MANAGING MULTIPLE VECTORS for MARINE INVASIONS in an
INCREASINGLY CONNECTED WORLD

Susan L. Williams\textsuperscript{1,2*},
Ian C. Davidson\textsuperscript{3,4},
Jae R. Pasari\textsuperscript{1},
Gail V. Ashton\textsuperscript{5},
James T. Carlton\textsuperscript{6},
R. Eliot Crafton\textsuperscript{7},
Rachel E. Fontana\textsuperscript{1,7,8},
Edwin D. Grosholz\textsuperscript{9},
A. Whitman Miller\textsuperscript{4},
Gregory M. Ruiz\textsuperscript{4},
Chela J. Zabin\textsuperscript{5,9}

\textsuperscript{1}Bodega Marine Laboratory, University of California-Davis, PO Box 247, Bodega Bay, CA 94923-0247,*\textsuperscript{(slwilliams@ucdavis.edu)}; \textsuperscript{2}Department of Evolution and Ecology, University of California-Davis, Davis, CA 95616; \textsuperscript{3}Environmental Sciences and Management, Portland State University, Portland, OR; \textsuperscript{4}Smithsonian Environmental Research Center, PO Box 28, Edgewater, MD 21037-0028; \textsuperscript{5}Smithsonian Environmental Research Center, 3152 Paradise Dr., Tiburon, CA 94920; \textsuperscript{6}Maritime Studies Program, Williams College and Mystic Seaport, PO Box 6000, Mystic, CT 06355-0990; \textsuperscript{7}Graduate Group in Ecology, University of California-Davis, Davis, CA 95616; \textsuperscript{8}Current address:
Keywords: invasive species, marine, vectors, propagule supply, management

Susan Williams, PhD, is a professor and coastal marine ecologist who studies the ecological effects of non-native species and applies results to management and policy.

Ian Davidson, PhD, is a Research Associate at the Aquatic Bioinvasion Research and Policy Institute. He is a benthic ecologist who focuses on marine invasive species, especially associated with vessels, and applies results to management and policy.

Jae Pasari, PhD, teaches and conducts research on ecological invasions in California's marine and terrestrial environments.

Gail Ashton, PhD, is a marine ecologist specializing in invasive species.

James Carlton, PhD, is a professor and marine biologist at Williams College and director of the Williams-Mystic Maritime Studies Program. His research focuses on marine invasions and extinctions.

R. Eliot Crafton is a PhD candidate modeling invasion risk for coastal marine and estuarine species.

Rachel Fontana, PhD, is an environmental oceanographer and a National Sea Grant Knauss Marine Policy Fellow in Washington, D.C.

Edwin Grosholz, PhD, is a professor and benthic marine ecologist who works on the science and management of biological invasions and coastal restoration.
A. Whitman Miller, PhD, is a Research Scientist who studies marine and estuarine invasions ecology with a strong focus on the role of commercial ships in the worldwide spread of invasive species.

Gregory Ruiz, PhD, is a Senior Scientist and head of the Smithsonian Environmental Research Center’s Marine Invasion Research Laboratory. He applies invasive species research results to management and policy.

Chela Zabin, PhD, is a marine ecologist interested in native species restoration and management of invasive species.
Abstract

Invasive species remain a major environmental problem in the world's oceans. Managing the vectors of introduction is the most effective means to mitigate this problem, yet current risk assessments and management strategies largely focus on species, not vectors, and certainly not multiple vectors acting simultaneously. To highlight the issue that multiple vectors are contributing to invasions, we analyzed the historical and potential contemporary contributions of eight maritime vectors to the establishment of non-indigenous species in California, where most species were associated with two to six vectors. Vessel biofouling looms larger than ballast water as a major vector and a management opportunity but aquaculture risk appears reduced from historic contributions. Standardized data on species abundances in each vector are lacking for a robust cross-vector assessment, which could be obtained in a proof of concept ‘vector blitz’. Management must shift away from one or two target vectors to coordination across multiple vectors.
Non-indigenous species (NIS) are widespread throughout Earth’s oceans and coasts, where they cause environmental impacts and economic damages (Carlton 1999). They have been associated with declines in marine populations (Kappel 2005), alteration of food webs (Nichols et al. 1990, Oguz et al. 2008), habitat modifications that affect community structure and function (Neira et al. 2006, Sousa et al. 2009), and delivery of toxic microorganisms of concern for sea life and human health (Ruiz et al. 2000).

Multiple vectors operating in an increasingly connected world

Increasing global trade, novel trade routes, climate change, habitat modification, fisheries, and invasions themselves can combine to create increasing opportunities for introductions of marine NIS. Global trade increased dramatically in the latter half of the 20th Century, driven by human population growth, changes in policies, and increased efficiency in shipping (Hulme 2009). Previously remote locales such as Antarctica, where many marine species are endemic, have come under increasing risk from NIS introductions (Smith et al. 2012). At the opposite pole, the Northwest Passage has been sufficiently ice-free for navigation since the summer of 2007, shortening the path between the Atlantic and Pacific oceans and increasing opportunities for human-mediated species introductions (Niimi 2004). As oceans warm, NIS can gain a foothold over native marine species (Sorte et al. 2010). New conservation strategies such as “assisted colonization” or “managed relocation” further promote transfers of species beyond their native ranges (Schwartz et al. 2012).
One by one- single species, single vector risk assessments

In this increasingly connected world, the most effective means to reduce future ecological and economic costs of NIS is to prevent their introductions by managing the vectors that deliver them, rather than focusing efforts on the management of individual species or even individual vectors (Ruiz and Carlton 2003, Reaser et al. 2008). Despite this widely accepted recommendation, most research and management tackles the problem of biological invasions on a species-by-species and vector-by-vector approach.

Species approaches have included “black listing” based on evidence that a species could be or is an injurious pest. This approach is usually based on previously-identified bad actors and it is laborious, being impractical for the large number of species that circulate in multiple vectors and especially those without an invasion history (Simberloff 2006, Reaser et al. 2008). A formal risk assessment, involving evaluation of the probability that a species will be introduced, establish, and cause ecological or economic harm, requires both more data and effort than is available for most species.

Various types of NIS risk assessments are being considered or applied by management authorities from states to nations (Kolar 2004, Gordon et al. 2012). Some assessments favor matching environmental conditions of native and non-native ranges to predict risk, some take a spatially-explicit landscape approach to identify sites that are vulnerable to invasions, some include management actions, and others focus on propagule pressure or address how the recipient community can shape the success or failure following an introduction. NIS risk assessment makes economic sense (Keller et al. 2007, Springborn
2011) and has made substantial progress over the past decade, but it is still based primarily on the risk posed by specific species or species characteristics related to invasiveness (Hayes 2002, Hayes and Sliwa 2002, Orr 2003, Keller et al. 2007, Campbell 2009, see Leung et al. 2012 for theoretical framework).

In this article, we highlight the challenge that multiple vectors pose in evaluation and management of invasions, using marine and estuarine (hereafter ‘marine’) NIS as a model. Maritime vectors are diverse. Major vectors include: 1) ballast water, which is already the subject of management to varying degrees (Miller et al. 2011), 2) ‘biofouling’ of large and small vessels by a community of sessile and associated mobile organisms that colonize and grow on any wetted surface of a vessel, such as hulls, anchors, storage lockers, or other colonizable locations (Mineur et al. 2008, Davidson et al. 2009, Wanless et al. 2010), 3) aquaculture (Naylor et al. 2001), 4) live seafood (Chapman et al. 2003), 5) live bait (Kilian et al. 2012), 6) ornamental species trade (Rhyne et al. 2012), and 7) marine debris (Barnes 2002). Maritime vectors are also temporally dynamic, with both gradual and punctuated changes, the latter demonstrated by biofouled debris from the 2011 Japanese earthquake and tsunami that washed ashore in North America. The tsunami debris instigated a rapid management response [25 June 2013; www.anstaskforce.gov/Tsunami/FINAL%20JTMD%20Biofouling%20Response%20Protocol_19%20Oct%202012.pdf], which is crucial to preventing introductions, but also highlighted the ad hoc manner in which limited management and scientific resources are allocated among multiple vectors when no decision has been made about vector
prioritization. Our analysis of maritime vectors helps explain why it is difficult to prioritize among vectors.

The plethora of existing vectors and temporal changes in operation is not generally recognized, except by the scientists who study them. It is safe to say that the broader public, the media, and the environmental, management and political communities are largely unaware of how little is known about these vectors in space and time. For example, the education campaigns that raised public awareness about ballast water as a possible vector for invasive species contrasts sharply with the lack of awareness about cultured non-native oysters that have become feral and can dramatically change marine environments (Ruesink et al. 2005). In a different example, the public is not likely to know that over 100,000 individuals of the quagga mussel (*Dreissena rostriformis bugensis*), over 100 sharks, and transgenic tilapia and salmon, all of which are restricted species in California, were permitted for importation in 2009, for research, exhibition including at public zoos and aquariums, or aquaculture (see below for data sources). Only recently have research facilities and public zoos and aquariums taken steps to prevent the release of NIS. The general incognizance of vector multiplicity is evident in regulatory frameworks based on single species or vectors. For instance, the Lacey Act administered by the US Fish and Wildlife Service (USFWS) regulates injurious pests species-by-species and the International Maritime Organization is advancing ballast water management. The value of these frameworks cannot be discounted, but they do not address the issue of managing multiple vectors.
How close are we to reliably comparing the relative risk of different maritime vectors or their cumulative risk? Which among the many operating vectors offer management opportunities or merit prioritization under the limited available resources? The relative importance of maritime vectors has been assessed most often by tallying the number of species attributed to vectors that are often defined in different ways (Bax et al. 2003, Ruiz et al. 2011), an approach also applied to freshwater and terrestrial NIS vectors (e.g., Keller et al. 2009). Although these studies have advanced the management of marine invasive species, they are largely retrospective analyses. A few quantitative risk assessments for single marine species have been accomplished (e.g., Herborg et al. 2007, 2009, Thierrault and Herborg 2008). A few other studies have undertaken a vector-based risk assessment by obtaining abundances of NIS in invasive pathways (Hayes 2002, Hayes and Sliwa 2002, Barry et al. 2008, Acosta and Forrest 2009). Hayes (2002) used shipping records and species distributions to estimate invasion potential, added a web-based questionnaire to assess economic, ecological, and health impacts for potential marine invaders in New Zealand, and estimated uncertainty using interval arithmetic. Single-vector management is certainly an improvement over single-species management, but might not substantially reduce invasions if many other vectors are in place. To our knowledge, there has been no attempt to quantify the relative or combined risk that multiple maritime vectors pose, beyond vector attribution tallies, or to evaluate their past, present and future changes.

To illustrate both the need for and the challenge of assessing the risk posed by multiple vectors, we compared available data for eight maritime vectors operating in California:
commercial vessel ballast water, commercial vessel biofouling, recreational vessel biofouling, fishing vessel biofouling, aquaculture, and trades in ornamental species, live seafood, and live bait. California provides a good model to illustrate the state of knowledge of multiple vectors for several reasons. California is a major introduction point for marine NIS and serves as a nexus for their establishment and spread. Furthermore, the state supports a relatively high level of activity across diverse vectors (Ruiz et al. 2011). Its large marine economy (Kildow and Colgan 2009) has already been taxed by marine invasive species (Anderson 2005, Fernandez 2008), which helped spur state government’s interest in a multiple-vector management approach. The vectors considered here operate globally; therefore, their comparison should provide a useful generalized illustration of the issue of multiple vectors.

Multiple vectors characterize California’s historical marine invasions

Data often limit quantitative NIS risk assessment (Gertzen and Leung 2011, Leung et al. 2012). The most readily available data are NIS lists that provide information on the species, introduced locales, and dates of first record (e.g., National Exotic Marine and Estuarine Species Information System [NEMESIS, 3 July 2013; http://invasions.si.edu/nemesis/index.html]; National Introduced Marine Pest Information System [NIMPIS, 16 June 2013; www.marinepests.gov.au/nimpis]). We analyzed California’s marine NIS invasion history based on a subset of data from NEMESIS (accessed 18 March 2013) for all non-freshwater, non-native invertebrates (except insects) and algae known to have established in California from 1853-2011. These taxa include the vast majority of marine NIS in California. We updated the study by Ruiz et al.
(2011) on vector attribution to individual species and expanded it to include multiple introduction events by including the dates and specific bays of introduction within the state, allowing finer parsing of vector attribution. We identified that at least 235 NIS have established in California’s marine and estuarine waters (Supplemental Material, Table A), including two species that were subsequently eradicated (the seaweed Caulerpa taxifolia, and the polychaete worm Terebrasabella heterouncinata).

We then addressed vector strength (the number of invasions attributed to a vector, Ruiz and Carlton 2003) in several ways. Based on life history traits, timing, and location of NIS detections and vector operations (see Ruiz et al. 2011 for description), 90 of the 235 species were classified as introduced to California almost certainly by only a single vector (figure 1a; Supplemental Material, Table A). The single-vector species provided the most conservative estimate of the historical strength of each vector. For these single-vector species, although ballast water was a major vector, non-ballast water vectors together accounted for more than twice the number of established NIS in comparison to ballast water alone. Furthermore, vessel biofouling was identified as the vector for as many established NIS as ballast water and aquaculture combined.

The other 145 NIS (61% of the total) were attributed to between two and six possible vectors. For these, we summarized vector strength in two ways. First, for each species, we summed the number of establishment events (non-transient presence of a species in a bay) attributed to each possible vector. For example, if a multiple-vector species was known from nine different bays and ballast was a sole or possible vector for three of these
bays, three invasion events were attributed to ballast for that species. This approach identifies the maximum number of establishment events per vector. Second, we weighted vectors proportionately by the number of events attributed to each for each individual species. When more than one vector was plausible for the presence of a species in a bay, it was treated as multiple events, each by a single vector. For example, if a species was known from 10 bays, including three associated with ballast alone, two with ballast and vessel biofouling together, and five with aquaculture only, ballast was weighted as 0.42 (5/12). Thus, each species is weighted equally (as 1.0), regardless of number of invasion events, and each plausible vector per introduction event has equal probability in its proportional contribution.

For these multiple-vector species, our unweighted estimate of possible vector importance indicated that ballast and vessel biofouling were the most common vectors involved (figure 1b). Of the 77 species introduced by two vectors, 49% were attributed to ballast water and vessel biofouling, 26% to aquaculture and vessel biofouling, and 8% to ballast water and aquaculture. Our weighted estimate highlights patterns that are not apparent from the previous, more traditional unweighted analysis alone. While the unweighted analysis demonstrates the magnitude of possible vector importance (for all invasion events), the weighted analysis is informative for generating hypotheses about probable vector importance on a per species basis. For example, the unweighted estimate indicates aquaculture was a potent possible vector, but the weighted estimate de-emphasized its vector strength relative to ballast water and vessel biofouling (figure 1c). To a lesser
degree the same can be said of ballast water, whereby its strength is reduced in the weighted estimate compared to vessel biofouling.

Although the historical data provided some new insights into the relative contributions of vectors introducing marine NIS to California, there are some obvious limitations for a robust comparison of vectors and their relative risk. First, the numbers of species on lists of introduced species such as NEMESIS and NIMPIS are undoubtedly underestimated (Carlton 2009). Second, a more serious limitation is that historical data do not necessarily match the species currently circulating in vectors today and rarely provide information on species abundances. Third, the nature of individual vectors themselves can change over time, both in magnitude and the per-capita transfer of organisms (see below). We thus considered contemporary fluxes of marine NIS to California.

Contemporary fluxes of marine NIS to California

Information on the abundance of organisms circulating in vectors is critical because abundance is highly correlated to the probability of an introduction (Ruiz et al. 2000, Colautti et al. 2006, Hayes and Barry 2008). For risk assessment, ideally both the number of individuals released in a single event (‘propagule size’) and the number of discrete release events (‘propagule number’) would be estimated for each species (Colautti et al. 2006). Although ballast water discharge events are recorded in countries including the US, data on release rates for biofoulers, marine ornamentals, seafood and bait are not available (Weigle et al. 2005). Thus, we focused on propagule flux as the numbers of species and individuals circulating in a vector per unit time (standardized to one year).
To investigate propagule flux we mined published data, federal and state records, and conducted field observations (vessel biofouling, air cargo). Flux estimates for recreational vessel biofouling were obtained from: 1) Last Port of Call (‘LPOC’) records of the US Customs and Border Protection (CBP) for small vessel arrivals to California in 2009, and 2) sampling hulls of 49 transient vessels between 2010-2011 for species identification and abundances. The flux of NIS through commercial fishing biofouling was estimated from numbers of arrivals to California in 2008, provided by the Pacific Fisheries Information Network [PacFIN, 1 March 2012; www.psmfc.org/program/pacific-fisheries-information-network-pacfin]. Flux estimates for commercial vessel biofouling and ballast water discharge were derived from hull surveys of 23 vessels during 2009-2011, the National Ballast Information Clearinghouse [NBIC, 30 January 2013; http://invasions.si.edu/nbic/search.html] arrival and discharge data, and using the midpoint of zooplankton concentrations in ballast arriving to the US (Minton et al. 2005). Ornamental species fluxes were estimated from: 1) USFWS’s Law Enforcement Management Information System (LEMIS) records for live marine fish and invertebrate (excluding scleractinian corals) importations into San Francisco and Los Angeles in 2009 (the most recent year of complete records) and observations of air cargo inspections in 2012, and 2) California Department of Fish and Game (CDFG) permits for restricted species from 1988 through 4 August 2011. We assessed the flux in aquaculture starting with CDFG records, which led to other sources (see below for details).
No common currency to compare propagule flux across vectors

At present, no single source of NIS information exists for any of these vectors. Also lacking is a common currency to estimate the flux (numbers of individuals and their identity) circulating annually in each vector, except as order of magnitude bounds (figure 2). We first identified a specific unit of NIS delivery for biofouling (vessels arriving), ballast water (vessels discharging), and ornamental species (shipments), but aquaculture import permits did not yield a useful unit of delivery (figure 2a). Next, the quantities of organisms associated with each unit of delivery were estimated for recreational and commercial vessels and the ornamental vector. Good records exist for volumes of ballast water discharged, but numbers of organisms in ballast water had to be extrapolated from another study (Minton et al. 2005). Vessel biofouling has been measured variously as the number of macroinvertebrate species in a biofouling community per vessel, the percent cover of biofouling in areas sampled on vessels, or the biomass of fouling per unit area (Davidson et al. 2009). For the ornamental species, LEMIS import permit records provide more indirect but readily available data than for biofouling. Although quantities of ornamental species in the LEMIS records are not always standardized to individual organisms and records do not account for subsequent transfers out of the state, they are probably close to actual quantities. Quantities could not be estimated for fishing vessels or aquaculture (figure 2b) because sampling access has been restricted to extremely few vessels to date and the numbers of organisms listed on aquaculture permits lacked sufficient standardization and specificity to derive quantities (see below).
Moreover, comparisons of measures of species richness are also problematic, having different approaches depending on the vector (figure 3c; see below). Taxonomic identification is best for the aquaculture vector in California, where permitted organisms are identified to the species level without exception. Species composition is problematic in live organism trades (Rhyne et al. 2012, Smith et al. 2012) but still far better than for most ballast water discharges, for which species composition is unknown. USFWS importation records concern only animals, the majority of which fall into generic taxonomic categories (“marine tropical fishes”, “crustaceans”). Plants fall under the jurisdiction of the US Department of Agriculture, where the same issues apply regarding labeling and transfers upon arrival into the country. Marine plants in general are mostly unidentified when observed and under-represented in vector sampling.

Small recreational and fishing vessels illustrate the fragmented nature of the data (table 1). There were 1182 recreational vessels of foreign origin that entered California and registered with CBP in 2009. This number is the same order of magnitude as commercial vessels (1822 reported in NBIC), yet the actual arrivals of recreational vessels in California and their intra-state movements are unknown but certainly higher than the number of foreign vessels that reported to CBP. CBP records include only the initial arrivals in California of vessels with a LPOC outside of the US. Such boats might travel to additional ports where further registration is not required yet NIS might be transferred. Similarly, vessel arrivals from other US states - either US vessels or foreign vessels that reported to CBP upon first arrival in a different state – are not captured by CBP’s California records. We also conducted surveys of certain marinas in the state, which
revealed that not all foreign arrivals were captured in the records. Fishing vessel data came from a different source (see above), were restricted to where catch was landed (and excluding other movements where fish were not landed), and included only vessels reporting to Washington, Oregon, and California. If a fishing vessel travels outside of these states, non-comparable CBP records should capture foreign voyages but there is no mechanism to capture voyages to other US states.

Aquaculture provides an example of both the lack of a common currency for contemporary fluxes and also the fragmented nature of the information (figure 3). We initially expected that the NIS flux in aquaculture could be estimated given that the organisms are intentionally imported or outplanted. We began assessing aquaculture NIS fluxes based on CDFG importation and private stocking permits from 1950 through 2011, only to realize that the records were incomplete and highly dispersed across multiple agencies that regulate various aspects of the industry in California. Different sectors of CDFG are responsible for import permits, private stocking permits, aquaculture inspection and planting certificates, and bottom lease records (“proof of use” reports for state-registered aquaculture facilities). Commercial aquaculture facilities, which must be registered with CDFG, must also file a management plan with the California Department of Public Health, a step we recognized only at the end of the data collection period. While these plans indicate potentially farmed acreage, they do not provide information on number of individuals outplanted or even number of acres actually farmed. The US Army Corps of Engineers (ACE) requires permits for aquaculture businesses placing structures that change the flow of water and/or affect the substratum in state or federal waters. We
examined ACE records held in the Los Angeles office through a Freedom of Information Act request, but the records provided no relevant information on NIS fluxes (records held in the San Francisco office were not readily retrievable). For aquaculture species imported from other countries, USFWS's LEMIS recorded no importations of invertebrate species for aquaculture between 2003-2011.

Even taken together, these numerous types of records for California marine aquaculture provided little information on NIS fluxes. Abundances were reported as cases, bushels or thousands of seed individuals. Although California aquaculture import permits must list the intended species and exporter location, there is no post-permit requirement to report the volume or number actually imported. Aquaculture “proof of use” reports specify the number of plantings for a subset of aquaculture facilities (figure 3), but listing the source is voluntary. To further complicate the issue, aquaculture leases were managed variously by CDFG, conservation districts, cities, and a private energy-generating company. The complexity of the aquaculture regulatory framework is challenging for both the industry and the regulators and is a cogent example of the long-recognized need for a authority for the international and interstate importation of live organisms (Schmitz and Simberloff 2001, Lodge et al. 2006), which ideally would also include intra-state movements of NIS.

Comparing invasions across multiple vectors – Apples and oranges

Although currently available data on NIS delivery by maritime vectors are too disparate for a rigorous cross-vector risk assessment, this assessment provided some rough comparisons across the vectors. Historical data indicate that ballast water, despite the
national and international focus on it as the primary vector for marine NIS, is by no means necessarily the most important vector for established marine NIS in California (figure 1). Indeed, this situation is likely true in other geographic locations (Bax et al. 2003). Managing ballast water, although necessary and an example of a vector-based approach, is clearly insufficient to prevent new introductions given the importance of other vectors. Although we found no common currency to allow highly quantitative comparisons of contemporary NIS presence and abundances circulating in each vector (figure 2), the available data support the conclusion that other vectors must be addressed in addition to ballast water. Flux data support ornamental species as a potentially risky vector (figure 2), which would not have been evident from historical data (figure 1).

Flux is often positively related to establishment rates (Colautti et al. 2006, Hayes and Barry 2008, Simberloff 2009) and reducing or eliminating flux is a prime management target. However, the risk of harm is also shaped in the consecutive stages along the invasion pathway of entrainment, transport, and release into the environment, and the contribution of each stage to overall risk differs among vectors (figure 5). Flux estimates for ornamental, live bait, and live seafood species are not necessarily good predictors of the probability that they will be introduced (released into the environment) because the available data on flux reflect only part of the full journey from source to destination waters (figure 5, #1, #2). Therefore, while these organisms are entering California, there is no information on their release into marine and estuarine habitats until their establishment as NIS is detected. Release rates are also unknown for marine ornamental species; only a few rates exist for freshwater ornamentals (e.g., Strecker et al. 2011).
Despite the high flux of marine ornamental species and their hardiness, their establishment has been low in California, perhaps because they are rarely released or that most of the species are tropical and do not survive release or they are transferred out of the state.

In contrast, ballast, fouling, and aquaculture organisms are released to, or directly contact, marine environments. Vessel biofouling carries a large number of species and individuals (high flux) but the quality of the vector’s habitat is variable for individuals, some of which are undoubtedly lost en route (Murray et al. 2012). Aquaculture differs in having a comparatively low flux but there is a strong economic incentive to ensure survival. However, data are lacking on the numbers of permitted aquaculture organisms that are actually placed in the environment (see above).

**Marine NIS impacts in California**

The ultimate goal of NIS risk assessment is to predict the probability of ecological, economic, and social harm. The perception that harm will occur often drives responses to invasions and motivates NIS management. Just as vectors differ in numbers and frequencies of non-native species, the impact of non-native species might not be delivered evenly among vectors. To assess whether the ecological and economic impacts of marine NIS in California could be differentiated by vector, we completed BIOSIS searches for impacts of mollusc, algal, and crustacean species (including alternate and synonymous species names) from 1926 through 2011 (see Supplemental Material, Table
B for search protocol and references for results). These taxonomic groups represent the majority of the NIS in California.

Published peer-reviewed information was too limited to assess the impacts of these taxa, let alone by vector (Supplementary Material, Table B). The majority of the information uncovered was devoted to only three or fewer species in each taxonomic group. Fifty publications concerning impacts were available for 11 of the 41 established molluscan species (Supplemental Material, Table B), with 34% of these publications devoted to one species, *Mytilus galloprovincialis*. The impact literature on algal species produced similar results, with three species (*Caulerpa taxifolia*, *Sargassum muticum*, *Codium fragile*) subspecies dominating 84% of the 124 impact publications. Impact data were available for just 17 out of 87 crustacean NIS, with 42% of papers dedicated to the European green crab, *Carcinus maenas*. Because only 17 publications on molluscs, two on algae, and six on crustaceans were specific to California, the relevance of the impact information may be limited given impacts can be highly context-dependent (Thomsen et al. 2011). Without better data, impacts cannot be apportioned across vectors, leaving vectors to be singled out for their impacts one at a time. For example, the ornamental trade vector has stood out as being responsible for introducing some of world’s worst aquatic invasive species (Padilla and Williams 2004, Semmens et al. 2004), including the seaweed *Caulerpa taxifolia*, which cost California over $6 million to eradicate (Anderson 2005) and lionfish (figure 4).
Vector management led to temporal changes in flux-

To the extent they have been taken, management approaches have also varied by vector.

Although historically aquaculture and ballast water were potent vectors for marine NIS introduction, these vectors have been deliberately interrupted to reduce their flux (figure 5, #3, #4). The drivers of change between historical and modern transport of bivalves and ballast water differed considerably; aquaculture vector changes were driven by industry practices and profitability, while the ballast water mechanism changed because of explicit vector management policy and regulation.

Historically, aquaculture shipments were a stronger vector than today because the intentional transfer of adult bivalve species was accompanied by an assortment of unintentional “hitchhiking” species (figure 5, #3), which benefited from the high-quality transport conditions needed for the bivalves. However, consciousness about NIS has heightened in the aquaculture industry with the result that under current practices the accidental introductions of associated species or ‘hitchhikers’, which were historically an important source of NIS, are now minimal. The vast majority of contemporary bivalve shipments consist of larvae or juveniles of one species, the commercial Pacific oyster *Crassostrea gigas*, with few (if any) additional entrained species, resulting in a dramatically lower risk of invasions (figure 5, #4). Analogous to current practices for aquaculture shipments, the elimination of biological packing materials (seaweeds, Haska et al. 2012) offers an opportunity to reduce the unintentional species that accompany intentional bait shipments, which could slow transfers of NIS from New England and Asia to California.
Historical ballast water entrained a large pool of planktonic species during a voyage that was reduced in species richness and abundance upon discharge by the net effect of interacting biological and environmental factors (figure 4, #5). The initiation of mid-ocean ballast water exchange (figure 4, #6) has reduced propagule delivery by enhancing interruption of the transport phase. Today, international, federal, and state ballast water regulations are among the few examples of active vector management in the marine realm; however, establishing such management practices has been the result of an arduous, ongoing, 30-year process.

A few marine and brackish ornamental species intended for sale or display are regulated by California as restricted species (alligators, sharks, gars) and the state has enacted legislation to ban importation, sale, and possession of nine species of the seaweed Caulerpa (Assembly Bill 1334, chaptered in 2001, CDFG Code 2300). Neither California’s nor the US Department of Agriculture’s Noxious Weed listing of Caulerpa taxifolia (invasive Mediterranean strain, 1999) has been effective (Diaz et al. 2012). The ornamental trade’s involvement in NIS management in California and elsewhere has not been as strong as industry involvement has been for aquaculture and ballast water, which is both a lesson to learn and an opportunity.

Conclusions

Way forward – Vector “blitz”, expert judgment, and management opportunities
Clearly, the many disparate sources of data available for each vector were not adequate for a rigorous risk assessment of multiple vectors, even for just the initial steps of entrainment and transfer of NIS in the invasion process, let alone their release and impacts. To contend with the lack of a common currency for a cross-vector comparison of the identity and abundances of organisms arriving in the multiple vectors and in recognition that managers must prioritize resource allocation in data-poor situations, we recommend a novel “vector blitz” to obtain comparable flux data rapidly and relatively inexpensively. Rapid assessments or “BioBlitzes”, in which the number of newly introduced and established NIS is quantified at a single field location over a short time interval (days), are common (Delaney et al. 2008). In an analogous vector blitz, the abundances and identity of organisms would be quantified in a coordinated manner across vectors over a standardized time period and location using a standard sampling unit to be resolved beyond the units we present in figure 3. While marine bioblitzes characterize what NIS have already arrived, the vector blitz would characterize the names and numbers of potential invaders on the way. Vector blitzes would force resolution of the common currency problem. For example, should the number of vessels, their volume, or wetted surface area be accounted for, or all three? The locale selected for the blitz would need to be sufficiently large to encompass representative vectors. Shipping ports generally do not support aquaculture because of poor water quality, but aquaculture often occurs in nearby bays. For a Californian example, aquaculture in Agua Hedionda lagoon and Tomales Bay is within striking distance of Los Angeles and San Francisco, respectively. A rigorous vector blitz would provide a concrete measure of the cost involved in collecting data for a longer-term cross-vector comparison or risk assessment.
Coordination of scientists, agency staff, and citizens would be necessary. Access to commercial ports, marinas and small vessels would need to be secured, which was an issue for our fishing vessel surveys. Taxonomic expertise would be required, as would Institutional Review Board approval (for human subject research) to survey vendors of seafood, bait, and ornamental species. A vector blitz is a perfect opportunity for a targeted educational campaign to raise awareness of the multiplicity of vectors in operation. Given a vector blitz would be the first of its kind, it would be a rigorous proof of concept and a step toward defining a common currency for NIS fluxes. Thereafter, however, vector blitzes should be repeated in time and space to capture the dynamics of NIS introductions and vector operation to evaluate management efficacy and to reprioritize vectors when necessary.

Although understanding the fluxes of organisms in vectors or propagule pressure is critical to managing vectors, other differences among vectors influence the probability of actual introduction, establishment, and impact. As we described earlier, these differences are known only qualitatively. In this data-poor situation, the tool of expert judgment offers a stopgap measure to help inform management decisions about vectors (Hayes 2002, Therriault and Herborg 2008, Acosta and Forrest 2009). Although expert judgment is inherently subjective, prone to systematic errors, and can lead to false confidence in the result, it can supplement limited data and help quantify uncertainties, as demonstrated in recent applications of Bayesian models to invasive species (Kuhnert et al. 2010). Unlike more commonly used statistical models, Bayesian models can incorporate prior knowledge about the variables, such as the results of an expert judgment elicitation on
NIS release rates and impacts, into the model development. A cross-vector Bayesian risk
model for California’s maritime vectors is under development, based on our results and
expert elicitation. Limitations of expert judgment are being addressed (Burgman et al.
2011), but for now, expert judgment is a crutch and not a substitute for data-driven
management.

Despite major data gaps, there are clear examples of changes in vector operations that
have caused sustained vector disruption for both aquaculture and ballast water (figure 5)
and further management opportunities exist. Our analysis revealed that vessel biofouling
was and is a very strong vector, supporting a compelling need to reduce its NIS flux
associated with both commercial vessels and small crafts. Similar to the management
progress made for aquaculture and ballast water, managing vessel biofouling to induce
more regular maintenance of submerged surfaces of commercial vessels and transient
boats could reduce propagule delivery (Johnson and Fernández 2011). A number of
countries have recognized that managing the biofouling on ships' hulls can reduce the risk
of marine invasions (Gollasch 2002, Floerl et al. 2005, Hewitt et al. 2009). In 2011, the
International Maritime Organization adopted biofouling management guidelines for ships
>24 m, which are primarily commercial vessels, and is working on guidelines for smaller
vessels. California now requires periodic removal of hull fouling organisms for vessels
over 300 gross registered tons and capable of carrying ballast water. An annual hull
husbandry report would also be required to enable better understanding of the extent of
the hull fouling flux in California (3 July 2013;
Our multi-vector analysis also revealed that reducing the risk from biofouling requires managing not only large vessels but also small craft. The small craft vector has roughly the same magnitude of vessels traveling from out-of-state as the commercial vessel vector (table 1, figure 2). These vessels can accumulate high biofouling loads when they sit in harbors for long periods (figure 6), yet they have not received any substantial management attention or even sustained outreach on NIS transfers to promote cleaner submerged surfaces, with the exception of efforts by the cooperative extension unit in California’s Sea Grant Program [3 July 2013; http://ca-sgep.ucsd.edu/focus-areas/healthy-coastal-marine-ecosystems/healthy-ecosystems-boating]. Our analysis highlights the need for better data on the movements of small crafts and the extent of biofouling to determine whether prioritization of this sector of the vector is merited.

Given that the majority of established species are associated with multiple vectors, the key to reducing future rates of new NIS introductions is to move away from approaches that target only commercial shipping and toward a more diversified approach that tackles all vectors simultaneously, or if sequentially, then in a prioritized manner, for example addressing biofouling of all vessel types next. Efficient, effective management is difficult to envision in the absence of good data and also an authority with the resources and accountability for the management of the multiple vectors in operation. Vector blitzes would result in better, more comparable data for estimating the flux of NIS arriving in multiple vectors, as required for a quantitative cross-vector risk assessment. Centralized permitting and data collection for NIS-associated sales of live bait, seafood, aquaculture, and ornamental species could also yield more standardized data. The need for centralized
regulatory authority is highlighted in the aquaculture example (figure 3), to echo recommendations repeatedly put forth (Schmitz and Simberloff 2001, Lodge et al. 2006). Severe impediments to centralization are the expense and effort to reorganize government bureaucracies and to fund external contractors, which has contributed to the expiration of several useful NIS web sites. In California, the Ocean Protection Council is serving at least in a centralized advisory role for maritime NIS. A more flexible and perhaps less costly alternative to centralization is a network of information distributed from nodes representing sites where data are collected routinely across vectors (Ruiz and Carlton 2003), ideally in standardized vector blitzes. Each node could be funded independently and the loss of one would be a regrettable data gap but would not collapse the entire network.

Maritime NIS risk assessment has been moving from single-species approaches to considering entire vectors (Floerl et al. 2009, Chan et al. 2012). The next opportunity for advancement in theory and practice lies in developing a rigorous assessment of multiple species in multiple vectors that represent the cumulative risk NIS pose in California and elsewhere. There is no substitute for good data, and our analysis highlights the need to establish a common currency to compare NIS abundances in different vectors and to collect data on NIS release rates. The invasion process is understood very well and there are good models and frameworks for how vector management can work, conceptually and practically. We need to join the various disparate components into an integrated system, allowing a strong basis for prioritization and science-based decisions for vector
management --- leaving behind the current *ad hoc* approach that leaves the door open to new invasions.

**Acknowledgments**

This work was supported by Proposition 84 funds made available to the California Ocean Science Trust by the California Ocean Protection Council with additional funding from the California Ocean Science Trust, the California Sea Grant Program, and the Smithsonian Institution. We thank many staff in federal and state agencies for their generous assistance, especially G. Townsend and K. Ramsey. Ocean Science Trust staff facilitated and helped shape the work, in particular S. McAfee, R. Gentry, E. Kramer-Wilt, and R. Meyer. We thank P. Fofonoff, K. Holzer, and B. Steves for critical database support. We also thank anonymous reviewers and T. Beardsley for clarifying comments.

**Supplemental Materials**

Table A. Non-indigenous estuarine and marine invertebrates and algal species established in California.

Table B. Literature search methodology and resulting references for information on impacts of marine and estuarine NIS molluscs, crustaceans, and algae established in California.
References


Gollasch S. 2002. The importance of ship hull fouling as a vector of species introductions
into the North Sea. Biofouling 18: 105-121.


Niimi, AJ. 2004. Environmental and economic factors can increase risk of exotic species introductions to the Arctic region through increased ballast water discharge.


Table 1. Comparison of vessel data used in Figure 2. This table provides details of the parameters and sources for vessel vectors that provide some of the basis for Figure 2. It also highlights the disparate nature of vector data, even among a subset of similar vectors.

<table>
<thead>
<tr>
<th></th>
<th>Recreational</th>
<th>Fishing</th>
<th>Commercial</th>
</tr>
</thead>
<tbody>
<tr>
<td># vessels</td>
<td>1182</td>
<td>134</td>
<td>1822</td>
</tr>
<tr>
<td># arrivals in CA</td>
<td>Unknown</td>
<td>Unknown</td>
<td>6002</td>
</tr>
<tr>
<td>Origin</td>
<td>Foreign</td>
<td>OR, WA</td>
<td>Outside CA</td>
</tr>
<tr>
<td>Date</td>
<td>2009</td>
<td>2008</td>
<td>2010</td>
</tr>
<tr>
<td>Data source</td>
<td>CBP</td>
<td>PacFIN</td>
<td>NBIC</td>
</tr>
</tbody>
</table>

**Fouling organism abundance**

<table>
<thead>
<tr>
<th>Abundance per vessel sampled</th>
<th># vessels</th>
<th># vessels</th>
<th># vessels</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>7</td>
<td>unknown</td>
<td>2</td>
</tr>
<tr>
<td>1-10</td>
<td>11</td>
<td>unknown</td>
<td>2</td>
</tr>
<tr>
<td>11-100</td>
<td>6</td>
<td>unknown</td>
<td>0</td>
</tr>
<tr>
<td>101-1000</td>
<td>13</td>
<td>unknown</td>
<td>2</td>
</tr>
<tr>
<td>1001-10,000</td>
<td>7</td>
<td>unknown</td>
<td>8</td>
</tr>
<tr>
<td>10,001-100,000</td>
<td>3</td>
<td>unknown</td>
<td>7</td>
</tr>
<tr>
<td>&gt; 100,000</td>
<td>2</td>
<td>unknown</td>
<td>2</td>
</tr>
<tr>
<td>Total vessels sampled</td>
<td>49</td>
<td>0</td>
<td>23</td>
</tr>
<tr>
<td>% with fouling NIS</td>
<td>86</td>
<td>unknown</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>Arrivals discharging</td>
<td>% with ballast NIS</td>
<td></td>
</tr>
<tr>
<td>--------------------------</td>
<td>----------------------</td>
<td>--------------------</td>
<td></td>
</tr>
<tr>
<td>non-CA sourced water</td>
<td>Not applicable</td>
<td>Not applicable</td>
<td>962</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Not applicable</td>
<td>Not applicable</td>
<td>Unknown</td>
</tr>
</tbody>
</table>


828 Note: No data were available for arrivals of fishing vessels from regions other than Oregon and Washington, although arrivals probably occur.
Figure 1. Vector attributions by taxa. (a) 90 marine NIS species established (including two subsequently eradicated) in California were attributed solely to a single vector ("single-vector species"). The "Protozoans" include Ciliophora. (b) 145 NIS in California were associated with two or more vectors ("multiple-vector species"). The graphed total exceeds 145 species because each species was assigned to all of the vectors considered possible transfer mechanisms at each location (n = 389 events). (c) For multiple-vector species (as in panel b), vector attribution was apportioned to each species by the number of unique place-times each vector was associated with an introduction. Taxa with < 10 species: "other". "Unascribed": a vector was not assigned to a species in the NEMESIS database (Supplemental material, Table A).

Figure 2. Annual NIS flux across vectors. Data illustrating the lack of a standardized metric to compare propagule flux across vectors: biofouling (recreational, fishing, and commercial vessels), ornamental species trade, aquaculture, and ballast water discharge as: (a) arrivals of units that could be managed for each vector (where available for biofouling, both the number of unique vessels (solid) and estimated number of arrivals (diagonal) are shown), (b) propagule flux associated with each arrival unit in panel a (kite diagrams illustrate the distribution of frequencies), and (c) likelihood of NIS associated with each unit of introduction. Note log scales in panels (a) and (b). Date range or the number of vessels sampled is indicated at the top of the figures. Fill indicates certainty, for example, we are confident of the number of ships discharging ballast into California waters (black), but accurate information concerning aquaculture permits in the state was not available (gray). White fill indicates ballast water data are from non-
California ports. No data were available for the number of individuals delivered by aquaculture or fishing vessels or the proportion of NIS in ballast water or fishing vessel fouling communities. See Table 1 for vessel data summary.

Figure 3. The process for importing animals and marine plants into (or moving within) California for aquaculture purposes. Dashed lines indicate import regulations for plants. Plants and animals imported into the United States must be cleared by the USFWS and/or the USDA. The California Department of Food and Agriculture (CDFA) maintains a noxious weeds list of species prohibited for importation. There are no restrictions on moving aquaculture species within the state. Marine animals and plants intended for placement into state waters must also be permitted through CDFG (Import Permit) if moved from out of state. CDFG Private Stocking Permits are required for organisms used for non-commercial purposes. Commercial facilities must file a management plan with the California Department of Health. CDFG manages aquaculture leases; leasees must file an annual Proof of Use Report. The ACE requires permits for structures placed in the water. Despite the numerous permits required in some cases, complete data on the source, species, and numbers of individuals actually placed in the water are not collected.

Figure 4. Lionfish (*Pterois volitans*) in its native Indo-Pacific region. Lionfish are an ornamental species that invaded the Caribbean, Gulf of Mexico, and US eastern seaboard. They can tolerate temperate waters and are being imported into California. Photographer: Bruce Nyden.
Figure 5. Conceptual diagram comparing maritime vectors and potential management control points. Eight contemporary maritime vectors (left column) are compared across (a) the relative size of source propagule pools (left-hand circles), (b) typical transit processes (polygons in middle section), and (c) relative inocula sizes during propagule delivery (right-hand circles). White circles and polygons: target species pools and deliberate transfer activities during *intentional* vector processes; gray circles and polygons: *unintentional* transfers of species; hatched polygons: intentional transfers of species with associated unintentional transfers. Circle diameter (left side) represents estimated species richness at the beginning of a typical transfer (small, medium, large circles reflect 1–9, 10-99, and 100-1000 species per shipment). For example, shipping vectors (ballast water and biofouling) and shipments of ornamental species are considered at present to have the highest richness while contemporary bivalve aquaculture shipments are single species transfers. Contemporary shipments of live bait include the target bait species and the associated unintentional entrainment of non-target species in packing material (1). A large influx of species via the seafood, ornamental, and bait vectors arrive into terrestrial hubs (airports, wholesalers) followed by an unknown attrition rate with releases into the sea by end-users (2). Biofouling of commercial, recreational, and fishing vessels transfers species into and within the state with invasion opportunities enhanced by constant vector contact with the marine environment. The dashed-line box shows historical operation of aquaculture (3) compared to the present (4) and historical ballast water (5) operation compared to modern (6).
Figure 6. Heavy biofouling on the hull of a transient recreational boat in California.

Photographer: Ian Davidson.
Figure 1.
Figure 2.
Figure 3.

CDFG: Import Permit (annual permit)

USDA/USFWS clearance (Federal Noxious Weed Act) or CDFA (state list) clearance

CDFG: Registered aquaculture facility

CA Department of Health (management plan)

US Army Corps of Engineers (5-year permit)

USFWS clearance

CA Department of Health (management plan)

CDFG: Proof of Use Report (annual report)

Structures in water

CDFA (state list) clearance

Other than CDFG managed lease

Private Stocking Permit

Non-commercial use

Within California (no regulations)

From overseas

From outside of California

Animal

Marine plant

No structures in water (no permit required)
Figure 4.
Figure 5.
Figure 6.