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Research Article

# A vector analysis of marine ornamental species in California

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## Abstract

The trade in marine and estuarine ornamental species has resulted in the introductions of some of the world's worst invasive species, including the seaweed *Caulerpa taxifolia* and the lionfish *Pterois volitans*. We conducted an analysis of the historical introductions and establishments of marine and estuarine ornamental species in California using a database ('NEMESIS') and the contemporary fluxes (quantities, taxa) based on government records, direct observations of aquarium-bound shipments, and internet commerce. California is the major port of entry of marine ornamental species in the United States, which is the major global importing country. The vector was considered possibly responsible for twelve species introduced between 1853–2011, nine of which successfully established, including *Caulerpa taxifolia* (Mediterranean invasive strain). The flux of imported ornamental species was over 11 million individual animals in 2009 and included 37 taxa from at least six temperate countries, although the majority originated from the Indo-Pacific region. Almost 4,000 individuals representing at least 149 species were imported into San Francisco on a single day in 2012. Estimates of imported quantities were probably accurate within an order of magnitude but could be improved with data on interstate shipments and internet commerce. Importations of high concern included *P. volitans*, live rock, *Chromis viridis* (green chromis), and *Cromileptes altivelis* (panther or humpback grouper). The low historical establishment rate for ornamental species hypothetically could be explained in part by a low release rate or temperature mismatch, but the flux remains high and is a growing concern that could be addressed by heightened public education.

**Key words:** invasive, marine, ornamental, aquarium, internet commerce, vector

## Introduction

The trade in ornamental ('aquarium') species can be a potent vector for the introduction of non-indigenous species (NIS) (Les and Mehrhoff 1999; Padilla and Williams 2004; Cohen et al. 2007; Gertzen et al. 2008; Maceda-Veiga et al. 2013). Exotic plants and animals are prized for their beauty and novelty, making the ornamental trade lucrative and resulting in its promotion as a means of potentially sustainable development for countries where specimens are collected (Edwards and Shepherd 1992; Kay and Hoyle 2001; Bruckner 2005; Wabnitz et al. 2003; Bunting et al. 2008; Secretariat of the Convention on Biological Diversity 2010). Most research on the ornamental species trade has focused on potential impacts to biodiversity from destructive collection and shipping practices in the source regions (Edwards and Shepherd 1992; Kolm and Berglund 2003; Shuman et al. 2005; Smith et al. 2008, 2009; Rhyne et al. 2012b, 2014). Far less attention has been devoted to the potential 'downstream' environmental effects of releasing marine NIS at their final destination (Andrews 1990; Semmens et al. 2004; Calado and Chapman 2006; Whittington and Chong 2007).

As a vector for invasive species, the marine and estuarine (hereafter 'marine') ornamental trade generally has received less attention from scientists and policy makers than other maritime and freshwater vectors such as ballast water (Ruiz et al. 2000; Weigle et al. 2005). However, NIS introduction via the ornamental trade is different from other aquatic vectors in at least two important ways. First, few if any ornamental species arrive in direct contact with the environment, unlike organisms fouling vessel hulls or entrained in ballast water. Second, although their release rate might be low, ornamental species are often hardy and large or fully-grown (Duggan et al. 2006), increasing the likelihood of survival and establishment if released (Keller and Lodge 2007).

This study describes and broadly assesses the ornamental trade as a vector for marine and estuarine (hereafter 'marine') ornamental species in California. The annual global flux of marine ornamental species is enormous and the majority is exported to the United States (US) and landed in California (Balboa 2003; Wabnitz et al. 2003; Tissot et al. 2010). The number of fishes alone imported into the entire US between 1997–2005 was estimated at millions of individuals (Wabnitz et al. 2003; Rhyne et al. 2012a). Examples of invasive ornamental species include lionfishes (*Pterois volitans* (Linnaeus 1758)/*P. miles* (Bennett 1828) (Albins and Hixon 2008; Schofield 2010) and the seaweed *Caulerpa taxifolia* (invasive Mediterranean strain) (Meinesz et al. 2001; Meusnier et al. 2002). *Caulerpa taxifolia* has been a costly invasive species; its successful eradication in California incurred at least $6 million over the four years required to treat two infestations (Jousson et al. 2000; Withgott 2002; Anderson 2005).

The specific objectives of this study were to characterize the marine ornamental vector and evaluate the sources and quality of data relevant for assessing the risk of NIS introductions to California. In addition to being a major port of entry for marine ornamental species, California is also a major introduction point for NIS to the west coast of North America (Ruiz et al. 2011). The large marine economy of California (Kildow and Colgan 2005) is potentially at risk, and significant resources have already been directed to managing invasive marine ornamental species, as cited above for *Caulerpa taxifolia*. We conducted a vector analysis of the organisms circulating in the trade and estimated vector strength, *sensu* Ruiz and Carlton (2003). Specifically, we assessed the 1) historical marine NIS introductions and establishments attributed to the ornamental vector, 2) contemporary flux as the number or biomass of taxa and individuals circulating in the vector including key species in internet commerce, and 3) literature on the ecological and economic impacts reported for the marine ornamental species established in California.

## Methods

### *Historical introductions: vector analysis and strength*

To conduct a historical vector analysis of the number of introductions attributed to the vector ('vector strength'), we extracted a list of the introduced and established non-native marine and estuarine species in California attributed to the ornamental trade from the National Exotic Marine and Estuarine Species Information System database ('NEMESIS', Fofonoff et al. 2013). NEMESIS includes non-native species that have been introduced, thought to have established, failed to establish, or have gone extinct or were eradicated since establishment. NEMESIS records were compiled from the peer-reviewed scientific and the gray literature from 1853 through 2011. To estimate vector strength, we used the NEMESIS assignment of vectors to species, which was based on evidence linking introductions to vectors, species' life history characteristics, and the history of vector operation in specific locations (Fofonoff et al. 2013; Williams et al. 2013). Additional information on dates of first and subsequent records on a bay-by-bay basis was included (P. Fofonoff and B. Steves, pers. com). NEMESIS records through 2006 have been comprehensively reviewed; species added from 2007 to present are still under review. Cryptogenic (i.e., of uncertain origin, Carlton 1996) and strictly freshwater were excluded from our analysis. We used the year of the first report in California as a proxy for year of introduction.

### *Contemporary fluxes*

To assess the flux of taxa and quantities of ornamental species currently circulating in the vector operating in California, we obtained importation inspection records from the US Fish and Wildlife Service (USFWS)'s Law Enforcement

Management Information System (LEMIS) through a Freedom of Information Act (FOIA). We requested records for 2009 (the most recent year for which records were complete) for the state's major ports of Los Angeles (LA) and San Francisco (SF), the only Californian ports inspected by USFWS (any importations into other ports are illegal). LEMIS records are derived from documentation required of importers 48 hours prior to the arrival of live animal shipments in the US. Documentation includes CITES (Convention on International Trade in Endangered Species) permits, country of origin (where the organism was collected) permits if appropriate, customs declaration, packing list for each box in shipment, and an invoice. We used the following USFWS fields and categories to obtain records from all exporting countries. In the 'wildlife description' field, we requested records for 'live specimen', 'fingerling', and 'live rock'; in the 'purpose' field, 'breeding', 'educational', 'personal', 'scientific', 'commercial', 'reintroduction', and 'zoos'. In the 'source' field, we requested records for 'bred in captivity', 'confiscated', 'source unknown', and 'wild captured'. Data were returned in a per shipment-by-'species'-code record format. 'Species' refers to the USFWS taxonomic code for imported animals, which can be scientific names or non-specific categories (e.g., 'marine tropical fish', 'crustaceans', 'substrates'). Each record included shipment code, taxa, and quantities (numbers or weight) imported, wildlife description, purpose of the import, country of origin, country of export, port of entry, and action taken by USFWS (e.g., cleared, seized). We removed exclusively freshwater species, based on FishBase (http://www.fishbase.org), World Registry of Marine Species (http://www.marinespecies.org), and Encyclopedia of Life (eol.org), tropical scleractinian coral species (unlikely to establish in California waters), and duplicate or incomplete records. We then compared the range for minimum and maximum Sea Surface Temperature (SST) of California and temperate countries of origin out to 80 km from the coasts based on Bio-Oracle Marine Environmental Raster Package (Bio-ORACLE; Tyberghein et al. 2012).

To further assess the ornamental trade as a vector of NIS, we observed a routine one-day inspection by USFWS of wildlife arriving in air cargo at San Francisco International Airport (SFO) in March 2012. We collected information on the common and scientific names of species shipped for the aquarium trade, quantities within each taxon, the condition of the organisms (dead, unlikely to survive, alive, active/responsive), taxonomic identification errors, and discrepancies between shipment contents and invoices (importer information redacted by USFWS).

We also reviewed California Department of Fish and Wildlife (CDFW, previously California Department of Fish and Game) records, which spanned 1988 through 4 August 2011, for marine animals prohibited for entry, importation, transportation, possession, and release except by a special Restricted Species permit (California Administrative Code, Title 14, Section 671). A Restricted Species is considered by CDFW or the California Department of Food and Agriculture (CDFA) to be an undesirable wild animal or one posing a menace to the state's native wildlife or agriculture. Permits contained information on permit type (purpose of possessing the species), species permitted, permittee's city, the number of animals allowed, origin of animal, port of entry, and age of animal. We extracted data for marine species according to permit type and year. We reported only the most recent data from 2000 through 2010 because only 1–2 permits were issued annually prior to this period.

To complement the information above on contemporary fluxes, we searched the internet for the online availability of marine ornamental NIS to California residents. First, we conducted a preliminary search of aquarium store websites to assess specimens available for sale in the San Francisco Bay area on 6–7 March 2012, using the Google search engine and the search terms '*aquarium stores in San Francisco Bay area*'. To constrain the search, we limited it initially to this major population center, which should be a representative subsample of the internet availability of marine ornamental species. The search was rerun on 23 June 2012 with the additional term '*pet stores in San Francisco Bay area*', which added major chain stores. We also estimated the availability of *Caulerpa* spp. on internet stocking lists on 8 March 2012, using the terms '*live Caulerpa for aquarium*' or '*live Caulerpa*'. Websites of vendors who appeared to be selling *Caulerpa* spp. were examined for further information including shipping availability to California and recommendations for appropriate disposal. Based on the results of these searches, between 27 August – 27 September 2012, we expanded the searches beyond the San Francisco Bay area and focused on *Caulerpa*, lionfish, and green chromis (*Chromis viridis*), as known invaders and/or importations potentially able to establish in California (see Results). Search terms were: '*live saltwater aquarium plants*',' *Caulerpa for sale*', '*live Caulerpa*', '*Caulerpa sale*', '*lionfish for sale*', '*live lionfish ebay*', '*lion fish for sale*', '*Green chromis*', '*Green damselfish for sale*', '*Chromis viridis for sale*', '*Live chromis viridis ebay*', '*Live chromis viridis*', '*Green chromis for sale*', '*Green damsel fish*', and '*Chromis viridis*'. To standardize the search effort, we included only the unique entries returned per unit time searched, similarly to Walters et al. (2006). We searched for online sales of each species for six hours over a five day period, for a total of 18 internet search hours, after which no new entries were uncovered for all species analyzed. We excluded informal exchanges occurring through online aquarium hobbyist forums. We recorded the number and type (wholesale, eBay) of vendors for each species, the stock availability for shipping within the US, information on general shipping restrictions, shipping restrictions to California, 'buyback' policies or other means to return unwanted organisms, and instructions for destruction of unwanted organisms.

### *Literature review of impacts of marine ornamental species established in California*

We used BIOSIS to search the peer-reviewed scientific literature from 1926 through 2011 for impacts of the marine ornamental seaweeds and molluscs recorded as established in California (see Results): *Caulerpa taxifolia* and molluscs *Busycotypus canaliculatus* (Linnaeus, 1758), *Bullia rhodostoma* (Reeve, 1847), *Littoridinops monroensis* (Frauenfeld, 1863), *Melanoides tuberculata* (O.F. Müller, 1774), *Potamopyrgus antipodarum* (J.E. Gray, 1843)). Molluscs and seaweeds represented the majority of the invasive species introduced to California as reported in NEMESIS. Search terms were: *Topic=(Adventive OR Alien* OR Bioinvasi* OR Biosecur* OR Exotic* OR Foreign OR Introduc* OR Incursion* OR Invad* OR Invasi* OR Nonendemic* OR Nonendemic* OR Non indigenous OR Nonindigenous OR Nonnative* OR Nonnative* OR Nuisance* OR Pest* OR Pest) AND Topic=(species name in quotes, e.g. 'Caulerpa taxifolia') AND Timespan=1926–2011.* Searches also were performed using synonyms for the current species name based on WoRMS (World Registry of Marine Species; http://www.marinespecies.org/) and AlgaeBase (http://www.algaebase.org/). After reviewing titles and abstracts, we extracted the following data from relevant impact studies on each species: recipient habitat type and location, impacted entity, the response variables, details on the types of environmental, ecological, human health, and economic impacts, direction of effect, study type, setting (laboratory, field), statistical analysis performed, and availability of means and variances. Study type was defined as observational (no statistical design), mensurative (statistical design, no experimental manipulations), or experimental (statistical design, experimental manipulations). A case was defined as a single result or effect for a single response variable; an experiment, study, or publication could include multiple cases. We excluded studies lacking replication. We tallied whether there was a change in each response variable and the direction of the change (positive, negative) if reported. We then interpreted the biological effect on the impacted entity to determine the number of cases in which there was an enhancement of the native species/ community or deleterious effect; a positive increase in a response variable can indicate a negative biological outcome and vice versa. We took a conservative approach of assigning the biological effect simply as 'changed' where the inferred biological response was in the opposite direction of the change in response variable or there was no consistent direction of change.

## Results

### *Historical vector strength: attribution of species to vectors*

Twelve marine NIS associated with the ornamental species trade were recorded as having been introduced to California (Table 1). Of these, nine (75%) established (including the eradicated seaweed *Caulerpa taxifolia*), two failed to establish, and the population status of the remaining species is unknown. The historical vector strength was weak; the successfully established ornamental NIS represented less than 4% of the 246 marine NIS considered established in California by 2011 (including 11 fishes added to numbers in Williams et al. 2013). Only three species of the 12 total were attributed solely to the ornamental species trade: *Caulerpa taxifolia*, the trumpet snail *Melanoides tuberculata* (Muller 1774), the sailfin molly *Poecilia latipinna* (Lesueur, 1821). The other species were associated with other probable vectors (Table 1). Six of the nine established species were reported from only one locale (San Francisco Bay); two have been found in at least two bays (Table 1). The

**Table 1.** Species introduced to California attributed to the ornamental species trade, the year of first record of the species in the state, population status, locales from which species were reported (*denotes bay of first record), and probable vectors, from NEMESIS database. Vector abbreviations: AQ = aquaculture; BF= biofouling; BW = ballast water; ORN = ornamental. Locale abbreviations: ES = Elkhorn Slough; SFB = San Francisco Bay-Delta.

| Species | Taxon | First Record | Status | Locale | Vectors |
|---|---|---|---|---|---|
| *Bullia rhodostoma* Reeve, 1847 | Mollusca – Gastropoda | 1966 | Failed | SFB* | BW, ORN |
| *Busycotypus canaliculatus* (Linnaeus, 1758) | Mollusca – Gastropoda | 1938 | Established | SFB* | AQ, ORN |
| *Caulerpa taxifolia* (M. Vahl) C. Agardh, 1817 | Chlorophyta – Bryopsidophyceae | 2000 | Eradicated | Oceanside | ORN |
| | | 2000 | Eradicated | LA-LB | ORN |
| *Cordylophora caspia* (Pallas, 1771) | Cnidaria – Hydrozoa | 1930 | Established | SFB* | AQ, BF, ORN |
| | | 1968 | Established | Humboldt Bay | AQ, BF |
| | | 1975 | Established | Trinidad | AQ, BF |
| | | 1975 | Established | Gualala | BF |
| | | 1998 | Established | ES | AQ, BF |
| *Limulus polyphemus* (Linnaeus, 1758) | Chelicerata – Merostomata | 1917 | Failed | SFB* | ORN, Fisheries |
| *Littoridinops monroensis* (Frauenfeld, 1863) | Mollusca – Gastropoda | 2005 | Established | SFB* | BW, ORN |
| *Lucania parva* (Baird & Girard, 1855) | Vertebrata – Actinopterygii | 1959 | Established | SFB* | ORN, AQ, BW |
| *Melanoides tuberculata* (Müller, 1774) | Mollusca – Gastropoda | 1989 | Established | SFB* | ORN |
| *Poecilia latipinna* (Lesueur, 1821) | Vertebrata – Actinopterygii | 1984 | Established | San Diego* | ORN |
| *Potamopyrgus antipodarum* (Gray, 1843) | Mollusca – Gastropoda | 2003 | Established | SFB* | BF, ORN |
| | | 2008 | Established | Trinidad | BF |
| *Uromunna* sp. A | Crustacea – Isopoda | 1989 | Established | SFB* | BF, BW, ORN |
| *Vallicula multiformis* (Rankin, 1956) | Ctenophora | 2007 | Unknown | San Diego* | BF, ORN |

hydrozoan *Cordylophora caspia* (Pallas, 1771) achieved the widest distribution and was associated also with biofouling and aquaculture vectors.

The first report of a NIS introduction to California coastal waters possibly linked to the ornamental vector was the horseshoe crab *Limulus polyphemus* (Linnaeus, 1758) in 1917. The ornamental vector attribution in NEMESIS was based on reports of *L. polyphemus* shipped to Europe for aquariums in the 1860s and released if not sold (Wolff 1977) and the reasonable assumption that the same was possible in California. Between 1917 and 1960 four species linked to the ornamental trade were reported from California bays. Of the eight new state records since 1960, four occurred after 1999. All first reports of the species were from the state's major population centers in San Francisco, Los Angeles, and San Diego.

### *Contemporary fluxes of marine ornamental NIS*

There was a high contemporary flux of live animals into California, as estimated from a total of 56,739 LEMIS records in 2009. A record can include one to thousands of individuals. Removal of strictly freshwater species and tropical scleractinians yielded 16,286 records (Figures 1, 2). These remaining records of interest included over 11 million individuals representing at least 102 species that entered the ports of LA and SF predominantly in air cargo as aquarium shipments (Appendix 1, Electronic Supplemental Material). At least 250,504 kilograms, and 10,700,366 individual specimens were imported into LA and 4,478 kilograms and 519,551 individual specimens to SF. The categories of 'Other Live Invertebrates', 'Marine Tropical Fish', 'Crustaceans', and 'Molluscs' together accounted for 86% and 47% of the records for LA and SF, respectively (Figures 1,2).

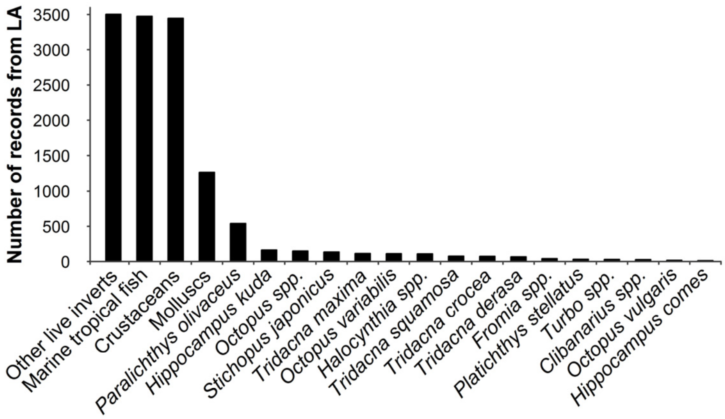


**Figure 1.** The number of records for the 20 most common species codes for marine animal imports into Los Angeles in 2009. A record can represent more than one individual. "Other live inverts" is the USFWS code for unspecified invertebrate taxa. Data source: USFWS LEMIS.

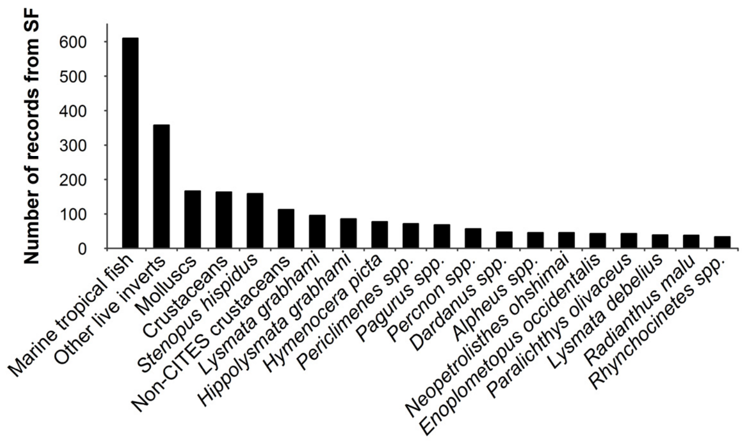


**Figure 2.** The number of records for the 20 most common species codes for imports into SF in 2009. A record can represent more than one individual. "Other live inverts" is the USFWS code for unspecified invertebrate taxa. Data source: USFWS LEMIS.

The LA records comprised 47 countries of origin, where organisms were collected, and 47 countries of export (from which organisms were exported); the SF records comprised 19 countries of origin and 21 countries of export. Origin and export countries can differ if a trans-shipment has occurred, i.e., beyond the initial port of entry. Indonesia and the Philippines were the most common countries of origin and export, but Vietnam, Sri Lanka, South Korea, China, and Australia were also major exporting countries (Figure 3).

Of special interest to California and regions with similar ocean climates was that 10 temperate countries of origin provided at least 37 unique 'species' codes in 16,286 records (Table 2). Over 90% of these records represented direct shipments of temperate species because the country of origin matched the country of export (Table 3). Among the remaining handful of records in which origin/export countries differed, there was one unequivocal trans-shipment record: *Holocanthus* spp. (angelfishes) recorded from 'France' (probably a French territory)

**Table 2.** Lists of species codes on LEMIS importation records for ports of Los Angeles (LA) and San Francisco (SF) from temperate countries of origin in 2009. Tropical species codes (primarily corals from Australia) were removed, except for 'tropical fishes' because it is a large, inclusive field. LEMIS codes are not necessarily currently accepted species names and do not include taxonomic authorities. "Other live inverts" is the USFWS code for unspecified invertebrate taxa.

| Taxon | Port |
|---|---|
| *Aurelia aurita* (moon jellyfish) | LA |
| *Casmaria species* (helmet shells) | LA |
| Crustaceans | LA |
| *Cucumaria miniata* (orange/red sea cucumber) | LA |
| *Cucumaria species* (sea cucumbers) | LA, SF |
| *Enteroctopus dofleini* (giant Pacific octopus) | SF |
| *Enteroctopus* species (giant octopuses) | LA |
| *Gymnothorax* species (moray eels) | LA |
| *Halocynthia* species (sea peach sea squirts) | LA, SF |
| *Haliotis* species | SF |
| *Heteractis* species (sea anemones) | LA |
| *Heterodontus* species (sharks) | LA |
| *Hippocampus abdominalis* (big-belly seahorse) | LA, SF |
| *Hippocampus barbouri* (zebra seahorse) | LA, SF |
| *Hippocampus breviceps* (knobby/short-head seahorse) | LA |
| *Hippocampus kuda* (common/estuary seahorse) | LA, SF |
| *Hippoglossus* species (right-eyed flounders) | LA, SF |
| *Holacanthus* species (angelfish) | SF |
| *Loligo species* (squids) | LA |
| *Macrocheira kaempferi* (Japanese spider crab) | LA |
| Non-CITES entry | SF |
| Non-CITES entry fish | LA |
| Non-CITES entry invertebrates | LA |
| *Octopus* species (octopuses) | LA, SF |
| *Octopus variabilis* (whiparm octopus) | LA, SF |
| *Octopus vulgaris* (common octopus) | LA, SF |
| Other live inverts | LA, SF |
| *Paralichthys olivaceus* (olive flounder) | LA |
| *Phycodurus eques* (leafy sea dragon) | LA, SF |
| *Platichthys stellatus* (starry founder) | LA, SF |
| *Scomber* species (mackerels) | LA |
| *Sebastes* species (rockfishes) | LA |
| *Stichopus japonicus* (Japanese sea cucumber) | LA |
| *Stichopus* species (sea cucumbers) | LA, SF |
| *Strombus* species (conchs) | LA |
| Tropical fish (marine species) | LA, SF |

routed through Mexico and then into SF. The other mismatches appeared to be typographic errors in the database (e.g., wild-caught, marine tropical fish in the land-locked Czech Republic). After accounting for these exceptions, there were six unequivocal temperate countries of origin. Survival of importations from these countries cannot be ruled out for California's waters based on coastal SSTs (Appendix 2, Supplemental Online Material). The range of minimum and maximum annual temperatures of Californian waters (7.41–15.25°C and 11.52–22.14°C, respectively) falls within those of all six unequivocal temperate countries of origin.

While most taxa from temperate countries of origin were imported for the home aquarium trade, a few were not. For example, the 'purpose' USWFS code for the large spider crab *Macrocheira kaempferi* (Temminck, 1836) was 'zoos' (one record) and 'commercial' for 160 records for the edible sea cucumber *Stichopus japonicus* (Selenka, 1867). Within the 'live specimen' code, a small number of taxa could be considered live food. Of these, the olive halibut, *Paralichthys olivaceus* (Temminck and Schlegel, 1846) accounted for the majority of the total imported weight, but only 3.6% of the total number of records of interest (Figures 1 and 2). Together, *P. olivaceus* and six other putative food taxa (*Octopus* sp., *O. variabilis* (Saski, 1929), *O. vulgaris* (Cuvier, 1797), starry flounder, *Platichthys stellatus* (Pallas, 1787), rockfishes *Sebastes* spp., *Stichopus japonicus*) accounted for only 3% of the imported individuals (Appendix 1, Supplemental material). These LEMIS numbers closely match an independent source of numbers of live seafood sold in California in 2011 (Cohen 2012). These taxa, however, cannot be unequivocally deleted as food importations because they have attracted the notice of hobbyists (http://aquarium.org/exhibits/sandy-shores/animals/starry-flounder; 21 November 2013; http://www.advanceaquarist.com/2003/1/inverts; 21 November 2013). Even *Paralicthys olivaceus,* which had the highest number of records for the putative food species, has attracted the attention of aquarists (http://en.microcosmaquariumexplorer.com/wiki/Your_Portal_to_Aquatic_Discovery; 21 November 2013). Given these considerations, it is reasonable to conclude that roughly 97% of the importation records were ornamental, not food, species.

Although the broad categories in LEMIS records underestimate the taxonomic diversity, at least 149 species were shipped into SF on one typical day, based on invoices (Figure 4; Appendices 1, 3, Supplemental material). The ornamental shipments we observed being inspected included solely marine species from the Philippines (29 boxes of live fishes) and Indonesia (nine boxes of corals/live rock and 29 boxes of 'live tropical fishes and others'). A total of 3,996 individual fishes and invertebrates were invoiced in the two shipments (Appendix 3, Supplemental material). This flux was considered a typical weekly or semi-weekly volume for the port of SF and equal to ~20% of the volume arriving in LA, one of the top three ports of entry

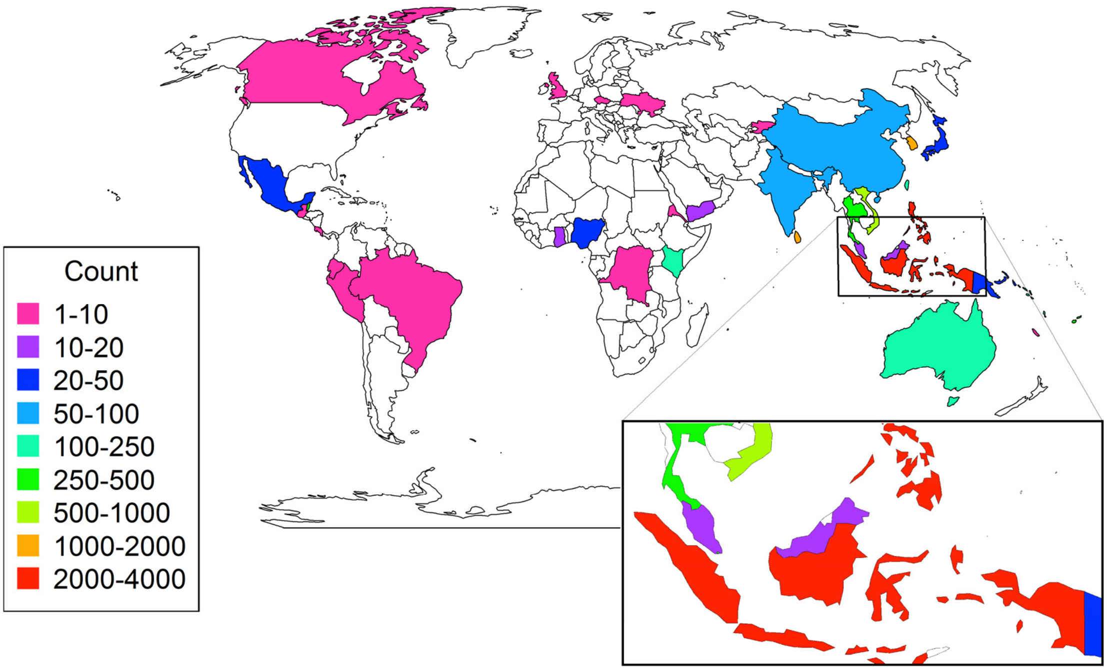


**Figure 3.** The number of records by country of origin for imports (source of organisms) into LA in 2009. The major source region is Indonesia and the Philippines. Data source: USFWS LEMIS.

**Table 3.** Countries of temperate origin and countries of export list on LEMIS importation records in 2009. Italicized countries likely represent typographical errors in which the country of origin was switched with the country of export. LA: Port of Los Angeles. SF: Port of San Francisco.

| Country of Origin | Country of Export | # LA Records | # SF Records |
|---|---|---|---|
| Australia | Australia | 11 | 5 |
| Canada | Canada | 5 | 3 |
| Czech Republic | Czech Republic | 1 | 0 |
| Germany | Germany | 0 | 1 |
| Great Britain | Great Britain | 1 | 0 |
| France | Mexico | 0 | 1 |
| Japan | Japan | 7 | 2 |
| *Norway* | *Philippines* | *3* | *0* |
| *Kyrgyzstan* | *South Korea* | *1* | *0* |
| South Korea | South Korea | 18 | 11 |
| Total | | 47 | 23 |

of ornamental species into the US, along with John F. Kennedy (JFK, New York) and Miami International Airports (MIA) airports (USFWS, pers. com.). The invoices included the USFWS ‘species’ code, the common name, scientific name, the quantity, unit price and total price per ‘species’ and, for some of the organisms, the size (‘sm/md/lg’). One importer provided a breakdown of the total number of organisms by taxa. The other provided a total number of specimens (172) only for live corals, which represented 35 genera and/or species and 137 ‘substrates/unidentified Scleractinia’. The survivorship of the organisms we inspected (n = 1657) was very high (98%). The survivors’ condition was also good; 97% were active. The few specimens exhibiting poorer condition were inactive fishes and one coral colony deemed unlikely to survive.

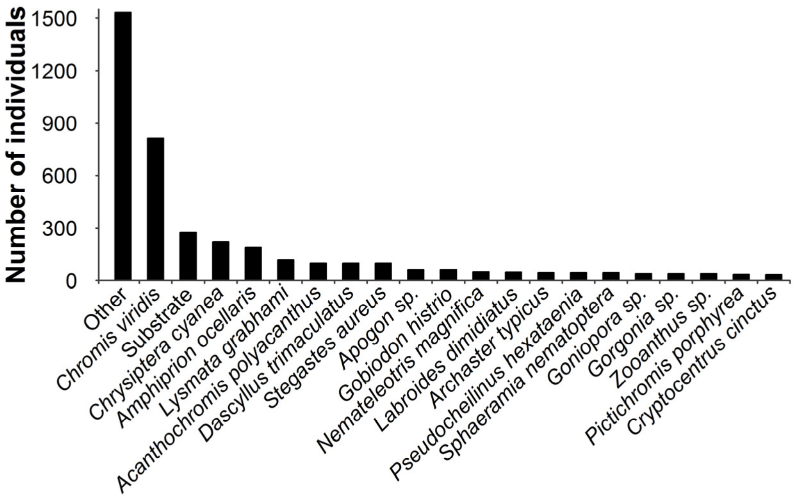


**Figure 4.** Taxa shipped to San Francisco International Airport from the Philippines and Indonesia on one day in March 2012, ranked by abundance. The total number of organisms was 3,996. 'Other' includes 129 taxa, each with < 33 individuals. 'Substrate' was abbreviated from 'substrate (unidentified scleractinia)' and refers to live rock. See Appendix 3, Electronic Supplemental Material, for complete taxonomic listing and quantities. Data source: USFWS LEMIS.

Labeling and identification of organisms by the exporters was problematic for 59% of the 34 boxes inspected by USFWS (of 67 total boxes in the combined shipments). Bags were not labeled and required identification by inspectors to confirm the invoice. The contents of the inspected boxes did not match the inventory, common names were sometimes incorrectly assigned to a family although the species name was correct, and organisms were listed with both incorrect common and scientific names. USFWS personnel noted that they can generally inspect ~25% of all live and perishable air cargo shipments, which includes their inspection of every bag (containing one organism each) within every box labeled 'live coral and other' for CITES-listed taxa.

The shipments we examined contained four notable specimen types. First, 20 lionfishes were imported, including five individuals of invasive *Pterois volitans* (as 'black peacock' or 'red'). Second, 815 green chromis, *Chromis viridis* (Cuvier, 1830), were imported. This high flux is notable because the green chromis is potentially able to survive in California waters (Chang et al. 2009). Third, eight small *Chromileptes altivelis* (Valenciennes, 1828), commonly known as 'panther grouper', 'humpback grouper', 'barramundi cod', were imported as ornamental species and could potentially survive in California waters (Johnston and Purkis 2013). Fourth, 137 pieces of 'live rock' labeled as 'substrate' and/or 'unidentified Scleractinia' were shipped. 'Live rock (coral rock)' is a USFWS designation that distinguishes any hard substratum and its attached community from a 'live specimen'. Importations labeled 'substrate' and 'unidentified Scleractinia' are inspected routinely by USFWS for CITES-listed corals, but not for associated organisms. The live rock in the shipments was covered with zooanthids and several seaweeds (*Halimeda* sp., coralline and fleshy red crusts), including algal turf, which is a diverse community of small (< 1–2 mm tall) species. In LA in 2009 alone, there were 435 LEMIS records under the 'live rock' wildlife designation.

Before this study, California Restricted Species were an unexamined potential pathway for marine ornamental NIS both from other countries and other states. No Restricted Species has been reported as introduced to date; thus, they probably represent a minor potential pathway. Because permits covered only the intent to transport, import, or possess a species and post-permit reports of actual quantities are not required, the allowable quantities represented an upper bound on potential fluxes. We found permits for 10 brackish and marine Restricted Species intended for display by residents, zoos, and aquariums (Table 4). After finding Restricted Species permits issued to zoos and aquariums, we identified at least 19 public display facilities in California, some of which routinely house non-native ornamental species or maintain water systems at least partially open to the environment (J. Moore, CDFW, pers. com.). Restricted Species were

**Table 4.** Marine and brackish Restricted Species permitted by California Department of Fish and Wildlife (CDFW) from 2000–2010 for possible purposes of display or brokering, by permit type and number. 'Permits by year' includes permit renewals, which are required annually by CDFW. AZA: Association of Zoos and Aquariums. Note: Restricted Species permits do not specify taxonomic authorities.

| Species | Common name | Permit type | # Permits | # Permits by year |
|---|---|---|---|---|
| *Alligator mississippiensis* | American alligator | AZA Detrimental Species/ Native Species Exhibiting | 1 | 1 |
| | | Exhibiting | 1 | 1 |
| | | Nonresident Exhibiting | 1 | 6 |
| | | Resident Exhibiting | 4 | 5 |
| *Caiman crocodilus* | Spectacled caiman | Nonresident Exhibiting | 1 | 1 |
| *Caiman sclerops crocodilus* | Spectacled caiman | AZA Detrimental Species | 1 | 1 |
| *Carcharhinus melanopterus* | Blacktip reef shark | Resident Exhibiting | 1 | 1 |
| | | Resident*Broker/Dealer | 3 | 3 |
| *Carcharhinus plumbeus* | Sandbar shark | AZA Detrimental Species | 2 | 3 |
| *Carcharhinus leucas* | Bull shark | Resident*Broker/Dealer | 1 | 5 |
| *Esox lucius* | Northern pike | Resident Exhibiting | 1 | 1 |
| *Lepisosteus oculatus* | Spotted gar | AZA Detrimental Species | 1 | 1 |
| *Lepisosteus tristoechus* | Longnose gar | AZA Detrimental Species | 1 | 1 |
| *Perca flavescens* | Yellow perch | Resident Exhibiting | 1 | 1 |

permitted under six of nine total permit designations (e.g., including aquaculture or research) for a total of 20 unique species-designation permits and 31 unique species-designation permits by year issued during 2000–2010. The higher number accounts for permit renewals, which are required annually. Most permits allowed fewer than 10 individuals of a given species. However, one permit allowed 20–40 sandbar sharks, *Carcharhinus plumbeus* (Nardo, 1827), and another allowed 100 blacktip reef sharks, *C. melanopterus* (Quoy and Gaimard, 1824), for State Resident Dealers/Brokers; neither shark is native to California.

Internet commerce also contributes to contemporary fluxes of marine NIS. Online information on numbers or volumes in stock or sold was not readily available. Only four of the seven independent aquarium stores in the San Francisco Bay area provided lists of live stock, only one of which regularly updated listings. Three of these four independent stores were selling or had sold lionfishes, listed by various common names. The fourth store specialized in brackish and freshwater species. The chain stores in the area were Petco, PetSmart, Pet Food Express, and Walmart. Petco and PetSmart were the most prominent chain stores, with over 60 store locations in the Bay Area. Searches indicated that only Petco sold marine animals and plants. Petco had an extensive online listing of live stock and internet sales, including five species of lionfishes under various common names. Three of these lionfish species- 'Dwarf (Fuzzy),' 'Volitan,' 'Dwarf Zebra'- were listed on the invoice for shipments into SFO and observed in the inspected boxes (see above).

We then targeted high-profile taxa (*Caulerpa*, lionfish, green chromis). Our initial search for live *Caulerpa* for internet sale revealed a total of 10 advertisements from five websites. Three of the 10 advertisements listed the legal shipping status of specific *Caulerpa* species being sold, but only one listed invasion risk as the reason for not shipping to California and only one other explained appropriate disposal of unwanted *Caulerpa*. In the expanded, more extensive search (Figure 5), which was not restricted to the San Francisco Bay location, we found 13 wholesale and eBay vendors for *Caulerpa*, but importantly none listed California addresses. Lionfish internet commerce was high, with the most unique entries and 13 vendors (four in California) offering 12 species of lionfishes. Twenty-two vendors were found for green chromis, of which three had California addresses.

Although green chromis was readily available through wholesale vendors, the only eBay vendors were located in the United Kingdom and did not provide shipping services. Information on stock availability (quantities held or sold) was limited for all three taxa. Wholesale vendors listed only whether an item was 'out of stock'. Sales were by item, which could be one or several fishes or non-standardized amounts (lengths, clump diameters) for *Caulerpa*. *Caulerpa* was also given

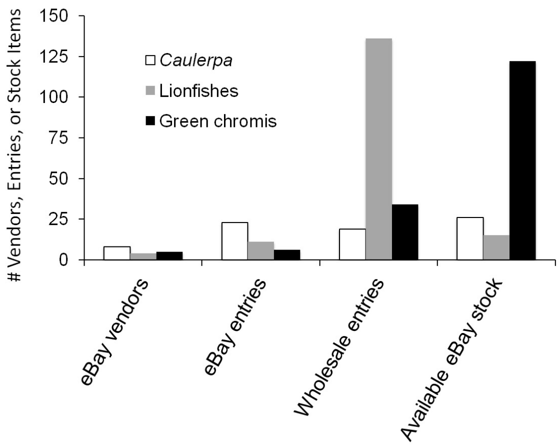


**Figure 5.** Number of eBay vendors, number of internet entries for eBay and wholesalers, and # of eBay stock items available for sale from 27 August – 27 September 2012 for each of three taxa. White bars: *Caulerpa (Caulerpa ashmeadii, Caulerpa cupressoides, Caulerpa lentillifera, Caulerpa prolifera, Caulerpa prolifera maxima, Caulerpa* sp.*, Caulerpa mexicana, Caulerpa paspaloides, Caulerpa racemosa, Caulerpa racemosa* var. *peltata, Caulerpa sertularoides).* Gray bars: lionfishes *(Pterois volitans, Dendrochirus brachypterus, Taenianotus triacanthus, Pterois miles, Pterois radiate, Dendrochirus zebra, Pterois antennata, Pterois russelli, Pterois mombasae, Dendrochirus biocellatus, Pterois sphex, Pterois lunulata*). Black bars: green chromis (*Chromis viridis*). Note: No taxonomic authorities were provided for species uncovered in searches and taxonomic identity is unconfirmed.

away or included in 'algae kits', and one wholesaler specialized in it. Across all entries for all three species in this search, we found a single wholesaler who provided information on destruction of an unwanted specimen (*Caulerpa*) and none indicated buy-back policies.

*Impacts of non-native species introduced by ornamental trade*

Our literature searches uncovered information for only two taxa: the seaweed *Caulerpa taxifolia* and the New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) of the five established molluscs (Table 1). Except for one study of *C. taxifolia* in California, the studies were conducted in Europe and Australia (*C. taxifolia*) or Oregon (*P. antipordarum*). The only available information on economic or societal impacts was the cost of the *C. taxifolia* eradication (Anderson 2005).

We found data on impacts of *Caulerpa taxifolia* in 49 of 149 articles uncovered in the search (Appendix 4, Supplemental material), yielding 137 independent mensurative and experimental cases within these 49 articles. The majority (83%, n = 114) of these cases showed an effect of the seaweed on the native community structure and species richness, and on the metabolic, developmental, reproductive, growth, and behavioral responses of organisms (primarily seagrasses, fishes, and an economically important bivalve). Of the cases demonstrating a positive or negative biological effect (n=67), the majority (70%, n=47 cases) was negative (reduced biological performance), but positive effects (enhanced biological performance) were evident in 30% (n = 20) of the cases.

Literature on impacts of *Potamopyrgus antipodarum* in estuarine systems was restricted to a single study in Youngs Bay in the Columbia River estuary (Brenneis et al. 2011), which provided eight cases and accounted for less than 1% of the 258 articles returned from the searches for all five molluscs in the vector. This single study indicated that the mud snail had insignificant impacts on native invertebrates a decade after it was introduced.

## Discussion

Excluding tropical hard corals, at least 11 million individuals of marine fishes and invertebrates were imported into California in 2009, including some with temperate origins and the invasive lionfish (*Pterois volitans*). This flux is higher than the global flux of ornamental marine fishes and invertebrates (including tropical hard corals) from 1998–2003 (Wabnitz et al. 2003) and as high as for tropical marine ornamental fishes imported into the entire US in 2005 (Rhyne et al. 2012a). Combining LEMIS records and our survey of imports into SFO, a minimum of 150 species were imported over the course of our study, which is undoubtedly underestimated due to the generic labeling of tropical marine aquarium fishes in the LEMIS data base (Rhyne et al. 2012). Based on our direct observations of shipment contents, virtually all of these animals are likely to survive the shipment or transfer phase of possible introduction. Yet, our analysis of historical vector strength indicates only nine ornamental species were found among the 235 marine NIS considered to have established in California (Williams et al. 2013), including the high-impact species, *Caulerpa taxifolia*. More marine ornamental species were introduced to the state in recent decades, perhaps due to the general increase in popularity of aquarium-keeping over this time period; thus, the historical record probably underestimates current and future trends. Although we considered only California, the ornamental trade to the state represents a major portion of the global marine ornamental flux, and the issues we discuss below can be applied to the vector in general.

Quantifying the flux of NIS via ornamental vectors is a first step toward estimating propagule pressure, which is strongly correlated to the probability of introducing non-native species (Lockwood et al. 2005; Colautti et al. 2006; Simberloff 2009; Wonham et al. 2013). The quantities reported in LEMIS are probably reasonable for the order of magnitude of the flux for the following reasons. Although LEMIS records contain errors, such errors resulted in overestimation of quantities by less than an order of magnitude in one analysis (27%, Rhyne et al. 2012a). Our analysis indicates that underestimation of quantities also can occur because exporters sometimes reported mass as opposed to numbers of organisms. However, this underestimation appeared too small to alter the order of magnitude of ornamental species entering the state (Appendix 1, Supplemental material). Possible trans-shipment is also not likely to decrease the magnitude, given the state's large size, major ports for importation, the availability of marine ornamental vendors within the state (~ 84; http://lfslocator.com/state.asp?st=CA, accessed 19 December 2013). Furthermore, large trans-shipments from JKF and MIA into California could be assumed to balance trans-shipment out of the state (USFWS, pers. com.). The trade should be encouraged to share its proprietary trans-shipment information (Murray et al. 2012) or USWFS could require it on the wildlife declarations. In any case, the high flux signals a potential invasion risk.

Contributions of Restricted Species to the overall flux were minimal. Our analysis however revealed that a number of non-native sharks were permitted, of which the sandbar shark could reasonably establish in the state's coastal waters. It also highlighted that public aquaria represent an underappreciated pathway that merits attention. The current permitting process is unlikely to support management objectives or future risk assessments but could be improved by requiring actual quantities entering the state.

Internet commerce in ornamental species continues to be a challenge to estimate (Kay and Hoyle 2001; Padilla and Williams 2004; Walters et al. 2006). The information currently available over the internet is very useful for tracking the popularity of species to anticipate potential species of concern. Certainly, prohibited *Caulerpa* spp., invasive lionfish, and green chromis are readily available for sale online in California. Abundances are however virtually impossible to assess. To illustrate in a gross comparison, internet entries and stocking numbers for green chromis exceeded the numbers (819) imported into SFO in a single day, both of which represent roughly a week of flux. The internet quantities for lionfish were similar to a year of LEMIS records (18 records for 136 individuals imported solely to SF in 2009). Web crawlers developed to apprehend illegal sales offer a means to track the species of ornamental marine NIS transiting through internet commerce, but not the quantities (J. Smith, Animal and Plant Health Inspection System, US Department of Agriculture (USDA), pers. com.). For now, the internet offers an under-utilized opportunity for education campaigns to prevent invasions of ornamental species, through vendor and hobbyist sites. The trade could follow the lead of the few vendors who posted information on invasiveness, disposal methods, and shipping restrictions.

Invasion risk is shaped by both the flux of organisms possibly being introduced and the likelihood of their successful establishment. The low historical establishment rate of ornamental marine NIS in California could be explained by a low release rate. To our knowledge, no data are available on marine ornamental release rates. Release rates for freshwater ornamental fishes vary widely across the few available studies (5% to 82% of fishes held, Gertzen et al. 2008; Strecker et al. 2011; Weeks 2012). Factors that increase the risk of release include the popularity of the species, size, aggressiveness, and distance between aquaria and waterways (Weigle et al. 2005; Duggan et al. 2006; Weeks 2012). Religious or other ceremonial releases of fishes, reptiles, and amphibians (Severinghaus and Chi 1999) can also occur and have been reported anecdotally in freshwater ponds around San Francisco. Surveys of marine hobbyists are sorely needed to estimate release rates and to determine attitudes toward release, which are useful for designing education campaigns as part of a management strategy.

If organisms have been released, temperature might have limited the establishment of the primarily tropical species circulating in the vector. At the very least, ornamental imports should not be considered a low invasion risk just because most come from the tropics. Invasion risk is increasing as the ocean warms (Stachowicz et al. 2002; Sorte et al. 2010). Although neither species-specific (de Rivera et al. 2011) or more general (Floerl et al. 2013) climate matching approaches to predict invasion risk are practical for the number of taxa being imported into California and were outside the scope of our study, the temperate countries of origin provide a first-cut proxy for the potential risk of successful survival in coastal Californian waters (Table 2; Appendix 2, Supplemental material). A small percentage of the organisms identified from temperate countries of origin could be live food importations, which still pose a threat. Others (mostly seahorses) probably originated from warmer regions of temperate countries (Australia), but the remainder represent a potential risk for introduction to California and elsewhere. Although the temperature tolerances of Indo-Pacific fishes are poorly known (Abesamis and Russ 2010), there is evidence they can recruit at temperatures of California's coastal environment (Russell et al. 1977). The green chromis (*Chromis viridis*) is our cautionary example because of its temperature tolerance (Chang et al. 2009), its high flux as a very popular ornamental species, and its internet availability. *Caulerpa taxifolia* and lionfishes (*Pterois volitans, P. miles*) also exceeded their primarily tropical native climate envelopes in their invaded habitats (Zaleski and Murray 2006; Johnston and Purkis 2011). When *C. taxifolia* invaded southern California, its northward expansion was probably limited by temperature (Williams and Schroeder 2004). A decade later, San Francisco Bay was warm enough for its overwintering and growth (http://www.nodc.noaa.gov/dsdt/cwtg/, Coastal Water Temperature Guide, NODC, NOAA, accessed 28 June 2013). Lionfishes can tolerate temperatures down to 10°C in the invaded habitat (Kimball et al. 2004) and could establish as far north as San Francisco Bay. Finally, the predatory panther or humpback grouper (*Chromileptes altivelis*, Appendix 3, Supplemental material) also can potentially survive in southern California, based on a climate-matching model for the western Atlantic Ocean (Johnston and Purkis 2013). This fish attains a large size, making it eventually unsuitable in a home aquarium and thus a risk for release.

Presently, the risk that marine ornamental species become invasive in the sense of causing ecological and economic impacts is defined only by conspicuous cases such as *Caulerpa taxifolia* (aquarium/Mediterranean strain) and lionfishes (not yet established in California). Experimental studies of marine introduced species in general are extremely limited (Williams et al. 2013). Assigning impact can be ambiguous except for reductions in the diversity and abundance of native species (Appendix 4, Supplemental material; Thomsen et al. 2009). Care must be taken because positive changes in some response variables can be interpreted unequivocally as potentially negative impacts. For example, the presence of *Caulerpa taxifolia* has resulted in increased sulfide concentrations that signal toxicity to seagrasses and animals. Similarly, increases in seagrass tannin cells and phenolics are a stress response. However, other cases are equivocal; an increase in seagrass epiphyte biomass could be interpreted simply as a positive biological effect or alternatively as negative given that epiphytes can be deleterious to seagrasses. Significant negative responses in seagrass leaf length and turnover in the presence of *Caulerpa* spp. are also ambiguous; in the right combination of responses, increases in primary production can be inferred. Finally, multivariate analyses of community structure revealed significant alterations to community structure, which are undoubtedly ecologically important. Yet, because the effect is not directional, they cannot be used to tally positive versus negative impacts.

The ornamental species vector is particularly diffuse and movements of NIS are difficult to track after entry into the US, particularly if through the internet, making the vector very challenging to manage. Even known invaders such as *Caulerpa* spp. (see Results, Williams and Smith 2007; Thomsen et al. 2009 and references therein) can slip through the fragmented federal and state NIS regulatory framework (Lodge et al. 2006; Jenkins et al. 2007; Walters et al. 2011; Diaz et al. 2012). For example, the aquarium/Mediterranean strain of *C. taxifolia* is the sole marine plant regulated as a Noxious Weed by the US Department of Agriculture (USDA), which points to a dire need to address non-native marine plants. Despite this federal regulation and that California also prohibits *C. taxifolia* (Mediterranean/invasive strain) plus eight congeners (Assembly Bill 1334, chaptered in 2001, CDFW Code 2300), *Caulerpa* remains available to Californians and others over the internet. The prohibited species do not even appear on California's Noxious Weed list (http://www.cdfa.ca.gov/plant/ipc/weedinfo/winfo_table-sciname.html, accessed 7 July 2014) presumably because it is managed instead by CDFW. The high flux of live rock, labeled as 'substrate' and 'unidentified Scleractinia', represents a risk of reintroducing *C. taxifolia* and introducing its congeners and other species (Bolton and Graham 2006; Zaleski and Murray 2006). Ornamental species can also introduce pathogenic organisms, an impact rarely addressed is the introduction of pathogenic organisms transmitted (Whittington and Chong 2007). Monitoring the fate of ornamental species post-border controls is one of the many recommendations made by these authors to reduce the risk of disease transmission, a recommendation supported by our study.

Given the ineffectiveness of ornamental species regulation, the high flux of species and potential impacts, and internet commerce, voluntary initiatives by the industry (Burt et al. 2007; Secretariat of the Convention Biological Diversity 2010) and public education offer viable alternative solutions to reducing the risk from this vector. Best Management Practices for the home aquarium trade focus on sustainable collection, husbandry practices, and certification programs (Shuman et al. 2004; Cohen et al. 2010; Sustainability Aquarium Industry Association (SAIA), http://www.saia-online.eu, accessed 14 August 2013; Marine Aquarium Council (MAC), http://www.aquariumcouncil.org/, accessed 14 August 2013). Best management practices would be greatly enhanced by guidelines on the disposal and release of aquarium organisms. For example, Habitattitude™, a partnership involving the Pet Industry Joint Advisory Council (PIJAC), the Federal Aquatic Nuisance Species Task Force (ANSTF), the USFWS, and the National Oceanic and Atmospheric Administration's National Sea Grant College Program, provides recommendations about procedures for releasing aquarium fishes. A specific challenge for education programs is engaging the participation of smaller independent aquarium stores. The adoption of industry-wide best management practices should also be applied to commercial and educational (and also research) aquaria.

The trade in marine ornamental species can be a lucrative business and a source of needed income in developing nations (Shuman et al. 2004; Tissot et al. 2010). For example, the invoiced value of the two SF aquarium shipments totaled over $2500 but the retail value was far higher. The invoiced value of a single emperor angelfish, *Pomacanthus imperator* (Bloch, 1787), was listed as $13 compared to its internet retail value ($90) at the time. Global trade in marine ornamental species grew rapidly through 2000 but then leveled off (Wabnitz et al. 2003; Rhyne et al. 2012b). Although the global recession is expected to affect trade (Floerl and Coutts 2009), our study indicates that the flux might not be decreasing.

## Conclusions

The high flux of marine ornamental species and the impacts of several high profile invaders make the vector a concern, even if few species have established historically. Further quantification of the risk the vector poses will require better species identification as well as attention to marine plants, which largely are overlooked in NIS monitoring and regulation. Major gaps include species identity, trans-shipment information, internet commerce, release rates, and environmental tolerances of high-flux species and known invaders. Hard-to-obtain impact information is desirable but not strictly necessary in a precautionary approach to management. If these data gaps continue to be addressed, a more formal risk assessment could be conducted to help guide industry and government decisions about increased self or mandatory regulation to reduce the threat of another costly invasion by a marine ornamental species.

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**Supplementary material**

The following supplementary material is available for this article.

**Appendix 1.** Annual sum of each species or taxonomic code by volume (kg, # specimens) imported into the ports of Los Angeles (section A) and San Francisco (section B) in 2009 from USFWS LEMIS data.

**Appendix 2.** Ranges in minimum and maximum Sea Surface Temperatures (SST, ºC) within 80 km from the coasts of California, the continental US, and temperate countries of origin for marine ornamental species imported into California in 2009.

**Appendix 3.** Taxa and number of organisms invoiced in shipments from the Philippines and Indonesia to San Francisco International Airport on a single day in March 2012.

**Appendix 4.** Summary of peer-reviewed literature (uncovered by a BioSIS search) addressing impacts of the seaweed *Caulerpa taxifolia* in invaded sites.

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