators can also be important. Perhaps the non-native species replaces a species that became extinct centuries or millennia ago (Perino et al. 2019) or environmental changes have created new habitats (like rivers turning into calm ponds or lakes). Whether the species are functional equivalents can of course no longer be tested.

In some situations, non-native species may actually benefit ecological restoration. Where non-native species do not unduly threaten other species, ecosystem functioning, or human interests or provide essential ecological or socioeconomic services, they can be tolerated or even used to good advantage (Ewel and Putz 2004). In highly degraded habitats, carefully selected non-native species could be used to accelerate restoration by nitrogen fixation or by acting as nurse plants for native species (Guo et al. 2018). There are always risks where potentially invasive non-native species are involved, but greater risks can be accepted by considering the functional properties of ecosystems rather than using the reconstruction of a biological community as the sole goal of restoration (Ewel and Putz (2004). Both ecosystem functions and the ecology of individual species should be considered in decisions about how (or whether) to manage invasive species.

# III. RECOMMENDATIONS

Our recommendations focus on *encouraging a broader, more forward-looking*, *integrated approach to invasive species science in the Delta that is coupled to management goals*. Broader means expanding to multiple species and ecosystems; forward-looking means developing predictions and forecasting in the context of changing drivers; and integrated means coordinating efforts into a cohesive program.

Several considerations underlie all of the following recommendations and must be included in discussions of how to implement the recommendations. First, climate warming, sea level rise, and more extreme environmental conditions will affect all species and habitats in the Delta, accelerating changes in species pools and facilitating the establishment of invasive species. Climate change scenarios should be incorporated into all management or policy actions regarding invasive species. Second, the initial step in implementing a recommendation is determining who has the responsibility and how the efforts will be supported and funded. Recommendations without responsibilities are unlikely to be effective. In some cases, work in the following areas is already underway in the Delta; implementing these recommendations should begin with a detailed assessment of what is currently being done. The wealth of knowledge and experience of Delta managers and researchers is a critical resource that should be brought to bear on future decision making about invasive species in the Delta.

We first offer several broad recommendations and then follow with some more specific questions that should be addressed through scientific research. While these recommendations and questions emphasize aquatic ecosystems, they apply broadly throughout the Delta.

## Recommendation 1

*Develop comprehensive quantitative models to predict potential impacts of new invaders on ecosystem structure and function.*

Forecasting the impacts of a potential invader requires better understanding of food-web disruption and interactions and insights into predation, competition, energy and nutrient flow, and habitat structure. A quantitative, spatially and temporally explicit food web model (such as ECOSIM with ECOSPACE) for the Delta would be a good place to start. These models can be used to assess the probability of successful invasion and potential impacts.

## Recommendation 2

*Assess the threat of new invasive species in the California Delta.*

The Delta is highly vulnerable to invasion by new aquatic species entering from San Francisco Bay or elsewhere in or beyond California. A quantitative risk assessment should be undertaken to identify 1) which species pose the greatest risk to the ecology and economy of the Delta, and 2) the primary vectors or corridors of entry. These could be the basis for developing risk-based decision models (e.g. Wu et al. 2010).

## Recommendation 3

*Develop programs to assess invasion probabilities in a dynamic Delta.*

Delta ecosystems and the species pools they contain are undergoing increasingly rapid change. The probabilities of invasion of different ecosystems by different kinds of invasive species and their shifting effects on ecosystem processes should be a focus of new research efforts. The changes in the Delta also emphasize the need to apply adaptive management practices throughout the Delta.

## Recommendation 4

*Expand comprehensive invasive-species coordination of planning and actions for the Delta.*

Currently, the Delta Interagency Invasive Species Coordination (DIISC) Team (part of the Sacramento-San Joaquin Delta Conservancy) acts to “foster communication and collaboration among California state agencies, federal agencies, research and conservation groups, and other stakeholders that detect, prevent, and manage invasive species and restore invaded habitats in the Sacramento-San Joaquin Delta”.[6]

DIISC provides a foundation for building broader integration of actions directed toward anticipating, detecting, controlling, and adjusting to invasive species in the Delta. Coordination of monitoring programs, rapid response teams, and corridor limitation cuts across agencies and across species. A comprehensive invasive-species coordination plan should be developed for the Delta. This should include a detailed Science Action Agenda for dealing with invasive species that defines short-term scientific priorities. An Invasive Species Task Force or Invasive Species Science Center could complement the communication and coordination functions of DIISC by developing protocols for prioritizing actions based, for example, on feasibility, risks, costs, and benefits; by integrating modeling efforts; by testing the effectiveness of new techniques for detecting and controlling invasive species; by developing and using maps of plant and animal biodiversity hotspots and coldspots in the Delta to show critical functions that could be

[6] DIISC Team Website: http://deltaconservancy.ca.gov/delta-inter-agency-invasive-species-team/

damaged by current or future invasive species; and by incorporating the information and lessons from efforts to deal with invasive species elsewhere and from the growing body of scientific theory and findings about invasive species and their effects.

### Recommendation 5

*Include invasive species assessment as a formal part of ecosystem restoration programs.*

The intent of many restoration projects is to use adaptive management to approach restoration goals as an iterative process. Specifying how invasive species entering proposed restoration sites will affect desired outcomes and can be managed should be part of all restoration plans. Restoration plans should also take advantage of opportunities to include field experimentation as part of the project design.

### Recommendation 6

*The Delta should join the monitoring effort being conducted by the National Wetland Condition Assessment.*

“Condition” includes assessment of non-native species. This effort already includes sampling stations in the Delta; expanding sampling will allow wetland conditions to be compared between the northern and southern Delta, as well as with the broader nation-wide array of monitoring sites.

## Science questions

Dealing with invasive species in the Delta can benefit from a science-based assessment of several overarching questions:

- How should actions to control invasive species be prioritized, based on what criteria?
- What new actions should be tested for controlling or eradicating an invader?
- When and how should field experiments involving invasive species be undertaken, using what safeguards?
- How can the cost-benefit tradeoffs of dealing with invasive species be determined?
- What factors determine when the presence of an invasive species should be accepted and managed adaptively?
- How can we assess or alter the vulnerability of Delta habitats and ecosystems to invasions?

- How does one manage an ecosystem with an ever-changing species pool?
- How do microorganisms act to facilitate or impede invading species?

**Box 5. Recommendations of Conrad et al. (2020)**

In a recent report on critical needs for the control of invasive aquatic vegetation in the Delta, Conrad et al. (2020) offered two recommendations. We support these recommendations and include them here for additional emphasis.

**Recommendation 1.***Prioritize and support regulatory authorization and identify funding to implement and evaluate new tools at two Fish Restoration Program sites.* Control programs often require consultation with multiple state and federal agencies, which creates time lags that can be costly in responding to a new invasive species. Testing new approaches with experimental adaptive-management approaches should be encouraged and streamlined.

**Recommendation 2.** *Identify funding for consistent Delta-wide monitoring.* Monitoring is essential to detect invasions early in the process, when eradication and control may be feasible, and to determine the effectiveness of costly control efforts. Monitoring requires reliable funding.

# IV. CONCLUSIONS

The species pool of any area within the Delta will continue to change. Some of these changes will involve the loss of native species, some the establishment of new immigrants. Of these, some will cause harm to the ecology and economy of the Delta. The challenge to science is to predict, detect, control, or adjust to these invasive species. Where should our efforts be placed, on what?

Imagine the following scenario: Some species (let's call it "Newtrina") may be the next invader to the Delta. It enters undetected and become fully established before it is noticed. It disrupts food webs and causes a decline in native species. Management will try to eradicate this species, but it may become permanently established in the Delta and harm ecosystem services valued by people.

How should we deal with such a prospect? We should have monitoring systems and food-web studies in place to be able to forecast the species' impact and its rate of spread. We should be able to predict changes in the food web and assess the changes once "Newtrina" has become permanently established, We should be able to tease out the impacts of "Newtrina" relative to ongoing and simultaneous changes in the ecosystem due to climate change, weather extremes, and other driving forces. We should develop protocols for dealing with unanticipated invaders like “Newtrina” that arrive unannounced.

At the present time, the management and scientific processes for preventing, detecting, minimizing the impacts, and adapting to individual invaders are well established and largely adopted at the state and national levels. The approach of focusing on individual invader species has been valuable, although not always effective. However, the rate of invasions and the impact of invaders on ecosystem structure and function are closely linked to other fundamental drivers of ecosystem change, including climate change, resource use, pollution, habitat alteration, and extreme events. Given that the Delta ecosystem has been largely modified, is already highly invaded, and like many other ecosystems is undergoing continual and increasingly rapid change, one might ask: What is the appropriate goal for invasive species management? We can expect that the species pool will continually change and management will need to adapt to the changes. Some of these changes may be predictable and others not. Developing more forward-looking scientific and management approaches will improve our ability to understand, predict, and adapt to those changing conditions.

## References [TO BE COMPLETE]

Akers, R. P., Bergmann, R. W., & Pitcairn, M. J. (2017). Biological control of water hyacinth in California's Sacramento–San Joaquin River Delta: observations on establishment and spread. *Biocontrol Science and Technology*, *27*(6), 755 to 768.

Anderson 2002

Arthur, J. F., Ball, M. D., & Baughman, S. Y. (1996). *Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta Estuary, California*. San Francisco State University.

Beck, K. G., Zimmerman, K., Schardt, J. D., Stone, J., Lukens, R. R., Reichard, S., ... & Thompson, J. P. (2008). Invasive species defined in a policy context: Recommendations from the Federal Invasive Species Advisory Committee. Invasive Plant Science and Management, 1(4), 414 to 421.

Borgnis, E., & Boyer, K. E. (2016). Salinity tolerance and competition drive distributions of native and invasive submerged aquatic vegetation in the Upper San Francisco Estuary. *Estuaries and coasts*, *39*(3), 707 to 717.

Boyer, K. E., & Burdick, A. P. (2010). Control of Lepidium latifolium (perennial pepperweed) and recovery of native plants in tidal marshes of the San Francisco Estuary. Wetlands ecology and management, 18(6), 731 to 743.

Boyer, K., & Sutula, M. (2015). Factors controlling submersed and floating macrophytes in the Sacramento-San Joaquin Delta. Southern California Coastal Water Research Project. Technical Report 870. Costa Mesa, CA.

Boyer, K., Miller, J., Borgnis, E., Patten, M., and Moderan, J. (2016). Salinity effects on native and introduced submerged aquatic vegetation of Suisun Bay and the Delta. Final Report to the CALFED Ecosystem Restoration Program and California Department of Fish and Wildlife. Romberg Tiburon Center for Environmental Studies, San Francisco State University Grant No.: E1183007/ERP-11-S11.

Brown, L. R. (2003). Will tidal wetland restoration enhance populations of native fishes?. *San Francisco Estuary and Watershed Science*, *1*(1).

Brown, L. R., Kimmerer, W., Conrad, J. L., Lesmeister, S., & Mueller–Solger, A. (2016). Food webs of the Delta, Suisun Bay, and Suisun Marsh: an update on current understanding and possibilities for management. *San Francisco Estuary and Watershed Science*, *14*(3).

Brown, L. R., & May, J. T. (2006). Variation in spring nearshore resident fish species composition and life histories in the lower San Joaquin watershed and delta. *San Francisco Estuary and Watershed Science*, *4*(2).

Brown, L. R., & Michniuk, D. (2007). Littoral fish assemblages of the alien-dominated Sacramento-San Joaquin Delta, California, 1980–1983 and 2001–2003. *Estuaries and Coasts*, *30*(1), 186 to 200.

California Department of Fish and Wildlife (CDFW). *Discovery of invasive nutria in California*. Retrieved from https://www.wildlife.ca.gov/Conservation/Invasives/Species/Nutria/Infestatio

Callaway and Parker 2012

Carlton, J. T. (1996). Biological invasion and cryptogenic species. *Ecology*, *77*(6), 1653.

Carlton, J. T., Thompson, J. K., Schemel, L. E., & Nichols, F. H. (1990). Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam Potamocorbula amurensis. I. Introduction and dispersal. *Marine Ecology Progress Series*, 81 to 94.

Carter, J. & Leonard, B.P. (2002). Review of the literature on the worldwide distribution, spread of, and efforts to eradicate the coypu (*Myocastor coypus*): *Wildlife Society Bulletin*, *30*(1), 162 to 175.

Charles, S. P., Kominoski, J. S., Troxler, T. G., Gaiser, E. E., Servais, S., Wilson, B. J., ... & Kelly, S. (2019). Experimental Saltwater Intrusion Drives Rapid Soil Elevation and Carbon Loss in Freshwater and Brackish Everglades Marshes. Estuaries and Coasts, 42(7), 1868 to 1881.

Cloern, J. E., & Jassby, A. D. (2012). Drivers of change in estuarine-coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics*, *50*(4).

Cloern, J. E., Knowles, N., Brown, L. R., Cayan, D., Dettinger, M. D., Morgan, T. L., ... & Jassby, A. D. (2011). Projected evolution of California's San Francisco Bay-Delta-River system in a century of climate change. PloS one, 6(9), e24465.

Cohen A.N., Carlton J.T., 1995 Nonindigenous Aquatic Species in a United States Estuary: A Case Study of the Biological Invasions of the San Francisco Bay and Delta. Connecticut Seagrant, Groton, CT.

Cohen, A. N., & Carlton, J. T. (1998). Accelerating invasion rate in a highly invaded estuary. *Science*, *279*(5350), 555 to 558.

Conrad, J. L., Bibian, A. J., Weinersmith, K. L., De Carion, D., Young, M. J., Crain, P., ... & Sih, A. (2016). Novel species interactions in a highly modified estuary: association of Largemouth Bass with Brazilian waterweed Egeria densa. *Transactions of the American Fisheries Society*, *145*(2), 249 to 263.

Conrad, J.L., D. Chapple, E. Bush, et al. 2020. Critical needs for control of invasive aquatic vegetation in the Sacramento-San Joaquin Delta. Report to the Delta Stewardship Council, May 2020.

Crooks, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, *97*(2), 153 to 166.

D'Antonio et al. 2016

Dahm, C. N., Parker, A. E., Adelson, A. E., Christman, M. A., & Bergamaschi, B. A. (2016). Nutrient dynamics of the Delta: effects on primary producers. *San Francisco Estuary and Watershed Science*, *14*(4).

Davis, M.A. (2011). Don't judge species on their origins. Nature, 474, 153 to 154.

Deems, E. F., & Pursley, D. (1978). North American furbearers: their management, research and harvest status in 1976: International Association of Fish and Wildlife Agencies in cooperation with the Maryland Department of Natural Resources-Wildlife Administration: College Park, University of Maryland.

Dick, J. T., Laverty, C., Lennon, J. J., Barrios-O'Neill, D., Mensink, P. J., Britton, J. R., ... & Dunn, A. M. (2017). Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology, 54(4), 1259 to 1267.

Diez et al. 2014

Dill, W.A., & Cordone, A.J. (1997). History and status of introduced fishes in California, 1871-1996. *Fish Bulletin 178,* 1 to 414.

Dukes 2011

Eller, F., Skálová, H., Caplan, J. S., Bhattarai, G. P., Burger, M. K., Cronin, J. T., ... & Lambertini, C. (2017). Cosmopolitan species as models for ecophysiological responses to global change: the common reed Phragmites australis. Frontiers in plant science, 8, 1833.

Eller, F., Lambertini, C., Nguyen, L. X., & Brix, H. (2014). Increased invasive potential of non-native Phragmites australis: elevated CO2 and temperature alleviate salinity effects on photosynthesis and growth. Global change biology, 20(2), 531 to 543.

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. University of Chicago Press.

Evans, J. (1970). *About nutria and their control* (No. 86). US Fish and Wildlife Service.

Ewel and Putz 2004 (p. 35)

Feyrer, F. (2004). Ecological segregation of native and alien larval fish assemblages in the southern Sacramento-San Joaquin Delta. In *American Fisheries Society Symposium* (pp. 67 to 80). American Fisheries Society.

Feyrer, F., & Healey, M. P. (2003). Fish community structure and environmental correlates in the highly altered southern Sacramento-San Joaquin Delta. *Environmental Biology of Fishes*, *66*(2), 123 to 132.

Fleenor et al. 2008 (p. 7)

Foxcroft, L. C. (2009). Developing thresholds of potential concern for invasive alien species: hypotheses and concepts. Koedoe, 51(1).

Galatowitsch, S. M., Anderson, N. O., & Ascher, P. D. (1999). Invasiveness in wetland plants in temperate North America. Wetlands, 19(4), 733 to 755.

Greenfield, B.K., Siemering, G.S., Andrews, J.C., Rajan, M., Andrews, Jr., S.P., & Spencer, D.F. (2007). Mechanical shredding of water hyacinth (Eichornia crassipes): effects on water quality in the Sacramento-San Joaquin River Delta, California. *Estuaries and Coasts, 30*(4), 627 to 640.

Grimaldo, L. F., Miller, R. E., Peregrin, C. M., & Hymanson, Z. P. (2003). Spatial and temporal distribution of native and alien ichthyoplankton in three habitat types of the Sacramento-San Joaquin Delta. In *American Fisheries Society Symposium* (pp. 81 to 96). American Fisheries Society.

Godoy, O. (2019). Coexistence theory as a tool to understand biological invasions in species interaction networks: Implications for the study of novel ecosystems. *Functional Ecology*, 33, 1190 to 1201.

Guo, Q., Brockway, D.G., Larson, D.L., Wang, D., & Ren, H. (2018). Improving ecological restoration to curb biotic invasion - a practical guide. Invasive Plant Science and Management, 11(4), 163 to 174.

Hammock, B. G., Moose, S. P., Solis, S. S., Goharian, E., & Teh, S. J. (2019). Hydrodynamic modeling coupled with long-term field data provide evidence for suppression of phytoplankton by invasive clams and freshwater exports in the San Francisco Estuary. *Environmental management*, *63*(6), 703 to 717.

Hestir, E.L., Khanna, S., Andrew, M.E., Santos, M.J., Viers, J.H., Greenberg, J.A., Rajapakse, S.S., & Ustin, S.L. (2008). Identification of invasive vegetation using hyperspectral remote sensing in the California Delta ecosystem. *Remote Sensing of Environment, 112*(11), 4034 to 4047.

Hestir et al. 2015 (p. 17)

Hickson, D., Keeler-Wolf, T., & Region, B. D. (2007). Vegetation and land use classification and map of the Sacramento-San Joaquin River Delta. Report prepared for Bay Delta Region of California Department of Fish and Game. *Vegetation Classification and Mapping Program, California Department of Fish and Game*, Sacramento, CA.

Holl, K. D., Howard, E. A., Brown, T. M., Chan, R. G., de Silva, T. S., Mann, E. T., ... & Spangler, W. H. (2014). Efficacy of exotic control strategies for restoring coastal prairie grasses. *Invasive Plant Science and Management*, 7(4), 590 to 598.

Hopper, J. V., Pratt, P. D., McCue, K. F., Pitcairn, M. J., Moran, P. J., & Madsen, J. D. (2017). Spatial and temporal variation of biological control agents associated with *Eichhornia crassipes* in the Sacramento-San Joaquin River Delta, California. *Biological control*, *111*, 13 to 22.

Hunter, S., Williams, N., McDougal, R., Scott, P., & Garbelotto, M. (2018). Evidence for rapid adaptive evolution of tolerance to chemical treatments in Phytophthora species and its practical implications. *PloS one*, 13(12), e0208961.

IPBES 2019

Janovsky and Larson 2019

Jassby, A. D., Cloern, J. E., & Cole, B. E. (2002). Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnology and Oceanography*, *47*(3), 698 to 712.

Khanna, S., Santos, M. J., Boyer, J. D., Shapiro, K. D., Bellvert, J., & Ustin, S. L. (2018). Water primrose invasion changes successional pathways in an estuarine ecosystem. *Ecosphere, 9*(9), 1 to 18.

Khanna et al. 2019

Kimmerer, W. J., Gartside, E., & Orsi, J. J. (1994). Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. *Marine ecology progress series*, *113*, 81 to 93.

Leidy, R. A., & Fiedler, P. L. (1985). Human disturbance and patterns of fish species diversity in the San Francisco Bay drainage, California. *Biological Conservation*, *33*(3), 247 to 267.

Loomis, C. M. (2019). Density and distribution of piscivorous fishes in the Sacramento–San Joaquin Delta. Thesis.

Luoma, S. N., Dahm, C. N., Healey, M., & Moore, J. N. (2015). Challenges facing the Sacramento–San Joaquin Delta: complex, chaotic, or simply cantankerous?. San Francisco Estuary and Watershed Science, 13(3).

Lund et al. 2010 (p. 7)

Mahardja, B., Conrad, J. L., Lusher, L., & Schreier, B. (2016). Abundance Trends, Distribution, and Habitat Associations of the Invasive Mississippi Silverside (Menidia audens) in the Sacramento–San Joaquin Delta, California, USA. *San Francisco Estuary and Watershed Science*, *14*(1).

Mann 2011

Marchetti, M. P., Light, T., Moyle, P. B., & Viers, J. H. (2004). Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecological Applications*, *14*(5), 1507 to 1525.

Moyle and Bennett 2008

Nichols, F. H., Thompson, J. K., & Scheme, L. E. (1990). Potamocorbula amurensis. 11. Displacement of a former community. *Mar. Ecol. Prog. Ser*, *66*, 95 to 101.

Nobriga, M. L. (2002). Larval delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. *California Fish and Game*, *88*(4), 149 to 164.

Nobriga, M. L., Feyrer, F., Baxter, R. D., & Chotkowski, M. (2005). Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. *Estuaries*, *28*(5), 776 to 785.

Noe, G. B. (2002). Temporal variability matters: effects of constant vs. varying moisture and salinity on germination. Ecological Monographs, 72(3), 427 to 443.

Noe, G. B., & Zedler, J. B. (2001a). Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. *Journal of Vegetation Science*, 12(1), 61 to 74.

Noe, G. B., & Zedler, J. B. (2001b). Variable rainfall limits the germination of upper intertidal marsh plants in southern California. *Estuaries*, 24(1), 30 to 40.

Norton, D. A. (2009). Species invasions and the limits to restoration: learning from the New Zealand experience. *Science*, 325(5940), 569 to 571.

Perino, A., Pereira, H. M., Navarro, L. M., Fernández, N., Bullock, J. M., Ceaușu, S., ... & Pe'er, G. (2019). Rewilding complex ecosystems. Science, 364(6438), eaav5570.

Pyšek, P., & Richardson, D. M. (2010). Invasive species, environmental change and management, and health. Annual review of environment and resources, 35, 25 to 55.

Rahel, F.J., and J.D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22: 521 to 533.

Rejmánek, M., & Pitcairn, M. J. (2002). When is eradication of exotic pest plants a realistic goal? In C.R. Veitch and M.N. Clout (Eds.), Turning the Tide: The Eradication of Invasive Species (pp. 249–253). Gland, Switzerland and Cambridge, UK International Union for Conservation of Nature and Natural Resources.

Ricciardi, A., & Simberloff, D. (2009). Assisted colonization is not a viable conservation strategy. *Trends in ecology & evolution*, 24(5), 248 to 253.

Ruiz, G. M., Fofonoff, P. W., Carlton, J. T., Wonham, M. J., & Hines, A. H. (2000). Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual review of ecology and systematics*, *31*(1), 481 to 531.

Ruiz, G. M., Fofonoff, P. W., Steves, B., Foss, S. F., & Shiba, S. N. (2011). Marine invasion history and vector analysis of California: a hotspot for western North America. *Diversity and Distributions*, *17*(2), 362 to 373.

Santos, M.J., Anderson, L.W., & Ustin, S.L. (2011a). Effects of invasive species on plant communities: an example using submersed aquatic plants at the regional scale. *Biological Invasions, 13*(2), 443 to 457.

Santos, M. J., Hestir, E. L., Khanna, S., & Ustin, S. L. (2011b). Image spectroscopy and stable isotopes elucidate functional dissimilarity between native and nonnative plant species in the aquatic environment. *New Phytologist*, *193*(3), 683 to 695.

Simberloff, D, and M. Rejmanek (Eds.). 2011. Encyclopedia of Biological Invasions. Berkeley, CA, University of California Press.

Sorte, C.J.B., I. Ibáñez. D.M. Blumenthal, et al. 2013. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters 16: 261 to 270.

Sousa, R., Gutiérrez, J. L., & Aldridge, D. C. (2009). Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions*, *11*(10), 2367 to 2385.

Spencer, D. F., Ksander, G. G., Donovan, M. J., Liow, P. S., Chan, W. K., Greenfield, B. K., ... & Andrews, S. P. (2006). Evaluation of waterhyacinth survival and growth in the Sacramento Delta, California, following cutting. *Journal of aquatic plant management*, *44*(1), 50 to 60.

Stohlgren, T.J., Barnett, D.T., & Kartesz, J.C. (2003). The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment,* *1*(1), 11-14. https://doi.org/10.1890/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2Ta et al. 2011 (p. 33)

Ta, J., Anderson, L.W.J., Christman, M.A., Khanna, S., Kratville, D….& Viers, J.H. (2017). Invasive Aquatic Vegetation Management in the Sacramento-San Joaquin River Delta: Status and Recommendations. *San Francisco Estuary and Watershed Science, 15*(4), 1 to 19.

Talley, T. S., Crooks, J. A., & Levin, L. A. (2001). Habitat utilization and alteration by the invasive burrowing isopod, Sphaeroma quoyanum, in California salt marshes. Marine Biology, 138(3), 561 to 573.

Thompson, J. K. (2005). One estuary, one invasion, two responses: phytoplankton and benthic community dynamics determine the effect of an estuarine invasive suspension-feeder. In *The comparative roles of suspension-feeders in ecosystems* (pp. 291 to 316). Springer, Dordrecht.

Underwood, E. C., Mulitsch, M. J., Greenberg, J. A., Whiting, M. L., Ustin, S. L., & Kefauver, S. C. (2006). Mapping invasive aquatic vegetation in the Sacramento-San Joaquin Delta using hyperspectral imagery. *Environmental Monitoring and Assessment*, *121*(1-3), 47 to 64.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., ... & Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology letters, 14(7), 702-708.Walther, G. R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., ... & Czucz, B. (2009). Alien species in a warmer world: risks and opportunities. Trends in ecology & evolution, 24(12), 686 to 693.

Wiens, J.D., R.G. Anthony, and E.D. Forsman. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monographs* 185: 1 to 50.

Winder, M., & Jassby, A. D. (2011). Shifts in zooplankton community structure: implications for food web processes in the upper San Francisco Estuary. *Estuaries and Coasts*, *34*(4), 675 to 690.

Winder, M., Jassby, A. D., & Mac Nally, R. (2011). Synergies between climate anomalies and hydrological modifications facilitate estuarine biotic invasions. *Ecology letters, 14*(8), 749 to 757.

Wolff, W. J. (1998). Exotic invaders of the meso-oligohaline zone of estuaries in the Netherlands: why are there so many?. *Helgoländer Meeresuntersuchungen*, *52*(3), 393.

Woo and Takeawa 2012

Workman, M. L., & Merz, J. E. (2007). Introduced yellowfin goby, Acanthogobius flavimanus: diet and habitat use in the lower Mokelumne River, California. *San Francisco Estuary and Watershed Science*, *5*(1).

Young, M. J., Conrad, J. L., Bibian, A. J., & Sih, A. (2018). The Effect of Submersed Aquatic Vegetation on Invertebrates Important in Diets of Juvenile Largemouth Bass Micropterus salmoides. *San Francisco Estuary and Watershed Science*, *16*(2).

Zedler, J.B. 2010. Tussock sedge: A restoration superplant? Arboretum Leaflet 22.

Zedler, J. B. (2017). What's new in adaptive management and restoration of coasts and estuaries?. Estuaries and Coasts, 40(1), 1 to 21.

Zedler, J.B., and S. Kercher. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30: 39-74.

Zedler, J.B., and M.L. Stevens. 2018. Western and Traditional Ecological Knowledge in Ecocultural Restoration. *San Francisco Estuary and Watershed Science* 16(3): 1 to 18.