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Unnatural History: Biological Invasions into Coastal Ecosystems

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Abstract

Biological invasions compromise the natural integrity of ecosystems, and can be viewed as both causes and consequences of ecological change. Estuaries are particularly vulnerable to invasion, accumulating species from the sea, land, and freshwater. The numerous estuarine systems of San Diego County, ranging from small coastal lagoons to large embayments, are no exception. There are now numerous marine, terrestrial, and freshwater invaders in these systems, which offer opportunities to broaden our understanding of biological invasions. At the same time, these invasions also challenge our ability to effectively manage the region's estuaries.

Keywords: Biological Invasions, Exotic Species, Tamarisk, Pacific Oysters

1. INTRODUCTION

Estuarine systems represent the one place on earth where the three major habitat types, - land, sea, and freshwater - all come together. Because of this, they are dynamic areas characterized by rich sets of abiotic and biotic interactions. However, management issues from these three different habitat types tend to converge here as well. One particularly problematic issue in estuaries is biological invasions, with estuaries accumulating invasive species from all sides. Herein we will consider the invasions within the numerous estuarine systems of San Diego County, California. This will focus on introduced, non-native species, but will also address invasions of native species due to changing environmental conditions.

Figure 1: Estuarine systems of San Diego County. These include several relatively small embayments and lagoons, such as the Tijuana River Estuary and Los Peñasquitos Lagoon, as well as large bays and harbors, such as Mission Bay and San Diego Bay.

2. INVASIONS BY UPLAND AND FRESHWATER SPECIES

Wetlands throughout the world tend to be invaded by some of the most problematic non-native weeds. One study indicated that although wetlands cover less than 6% of the land surface on earth, 24% of the most problematic exotic plant species are invaders of wetlands habitat [1]. Of the non-native plants in San Diego's tidal wetlands, there are few that are actually restricted to these marine habitats. One obligate wetland invader is the grey mangrove, *Avicennia marina*, which was intentionally introduced into Mission Bay wetlands in the late 1960s. Much more common are invaders from adjacent habitat types. One set of plants invading salt marshes are those more typically found in higher-elevation, non-tidal habitats. In general terms, the salt marsh - upland ecotone is known to be a site vulnerable to invasion [2], and is also a sensitive indicator of changing environmental conditions [3]. Another suite of plant invaders into marshes are those associated with fresh or brackish water conditions [4,5]. The incursion of both upland and freshwater plants into salt marshes is often limited by soil or water salinity [6,7].

2.1. Tamarisk

One of the more problematic of the region's salt marsh-encroaching non-natives is tamarisk, or salt cedar, (*Tamarix chinensis* and *Tamarix ramosissima* x *T. chinensis*; [8]). This shrub or small tree is an ecosystem engineer native to Eurasia and African, and can dramatically alter invaded ecosystems [9,10]. It has not typically been considered an invader of tidal areas, but in salt marshes such as the Tijuana River Estuary and San Dieguito Lagoon (Fig. 1) it has become an abundant element of the plant community. Here it can completely alter the structure of invaded habitats, converting the low-lying salt marsh plain, dominated by pickleweed (*Salicornia pacifica*), into dense tamarisk thickets [9,10]. This thick, tall vegetation affects soil characteristics and light regimes, decreases understory plant cover, alters food webs, and attracts birds which may compete with or prey upon sensitive marsh-dependent birds (such as the Ridgway's rail and Belding's savannah sparrow). It also alters associated invertebrate assemblages, including benthic macrofauna [8,11], as well as arthropods associated with vegetative canopies (Fig. 2). Sweep-net sampling of native pickleweed and invasive tamarisk in the intertidal revealed dramatically higher total densities of arthropods (primarily insects and arachnids), including the also-invasive tamarisk leafhopper (*Opsius stactogalus)*, within tamarisk. An abundant treehopper (Membracidae) was found in lower abundances within tamarisk compared to pickleweed.

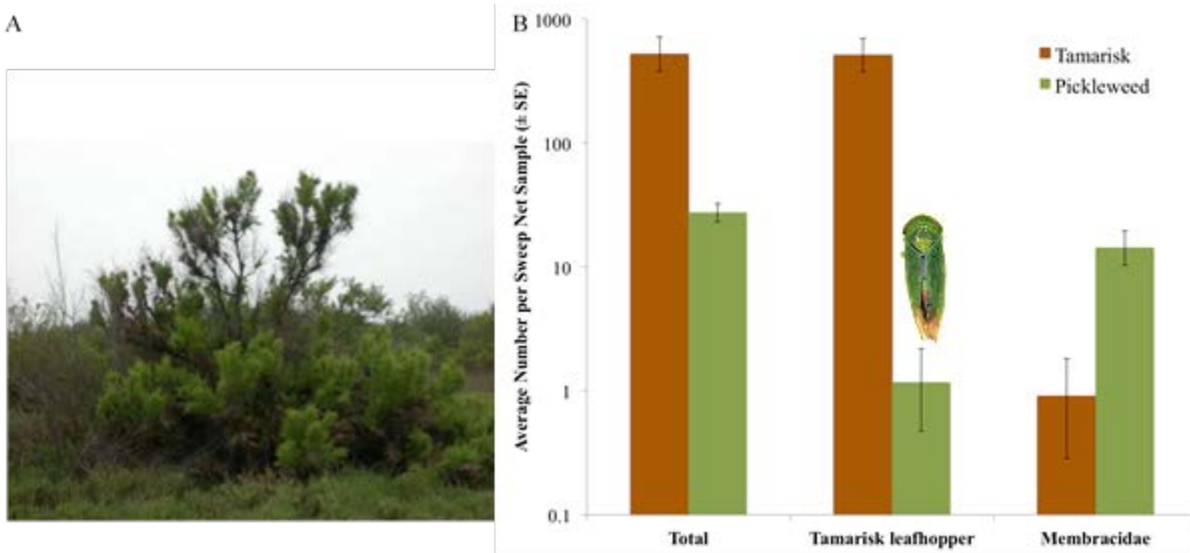

Figure 2: A) Tamarisk (Tamarix spp.) growing in intertidal pickleweed (Salicornia pacifica) in the Tijuana River Estuary. B) Number of arthropods found in timed sweep net samples of tamarisk vs. pickleweed, including total arthropods, numbers of the non-native tamarisk leafhopper, Opsius stactogalus*, and numbers of treehoppers (Membracidae). Tamarisk photo by J. Crooks, Opsius photo by Jason Eckberg, Creative Commons.*

Because of the problems associated with tamarisk in the Tijuana Estuary, there has been an effort to remove this plant over the last 15 years. The tamarisk invasion, and its control, provide an opportunity to evaluate the context for invasion species management. Typically, the goal of such efforts should not stop at invasive species removal *per se*, but instead focus on recovering native species. In many instances, it will be necessary to replant with native vegetation after removal of invaders. In some cases, though, removal of a target invader may be sufficient to achieve the goal of native species recovery. This is clearly seen with tamarisk removal in the Tijuana Estuary. Tamarisk had heavily invaded a site that included both intertidal salt marsh and adjacent upland transition zone. Monitoring of the site after a tamarisk clearing effort showed that in the upland, the only plants that returned immediately after the control effort were non-natives, primarily annual weeds (Fig. 3). In the lower-elevation, higher-salinity intertidal site, just a few meters away, the only plants that returned were native marsh species, such as pickleweed. This has important implications for management, which is typically resource-limited. In this case, re-vegetation efforts were focused on the upland site, while the intertidal site was left to recover naturally.

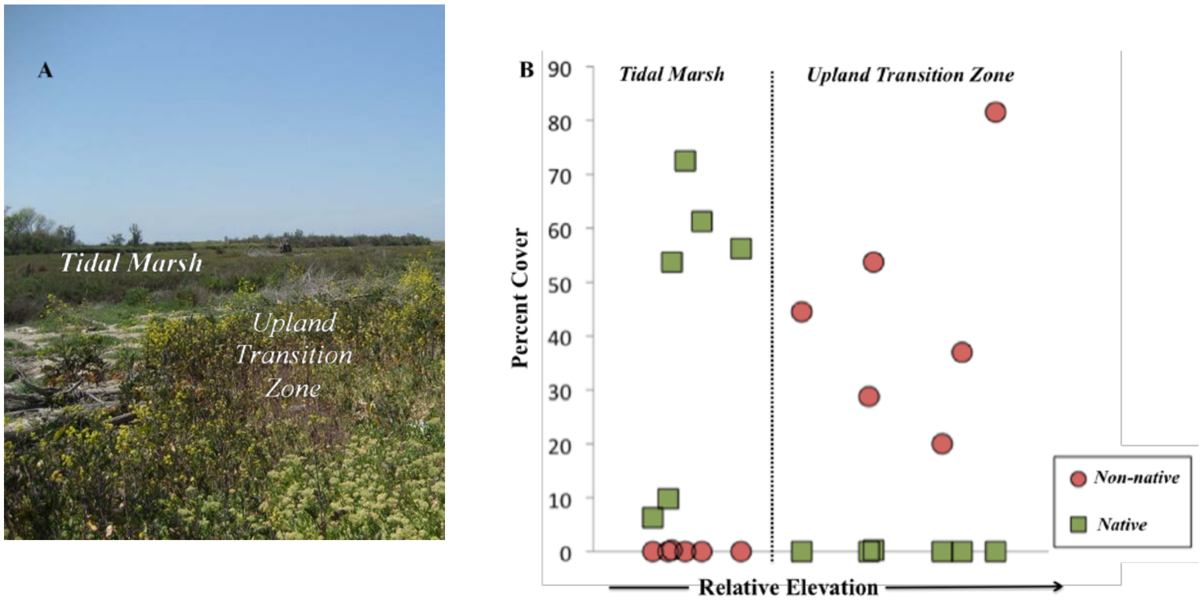

Figure 3: A) A site in the Tijuana Estuary after tamarisk (Tamarix spp.) removal, showing the upland transition zone heavily invaded by non-native annual plants, and the tidal marsh with recovery of native pickleweed (Salicornia pacifica). B) Post-tamarisk removal monitoring results, showing differences in percent cover of natives and non-natives along the elevation gradient from intertidal to upland. Photo by J. Crooks.

2.2. Invasions Associated with "Urban Drool"

In addition to invasion of marshes via the upland / marsh ecotone, lowering salinities in coastal salt marshes also can facilitate invasions and changes in plant communities. One major issue in the semi-arid, Mediterranean-climate systems of Southern California is the addition of anthropogenic freshwater. San Diego imports over 80% of its water, primarily from the Sacramento - San Joaquin Rivers and Colorado River. When this water is used outdoors, such as for irrigation, it can dramatically alter both the amount and timing of water entering coastal wetlands. In Los Peñasquitos Creek, one of the tributaries of Los Peñasquitos Lagoon (Fig. 1), a United States Geological Survey stream gage shows dramatic increases in the amounts of freshwater flowing in the creek (Fig. 4). This is particularly pronounced during the dry-season (June 1 - September 30; [12]), when creek flow should essentially be zero. This "urban drool" is effectively perennializing the normally ephemeral streams of the region.

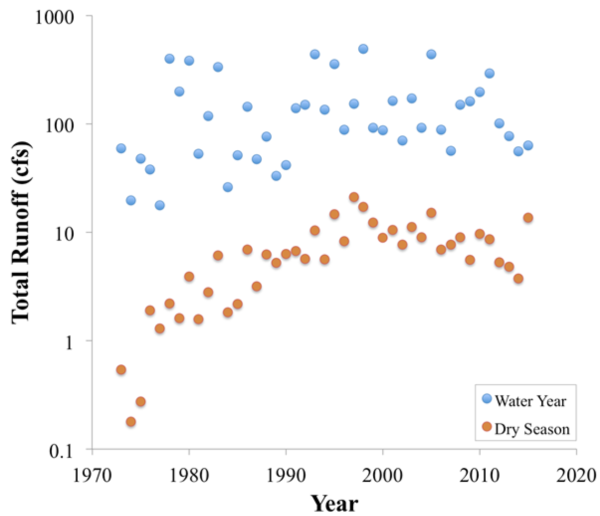

Figure 4: Runoff (cubic feet per second) at the United States Geological Survey's Los Peñasquitos Gage, including the water year (October 1 - September 30) and the dry season (June 1 - September 30). Adapted from White and Greer [12].

Numerous management issues arise from this input of freshwater into naturally more saline systems. These include allowing non-native freshwater-associated animals, such as mosquitofish (*Gambusia affinis*), red swamp crayfish (*Procambarus clarkii*), and disease-carrying mosqituoes (*Aedes aegytpi* and *A. albopictus*) to push further downstream into formerly more saline habitats. Another major impact is vegetation type conversion. Using remotely-sensed imagery, Greer and Stow [5] have documented large-scale type conversion of Los Peñasquitos Lagoon habitats since 1927, due to this anthropogenic freshwater input. Haline community-types, such as salt panne and salt marsh, have decreased in recent decades, while fresh-brackish marsh and riparian habitat types have increased. Changes in plant species composition in field transects that have been monitored annually since 1991 are consistent with this pattern (Fig. 5). The former dominant at the site, the characteristic salt marsh plant, pickleweed (*Salicornia pacifica*), has been replaced by cattails (*Typha* spp.), which is characteristic of freshwater marshes, and jaumea (*Jaumea carnosa*). Although these two species are both native, freshwater-impacted areas of Los Peñasquitos Lagoon also have a much greater representation of non-native species known to increase with freshwater input in salt marshes [4,13], including rabbitsfoot (*Polypogon monspeliensis*) and brass buttons (*Cotula coronopifolia*)

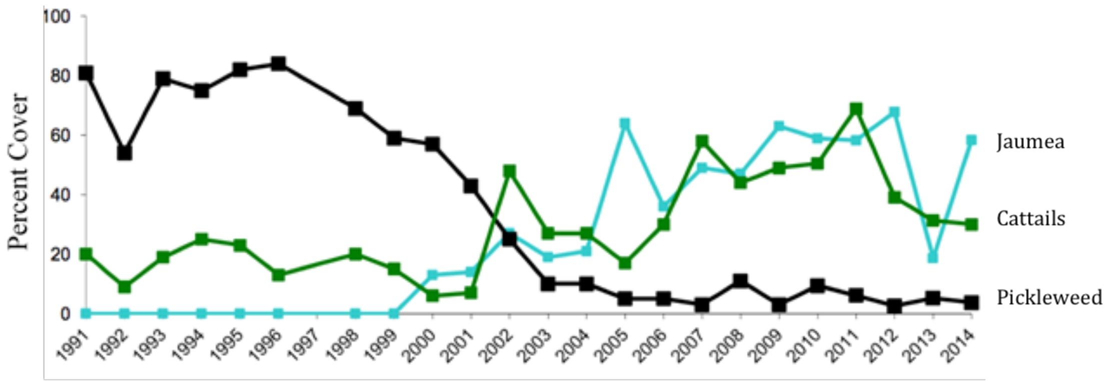

Figure 5: Long-term trends in vegetative cover of pickleweed (Salicornia pacifica), cattails (Typha sp.) and jaumea (Jaumea carnosa) at a transect increasingly affected by freshwater in Los Peñasquitos Lagoon. Source: Pacific Estuarine Research Lab (San Diego State University), Los Peñasquitos Lagoon Foundation, and the Tijuana River National Estuarine Research Reserve.

Habitat-type conversion from anthropogenic increases in freshwater flow is a complex issue, dealing with urbanization, land use, and, very importantly for Southern California, water. These watershed changes have also increased sediment loading to Los Peñasquitos Lagoon, and the California Water Quality Control Board has recently issued a Total Maximum Daily Load (TMDL) Waste Load Allocation for sediment. This explicitly recognizes that "impacts due to sedimentation are not clearly differentiated from the impacts associated with other stressors on the Lagoon such as freshwater inputs and physical barriers within the Lagoon." Planning for control of freshwater and sediment is currently underway, and implementation of the TMDL will occur over the next twenty years.

3. Invasions by Marine Species

The coastal waters of San Diego County now have over 130 recognized non-native marine species. As is seen in ecosystems across the globe, the rate of invasion in San Diego appears to be steadily increasing over time [14], with over 50 new species reported since 2000 (Fig. 6). This is due in part to an increasing ability to find and identify new species (e.g., using molecular tools), but also undoubtedly reflects an increase in the anthropogenic transport of species. Most of San Diego's non-natives are found in estuarine systems, rather than the open coast, likely arising from transport vectors that operate between estuaries (e.g. ship traffic) as well as disturbance that facilitates invasions within estuaries [15,16,17]. Fouling organisms, such as tunicates, bryozoans, and polychaetes, are well-represented in local waters, particularly associated with marinas [18]. Other invaders include the newly-discovered Japanese mud snail, *Batillaria attrimentaria* (Lorda, pers obs.) and the Manila clam, *Ruditapes phillinarum* [19] . Some invasive ecosystem engineers, which can cause dramatic, cascading effects on resident biota through their alteration of the physical nature of habitats [20], include the mat-forming Asian mussel, *Musculista* (=*Arcuatula*) *senhousia* [21, 22, 23] and the salt marsh burrowing isopod *Sphaeroma quoianum* [10, 24, 25].

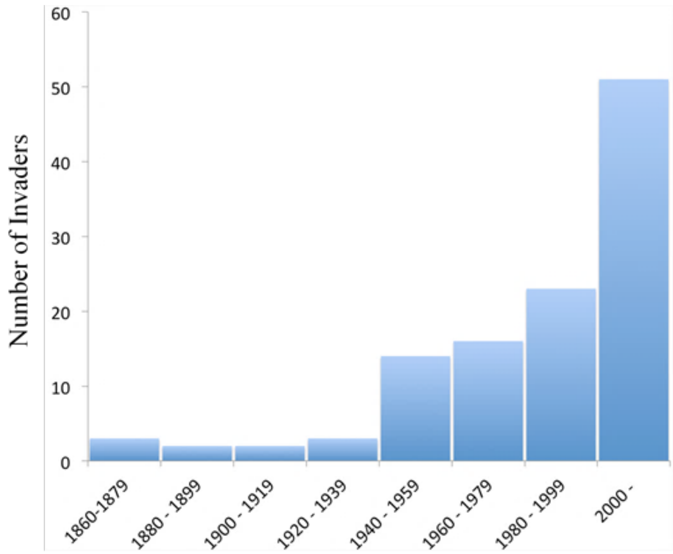

Figure 6: Dates of first record for non-native marine species in San Diego County.

3.1. El Niño

The warm waters associated with the recent El Niño caused remarkably quick changes in the local biota, including appearance of tropical species. Many of these represent natural invasions via temporary expansions of the northern limits of species native to the North American west coast. Some examples of tropical species appearing during the El Niño include a yellow-bellied sea snake (*Pelamis platura*) found on the beach north of the Tijuana Estuary, a bullseye puffer (*Sphoeroides annulatus*) found in the Tijuana Estuary itself (Deza pers. comm.), and a longnose puffer (*S. lobatus*) found in Mission Bay (Tuskes pers. comm.). There was also a bloom of the non-native Australian spotted jellyfish, *Phyllorhiza punctata*, in both San Diego and Mission Bays. This tropical species was first reported in the 1980's [26, 27], and the recent bloom, which became a local news story, likely represents the temporary ecological release of invader when conditions become more favorable. In general, biotic responses during this El Niño indicate how quickly changes can occur, both through expanding ranges as well as altered dynamics of already-present species. Such events offer intriguing opportunities to examine and anticipate potential effects of climate change [28].

3.2. Lag Times and the Invasion of Pacific Oysters

Biological invaders are notorious for causing "ecological surprises" that challenge both our understanding and management of invaders [29,30]. While some invasions can occur very quickly, some biological invaders are notorious for having long lag times before sudden changes in invasion dynamics. An example of a long lag in invasion is provided by the invasion of the Pacific (or Japanese) oyster, *Crassostrea gigas*, in Southern California [31]. In the early 20th century, there were repeated efforts to establish this large, commercially-desirable species throughout the west coast of North America. In the Pacific Northwest, the oyster has established and become an important fishery resource. In California, however, despite early introduction attempts and continuing grow-out of Pacific oysters, the species was deemed not able to survive in California waters. In the early 21st century, however, reports of Pacific oysters began to come from several systems in southern California. Today, the Pacific oyster is becoming a conspicuous element of the biota living in the estuarine systems of San Diego County (Fig. 7) [31].

Figure 7: Non-native Pacific oysters (Crassostrea gigas) in San Diego, including (A) growth on roots of marsh plants in Los Peñasquitos Lagoon and (B) cover on rip-rap in Tuna Harbor, San Diego Bay. Photos by J. Crooks.

3.3. Management of Non-Native Marine Species

Typically, it is very difficult to remove an invader in a marine setting once it has established itself, although one of the few success stories comes from San Diego's coastal lagoons - the eradication of the "killer alga" *Caulerpa taxifolia* [32]. Therefore, management of invasion vectors, such as ballast water and ship fouling, remain the key management interventions for marine invasions [15]. Another management approach relies on the observation that invaders - which are often "weedy" species - tend to outperform natives in disturbed, polluted areas. This suggests that improving environmental conditions might, among other things, help limit invader success [17].

While the process of unchecked invasions into ecosystems is undesirable, it is possible that individual invasive species might have benefits deemed desirable. This is well illustrated with the Pacific oyster, *Crassostrea gigas* [31]. This large shellfish is a highly sought-after, edible species. In fact, much of the concern regarding potential effects of ocean acidification on shellfisheries in western North America comes from impacts to this non-native species. In Southern California, the oyster might present a similar resource, but food safety concerns related to pathogens (e.g. Vibrio bacteria) and uptake of contaminants in the urbanized and warmer conditions of Southern California need to be addressed [31]. Oysters also represent quintessential ecosystem engineers, creating dense biogenic beds through shell production. Oyster beds are valued throughout the world, and there are proposals to utilize already-introduced Pacific oysters in Northern Europe to create "living shorelines" that can help filter water, prevent erosion, and, importantly, dynamically respond to changes in sea level. Similar efforts to create living shorelines are underway in southern California, focusing on restoration of the smaller, native oyster, *Ostrea lurida*. The potential impact, negative or positive, of the invasive Pacific oyster on these efforts is being considered, with attention being paid to the role of invaders in causing unintended consequences.

4. Conclusion

Invasions are changing the face of the globe - homogenizing the Earth's biota and compromising diversity at a global level. San Diego Bay is looking more and more like Tokyo Bay, and Tokyo Bay like Sydney Harbor. In light of the massive changes that have occurred, and will continue to occur, there is a growing chorus suggesting that we be less concerned about where a species is from, and be more concerned about what it does [33]. Lessons from invasion biology indicate that origin does matter, however [34]. Invaders erode the unique sets of species and interactions that characterize different systems across the globe, are prone to ecological surprises due to lack of co-evolved relationships, and can fundamentally transform invaded ecosystems. But it is counterproductive to argue that each and every invader is "bad" [35], especially when faced with the implications of climate change. A robust conversation is needed, informed by our understanding of the changing nature of ecosystems, how we can protect them, and how ecosystems can in turn can benefit human well-being.

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References

[1] Zedler, J.B. and Kercher, S. "Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes," *Critical Reviews in Plant Sciences*, 2004, 23(5), p. 431–452.

[2] Wasson, K. and Woolfolk, A. "Salt marsh-upland ecotones in central California: Vulnerability to invasions and anthropogenic stressors," *Wetlands*, 2011, 31(2), p. 389–402.

[3] Wasson, K., Woolfolk, A., and Fresquez, C. "Ecotones as indicators of changing environmental conditions: Rapid migration of salt marsh–upland boundaries", *Estuaries and Coasts*, 2013, 36(3), p. 654–664.

[4] Zedler, J.B. "Freshwater impacts in normally hypersaline marshes," *Estuaries*, 1983, 6, p. 346–355.

[5] Greer, K. and Stow, D. "Vegetation type conversion in Los Peñasquitos Lagoon, California: An examination of the role of watershed urbanization," *Environmental Management*, 2003, 31(4) p. 489–503.

[6] Noe, G.B. and Zedler, J.B. "Differential effects of four abiotic factors on the germination of salt marsh annuals," *American Journal of Botany*, 2000, 87(11), p. 1679–1692.

[7] Uyeda, K.A., Deutschman, D.H., and Crooks, J.A. "Abiotic Limitation of Non-native Plants in the High Salt Marsh Transition Zone," *Estuaries and Coasts*, 2013, 36(6), p. 1125–1136.

[8] Asef, T.S. Associating Genetically Diverse Tamarisk Invaders with their Impacts in A Salt Marsh Ecosystem: M.S. Thesis, California State University, Long Beach, California, 2013.

[9] Whitcraft, C.R., Talley, D.M., Crooks, J.A., Boland, J., and Gaskin, J. "Invasion of tamarisk (*Tamarix* spp.) in a southern California salt marsh," *Biological Invasions*, 2007, 9(7), p. 875–879.

[10] Levin, L.A. and Crooks, J.A. “Functional consequences of invasive species in coastal and estuarine systems,” In Treatise on Estuarine and Coastal Science Vol. 7, Wolanski, E. and McLusky, D.S., Eds. Burlington, Massachusetts: Academic Press, 2011, pp. 17-51.

[11] Whitcraft, C.R., Levin, L.A., Talley, D.M., and Crooks, J.A. “Utilization of invasive tamarisk by salt marsh consumers,” *Oecologia*, 2008, 158(2), p. 259–272.

[12] White, M.D. and Greer, K.A. “The effects of watershed urbanization on the stream hydrology and riparian vegetation of Los Peñasquitos Creek, California,” *Landscape and Urban Planning*, 2006, 74, p. 125–138.

[13] Callaway, J.C. and Zedler, J.B. “Interactions between a salt marsh native perennial (*Salicornia virginica*) and an exotic annual (*Polypogon monspeliensis*) under varied salinity and hydroperiod,” *Wetlands Ecology and Management,* 1997, 5(3), p. 179–194.

[14] Crooks, J.A. and Suarez, A.V. “Hyperconnectivity, invasive species, and the breakdown of barriers to dispersal,” In Connectivity Conservation: Maintaining Connections for Nature, Crooks, K.R. and Sanjayan, M.A., Eds. New York: Cambridge University Press, 2006, pp. 451-478.

[15] Ruiz, G.M. and Crooks, J.A. “Marine invaders: Patterns, effects, and management of non-indigenous species,” In Waters in Peril, Gallagher, P. and Bendell-Young, L., Eds. Dordrecht, The Netherlands: Kluwer Academic Publishers, 2001, pp. 3-17.

[16] Preisler, R.K., Wasson, K., Wolff, W., and Tyrrell, M.C. “Invasions of estuaries versus the adjacent open coast: A global perspective,” In Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives, Rilov, G.and Crooks, J.A., Eds. Heidelbderg, Germany: Springer, 2009, pp. 587–617.

[17] Crooks, J.A., Chang, A.L., and Ruiz, G.M. “Aquatic pollution increases the relative success of invasive species,” *Biological Invasions*, 2010, 13, p. 165-176.

[18] de Rivera, C.E, Ruiz, G.M., Crooks, J.A., Wasson, K., Lonhart, S., Fofonoff, P., Steves, B.P., Rumrill, S.S., Brancato, M.S., Pegau, W.S., Bulthuis, D.A., Preisler, R.K., Schoch, G.C., Bowlby, E., DeVogelaere, A., Crawford, M.K., Gittings, S.R., Hines, A.H., Takata, L., Larson, K., Huber, T., Leyman, A.M., Collinetti, E., Pasco, T., Shull, S., Anderson, M., and Powell, S. Broad-Scale Non-Indigenous Species Monitoring Along the West Coast in National Marine Sanctuaries and National Estuarine Research Reserves, Report to National Fish and Wildlife Foundation, 2005.

[19] Novoa, A., Talley, T.S., Talley, D.M., Crooks, J.A., and Reyns, N.B. “Spatial and temporal examination of bivalve communities in several estuaries of Southern California and Northern Baja California, MX”, *PLoS ONE*, 2016, 11(2), p. e0148220.

[20] Crooks, J.A. “The role of exotic marine ecosystem engineers,” In Biological Invasions in Marine Ecosystems. Ecological, Management, and Geographic Perspectives, Rilov, G. and Crooks, J.A., Eds. Heidelbderg, Germany: Springer, 2009, pp. 287–304.

[21] Dexter, D.M. and Crooks, J.A. “Benthic communities and the invasion of an exotic mussel in Mission Bay, San Diego: A long-term history,” *Bulletin of the Southern California Academy of Sciences*, 2003, 99(3), p. 128–146.

[22] Crooks, J.A. “The process of biological invasion: The arrival, establishment, and integration of exotic species into ecosystems,” *Bulletin of the Japan Ecological Society, Kanto Division*, 2002, 50, p. 15-22.

[23] Crooks, J.A. “The arrival, establishment, and integration of an invasive marine mussel into foreign ecosystems,” In Proceedings of the International Conference on Assessment and Control of Invasion Risks, Koike, F., Clout, M.N., Kawamichi, M., De Poorter, M.,and Iwatsuki, K., Eds. Kyoto, Japan: Shoukadoh Book Sellers and IUCN Press, 2006, pp. 113-115.

[24] Talley, T.S., Crooks, J.A. and Levin, L.A. “Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes,” *Marine Biology*, 2001, 138(3), p. 561–573.

[25] Talley, T.S. and Crooks, J.A. “Habitat conversion associated with bioeroding marine isopods,” In Ecosystem Engineers: Plants to Protists, Cuddington, K.M.D., Byers, J.E., Hastings, A., and Wilson, W.G., Eds. Burlington, Massachusetts: Academic Press, 2007, pp. 185-202.

[26] Larson, R.J. and Arneson, C. “Two Medusae new to the coast of California: *Carybdea marsupialis* (Linnaeus, 1758), a Cubomedusa and *Phyllorhiza punctata* von Lendenfeld, 1884, a Rhizostome Scyphomedusa,” *Bulletin of the Southern California Academy of Sciences*, 1990, 89(3), p. 130-136.

[27] Bolton, T.F. and Graham, W.M. “Morphological variation among populations of an invasive jellyfish,” *Marine Ecology Progress Series*, 2004, 278, p. 125-139.

[28] Lonhart, S. “Natural and Climate Change Mediated Invasions,” In Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives, Rilov, G. and Crooks, J.A., Eds. Heidelbderg, Germany: Springer, 2009, pp. 57-69.

[29] Crooks, J.A. “Lag times and exotic species: The ecology and management of biological invasions in slow-motion,” *Ecoscience*, 2005, 12(3), p. 316–329.

[30] Crooks, J.A. “Lag times,” In Encyclopedia of Introduced Invasive Species, Simberloff, D. and Rejmanek, M., Eds. Oakland, California: University of California Press, 2010, pp. 404–410.

[31] Crooks, J.A., Crooks, K.R. and Crooks, A.J. “Observations of the non-native Pacific oyster (*Crassostrea gigas*) in San Diego County, California,” *California Fish and Game*, 2015, 101(2), p. 101–107.

[32] Anderson, L.W.J. “California’s reaction to *caulerpa taxifolia*: A model for invasive species rapid response,” *Biological Invasions*, 2005, 7(6), p. 1003–1016.

[33] Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Arroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Del Tredici, P., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J., and Briggs, J.C. “Don't judge species on their origins,” *Nature*, 2011, 474, p. 153-154.

[34] Simberloff, D. and 141 signatories. “Non-natives: 141 scientists object,” *Nature*, 2011, 475, p. 36.

[35] Crooks, J.A. and Rilov, G. “Future directions for marine invasions research,” In Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives, Rilov, G. and Crooks, J.A., Eds. Heidelbderg, Germany: Springer, 2009, pp. 621-625.