

# Aquaculture as a vector for marine invasions in California

Edwin D. Grosholz · R. Eliot Crafton ·  
Rachel E. Fontana · Jae R. Pasari ·  
Susan L. Williams · Chela J. Zabin

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**Abstract** Although ballast water and hull fouling are widely recognized as important vectors for marine invasions, the risk posed by commercial aquaculture remains poorly quantified. To understand the importance of aquaculture as an invasion vector in California, we conducted an analysis of both current and historical introductions of marine and estuarine species associated with aquaculture using a comprehensive database ('NEMESIS') and permitting records for species imported into California. Our results showed that 126 non-native species associated with commercial aquaculture have been reported from California waters and 106 of these have become established. The vast majority are unintentional introductions linked to historical importation practices of the aquaculture industry. To understand the consequences of these

invasions, we reviewed the literature on the impacts of mollusk and algal species introduced into California via aquaculture. Of the few studies we found, the majority demonstrated negative impacts on native species. Finally and significantly, we found that changes in aquaculture importation practices over the past decade have resulted in most shellfish currently being imported as larvae or juveniles. Consequently, rates of unintentional introductions have been reduced. We cautiously conclude that current aquaculture importation in California represents a minor risk as a vector for introductions of NIS.

**Keywords** Invasive · Marine · Aquaculture · Vector · Impacts · California

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E. D. Grosholz (✉) · C. J. Zabin  
Department of Environmental Science and Policy,  
University of California at Davis, Davis, CA 95616, USA  
e-mail: tedgrosholz@ucdavis.edu

R. E. Crafton · R. E. Fontana  
Graduate Group in Ecology, University of California at  
Davis, Davis, CA 95616, USA

R. E. Fontana · J. R. Pasari · S. L. Williams  
Bodega Marine Laboratory and Department of Evolution  
and Ecology, University of California at Davis,  
PO Box 247, Bodega Bay, CA 94923, USA

R. E. Fontana  
Office of Oceanic and Atmospheric Research, National  
Oceanic and Atmospheric Administration, Silver Spring,  
MD 20910, USA

C. J. Zabin  
Smithsonian Environmental Research Center, Tiburon,  
CA 94920, USA

## Introduction

Although aquaculture continues to be an important economic driver in many coastal areas, the aquaculture industry has had a long history as a major vector for the introduction of non-indigenous species (hereafter NIS) around the world (Carlton and Mann 1996; Naylor et al. 2001; Ruesink et al. 2005; Minchin 2007; Miller et al. 2007). Numerous introductions of NIS have resulted from the intentional importation of novel species for the purposes of developing new aquaculture markets, but also due to unintentional introductions of associated or ‘hitchhiking’ species accidentally transferred with the intentionally introduced species. As a vector for introductions, aquaculture has not been studied as extensively as ship-based vectors, such as ballast water (Carlton 1996; Ruiz et al. 2000; Minchin et al. 2009; Miller et al. 2011; Ruiz et al. 2013). However, the importance of aquaculture introductions as a vector for invasions has had international recognition and resulted in cooperative efforts such as the ICES Codes of Practice (ICES 2005) to limit the spread of NIS associated with aquaculture. Intentional aquaculture introductions, although fewer in terms of number of species, are likely to have a higher probability of establishment than ballast introductions, since the goal is to create new fisheries production. The choice of species for importation is made based on matching habitats with the native range and the conditions of transport and planting into the new environment, both of which are aimed at maximizing survival. Species used for commercial aquaculture are also more likely to be hardy, fast-growing and larger bodied than many of their native analogs.

The goal of this study is to quantify both the historical and current importance of aquaculture as a vector for invasions by NIS in the coastal waters of California. Importation of aquaculture species in California began in the 1850s and has included a wide range of shellfish as well as many NIS from around the world (Carlton 1992; Carlton and Cohen 1995; Miller et al. 2007). Many of these imported species have become established in California waters. In addition to these species being intentionally introduced to develop new fisheries, aquaculture importation also resulted in the introduction of many non-native ‘hitchhikers’ that were unintentionally introduced with the shipments of aquaculture species (Ribera 1995; Minchin 2006; Ruesink et al. 2005; Miller et al.

**Table 1** Permits relevant to California aquaculture managed by the California Department of Fish and Wildlife

Data type	Information covers	Time period for which records were available	Data fields
Import permits	State	1989 to June 2011, records mostly complete	Importer, exporter, species, some volume
Proof of use reports	For leases managed by CDFW	Records incomplete, 1977–2010	Importer, exporter, species, dates, volume
Inspection and planting certificates	State	Records incomplete, 1964–1983	Species, dates, volume
Private stocking permits	State	1992–2009	Importer, exporter, species, dates, volume

2007). Because these hitchhikers survive in the same environment as the species intentionally introduced, it is likely the same habitat matching used to choose species for intentional introduction likely also applies to the hitchhikers. Unfortunately, these hitchhikers included many fouling species as well as parasites, pathogens and predators of the species intended for introduction and many of these have also become established in California. Species such as the Atlantic oyster drill (*Urosalpinx cinerea*) and Pacific oyster drill (*Ocenebra inornata*) were historically introduced with oyster shipments from the respective regions. The polychaete worm parasite of cultured abalone, *Terebrasabella heterouncinata*, was introduced in the 1980s by shipments of abalone from South Africa (Moore et al. 2007). Other major shellfish pests likely introduced via aquaculture include the predatory flatworm *Pseudostylochus ostreophagus* and the parasitic copepod *Mytilicola orientalis*.

The immediate objectives of this study were to estimate the number of species and individuals of NIS introduced into California as the result of aquaculture importation in order to characterize the relative risk of this as a vector for NIS. We then compared the historical records of invasions with the current data to

assess the relative risk of aquaculture as a vector both historically and under current importation practices, which have changed substantially over the past decades. We used a state of the art database, the National Exotic Marine and Estuarine Species Information System ('NEMESIS' managed by Smithsonian Environmental Research Center 'SERC'), existing literature and available importation and permitting data managed by state and federal agencies operating within California to assess: (1) the number of NIS introduced as the result of aquaculture importation, (2) historical and current flux of species and individual organisms, and (3) the impacts of NIS introduced via aquaculture importations on native species in CA.

## Methods

Our approach involves bringing together several lines of information to characterize the NIS both currently and historically used in California aquaculture. The primary goal was to obtain data on species, numbers of individuals per species, and the distribution of these species in time and space in California waters. We reviewed several categories of state and federal permits required for aquaculture (Table 1) and determined current and historical use of these permits based on conversations with staff at several state and federal agencies.

### California Department of Fish and Wildlife Aquaculture Permits

The California Department of Fish and Wildlife (CDFW) regulates the interstate transfer of aquaculture species, including shellfish, through its import permit process. Commercial aquaculture facilities must submit additional permits and statements including information on their yearly plantings and harvesting with species and volume. We examined records relevant to aquaculture leases as well as importation of aquaculture species searching specifically for the following information: (1) species that have been or are currently brought into the state and transferred between bays for aquaculture, (2) the quantity of each species over time (listed variably as number of individuals, pounds, bushels, etc.), (3) origin of individual species (i.e. source of individual shipment rather than their original native range), (4) locations

where aquaculture species have been or are being placed and the size of these operations, and (5) current and historic regulations that were intended to prevent the spread of NIS via aquaculture.

### *Import permits*

CDFW Import Permits are required for the interstate transfer of aquaculture species into California waters. We found a total of 328 import permits (standard, one-time shipments and long-term, yearly multi-shipments) for aquaculture related species were issued between 1989, the earliest date for which significant records were available, and 2011. Many of the permits neither indicated nor required the reporting of which species or quantities were imported or planted. Some aquaculture companies applied for a single permit for multiple species from one source location, whereas others applied for multiple single-species permits. Thus, for each year from 1989–2011, we tallied the number of permits for each species, the number of permits for each importation source region, as well as the intended California coastal destination for the species listed on the permits.

### *Inspection and planting certificates*

Prior to the mid-1980s, CDFW required Inspection and Planting Certificates for transfers of organisms from outside California and within state waters for all aquaculture activities in CA. These certificates listed species names, volume, source, destination and use. Sources for importation during this period included eastern and western U.S. as well as Japan and Canada. We entered and analyzed all available Inspection and Planting records from 1964 until 1983, after which these permits were discontinued.

### *Proof of use reports*

Beginning in the 1980s, Proof of Use (POU) reports replaced the Inspection and Planting Certificates. However, only a subset of aquaculture leases that are managed by CDFW are required to submit POU reports, which lists all planting and harvesting activities by date and year, a map of the site, and a narrative of the activities. POU reports represent the only source of data on the actual volume of species used in aquaculture plantings, unfortunately, these

reports are required only for this small subset of lease holders. Also, variation in reporting requirements over time made it difficult to evaluate trends in aquaculture practices even for this subset of aquaculture facilities.

#### *Private stocking permits*

Private stocking permits are issued by CDFW when organisms intended for aquaculture are placed in state waters by a person or agency that is not a registered commercial aquaculture facility. The most common use of these permits is for research and restoration, including species native to California, such as the Olympia oyster *Ostrea lurida*.

#### United States Army Corps of Engineers Permits

Since 1890, shellfish growers who placed structures in the water or otherwise changed water flow and/or impacted the substrate in state or federal waters were obliged to obtain federal permits. To estimate historic and current acreage in aquaculture, we attempted to obtain information from the U.S. Army Corp of Engineers (USACE), which provided records for permit applications from 1993 to 2011. However, these only included a handful of permits and so provided little additional information, so these data were not used in further analysis. This included four offshore aquaculture permits that were denied or withdrawn and two permits for salmon pens and abalone culturing facilities that were approved.

#### United States Fish and Wildlife Service Importation Records

The United States Fish and Wildlife Service (USFWS) is required to inspect all animal species imported into the United States. However, since 1989, very few imports into California have involved invertebrate species for aquaculture purposes, and none at all since 2003. Since there are so few data related to aquaculture from USFWS, we did not include data from this agency in our analysis.

#### Temporal and spatial patterns of invasion

To characterize temporal and spatial trends in introduction and establishment of NIS associated with shellfish

aquaculture, we used the NEMESIS database to create a list of established NIS likely to have been introduced to California via the aquaculture trade. NEMESIS is a database of marine and estuarine invasions in the continental U.S. and Alaska (<http://invasions.si.edu/nemesis/index.html>). This database is compiled from peer-reviewed scientific literature and the gray literature from approximately 1853 through the present (see Online Resource 1). We used a subset of the NEMESIS data involving species introduced to California (CA NEMESIS) with updates through 2011. This database includes species known to be non-native, those thought to have established populations, as well as species that have failed to establish or have gone extinct since becoming established. We did not include ‘cryptogenic’ (species whose non-native status is uncertain).

We cross-referenced NEMESIS with two related databases: (1) one compiled for a literature review that included non-native and cryptogenic invertebrate species from estuaries and bays within California, (Williams and Grosholz, unpub. data) and (2) a list of non-native algal species based on literature review (1995–2006) compiled by Williams and Smith (2007). We updated the algal database with a search of the literature from 2006 through 2011.

To examine spatial trends in invasion, we examined first reports on both a statewide (reported from anywhere in California) and a bay-wide (reported from a specific bay or water body) basis. Because the dates of first introduction and/or establishment are not known accurately for most species, we used the year of the first report as a proxy for year of introduction into CA. We also examined these data to determine the spatial extent of aquaculture-associated NIS across bays or other water bodies. Lastly, due to industry-wide changes in importation practices since approximately 2000 that dramatically reduced opportunities for unintentional introductions (defined as ‘hitchhikers’), we compared the number of species of hitchhikers via aquaculture prior to 2000 with the number of hitchhiker species recorded in California after 2000.

#### Impacts of NIS introduced via aquaculture

Using our updated lists of non-native algae and mollusc species introduced to California, we searched the peer-reviewed scientific literature and created a database of studies addressing the impacts of non-

native molluscs and macroalgae on native communities. A similar database had been created for crustaceans in an associated project and together these broad taxonomic groups made up the majority (>60 %) of the NIS in California.

Between November 2011 and March 2012, we conducted the searches using BIOSIS using a time interval for the search from 1926 through 2011. All searches were completed with the following search terms in BIOSIS: *Topic = (Adventive OR Alien\* OR Bioinvasi\* OR Biosecur\* OR Exotic\* OR Foreign OR Introduc\* OR Incursion\* OR Invasi\* OR Nonendemic\* OR Non indigenous OR Nonindigenous OR Non native\* OR Nonnative\* OR Nuisance\* OR Pest\*) AND Topic = (species name in quotes, e.g. “Sargassum muticum”) AND Timespan = 1926–2011.* We carried out searches using synonyms for the current species name using WoRMS (World Registry of Marine Species) for lists of synonyms.

We performed an initial sort by reading through the selected titles of which >95 % of papers were irrelevant. We then reviewed abstracts to choose articles for data extraction and entry. For each study, we extracted the following data: authors, publication year, introduced species name, vector and species origin if listed in article, recipient habitat (e.g. bay, intertidal, etc.) and location, impacted entity, name, metric, impact category, direction of effect, study type and setting, statistical analysis, mean effect size, and error term for the mean effect size if reported. These studies were categorized as observational, mensurative, or experimental (Williams 2007; Williams and Smith 2007). Mensurative and experimental studies included a replicated statistical design and experimental studies involved manipulations of native organisms and/or NIS. We included only mensurative and experimental studies in the analyses. Studies could contain multiple ‘cases’, which we define as a single result or effect for a single response variable, therefore a single publication could contain multiple cases. We tallied whether there was a change in each response variable and the direction (positive, negative) of the change if reported. We interpreted the biological effect of the NIS 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 visa versa. Of the total number of cases available, we calculated the percentage of studies that

**Table 2** Number of import permits for each species issued by CDFW from 1989 to 2011

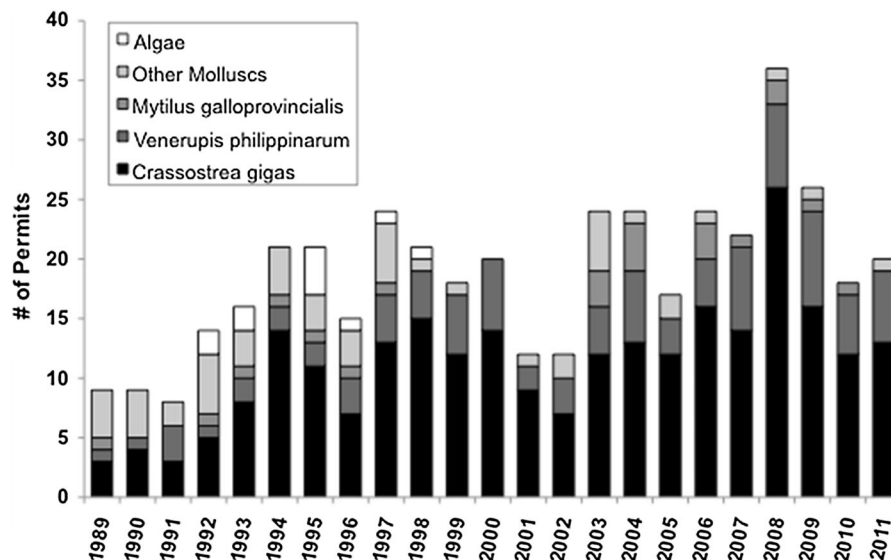
Taxon	No. of permits	Status
<i>Crassostrea gigas</i>	43	NIS, unknown
<i>Venerupis philippinarum</i>	21	NIS, established
<i>Crassostrea sikamea</i>	17	NIS, unknown
<i>Mytilus galloprovincialis</i>	5	NIS, established
<i>Crassostrea virginica</i>	5	NIS, unknown
<i>Ostrea edulis</i>	3	Native
<i>Panopea generosa</i>	2	Native
Algae	2	
<i>Mercenaria mercenaria</i>	1	NIS, established
Other molluscs	1	

Permits do not indicate the number of individuals imported or planted. ‘Other Molluscs’ make 1.6 % of the imports and include *Haliotis rufescens*, *H. discus hannai*, *Patinopectin caurinus*, *Ruditapes decussatus*, *Crassodoma gigantea* and *Crassostrea rivularis*. ‘Algae’ constitute 2.5 % of the total number of imports and include two species, *Nereocystis luetkeana* and *Palmaria mollis*. Status includes native species (Native), non-indigenous species that have become established in California (NIS, established), NIS that have been introduced to California (reported from non-aquaculture environments) with current status unknown (NIS, unknown) according to NEMESIS

reported positive versus negative changes in the response variables separately for mollusc and algal aquaculture species.

## Results

We found that even the most detailed data available from California Department of Fish and Wildlife (CDFW) and United States Army Corp of Engineers (USACE) were insufficient to estimate with accuracy the identity of species or the number/volume of aquaculture species imported into California transferred between bays, or planted in state waters. Further, quantitative examination of temporal and spatial trends for aquaculture importation use or even acreage in California was in most cases not possible with these limited data. In large part this was due to a lack of state regulations requiring permit-holders to provide follow-up information to CDFW and low rates of compliance with federal regulations (USACE) even when aquaculture facilities are required to be under permit with USACE.



**Fig. 1** Number of import permits issued in California per year by California Department of Fish and Wildlife (CDFW) between 1989 and 2011. ‘*Crassostrea gigas*’ includes *Crassostrea gigas* and *Crassostrea sikamea*. ‘Other Molluscs’ include *Haliotis rufescens*, *H. discus hannai*, *Patinopectin caurinus*,

*Ruditapes decussatus*, *Crassodoma gigantea* and *Crassostrea rivularis*, *Ostrea edulis*, *Mercenaria mercenaria*, *Panopea generosa*, *Crassostrea virginica*. ‘Algae’ include two species, *Nereocystis luetkeana* and *Palmaria mollis*

### Import permits

Our data show that the most permits were issued for Pacific oysters with *Crassostrea gigas* accounting for 43 % of all aquaculture import permits issued by CDFW for the time period for which we have importation data (1989–2011) (Table 2). The second and third most common species on import permits were Manila clams *Venerupis philippinarum* (21 %) and Japanese oysters *Crassostrea sikamea* (17 %). These three species represent 81 % of all CDFW import permits from 1989–2011. By the mid-1990s, oysters and Manila clams alone represented the majority of imported species (Fig. 1). Importantly, although species imported for aquaculture have become less diverse since 1989, the total number of permits issued annually has been relatively unchanged. When we tested the difference between numbers of import permits from the years before versus after 2000, we found no significant difference (*t* test;  $t_{21} = -2.07$ ,  $p > 0.05$ ).

Our results indicate the importation of NIS via aquaculture has been disproportionately greater into northern California bays and estuaries in comparison to central and southern CA. For the period from 1989–2011, the greatest number of permits issued was for companies based in Humboldt Bay (400 km north

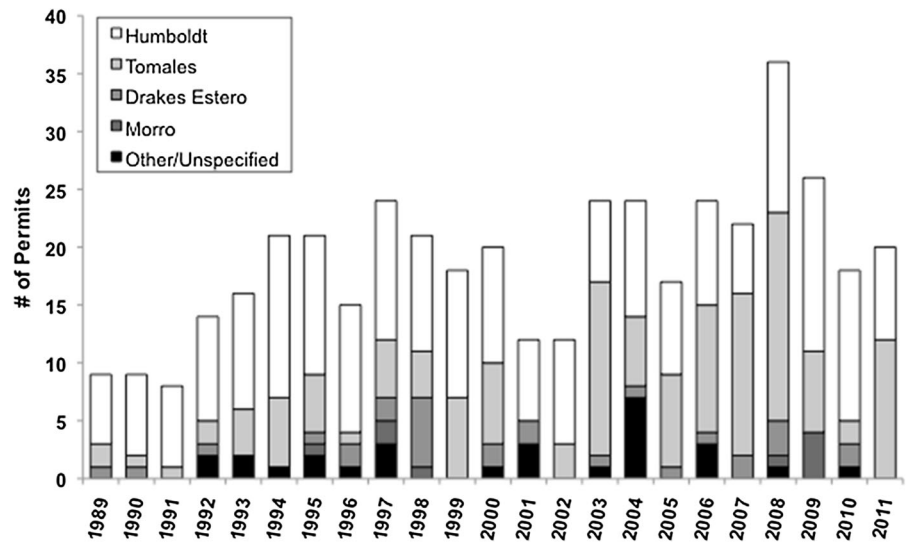
of San Francisco), with Tomales Bay (100 km north of San Francisco) as a close second (Fig. 2). During this period, Humboldt and Tomales Bays were the destinations listed on 52 % and 33 % of the aquaculture-related import permits, respectively. With few exceptions, other California bays had five or fewer permits issued per year.

We found that the Pacific Northwest was the primary source of most aquaculture imports to California from 1989–2011 with the majority from Washington (56 %) and a total of 80 % from Washington and Oregon collectively (Fig. 3). Since 2007, the source for aquaculture importations has shifted with a greatly increasing portion coming from Hawaii, while imports from Mexico have ceased since 2003. The eastern U.S. was an important source during the early years of California aquaculture (Gordon et al. 2001), but imports from Maine appeared in only two years in our data. During this period from 1989–2011, smaller numbers of imports have come from Japan, Australia and Canada (British Columbia).

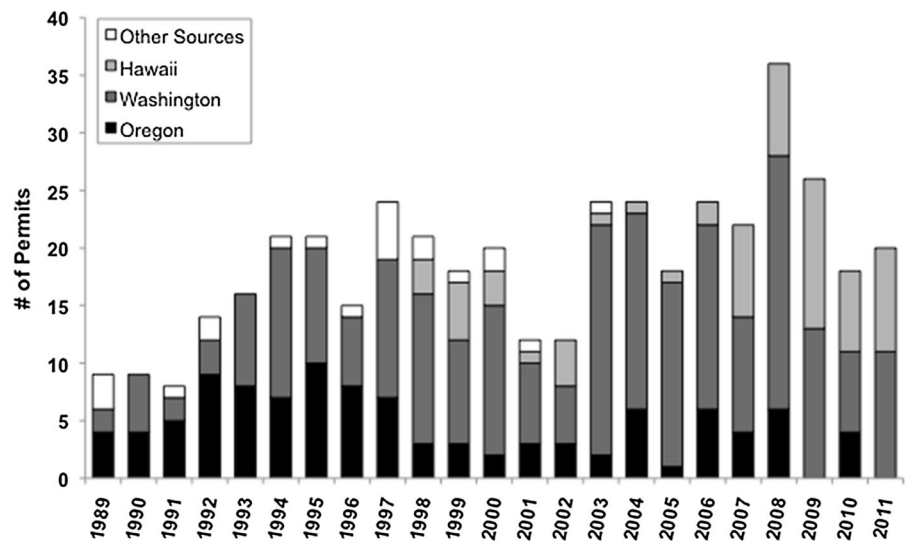
### Proof of use reports

We were unable to quantify the total number of aquaculture businesses or the volume of organisms

**Fig. 2** Number of import permits issued in California per year by CDFW by destination (water body). ‘Other/Unspecified’ includes destinations to Santa Barbara, San Diego, and unspecified bays



**Fig. 3** Origins of aquaculture species imported into California by year based on CDFW import permits. ‘Other Sources’ include imports from Alaska, Maine, Mexico, Canada, Japan, and Australia

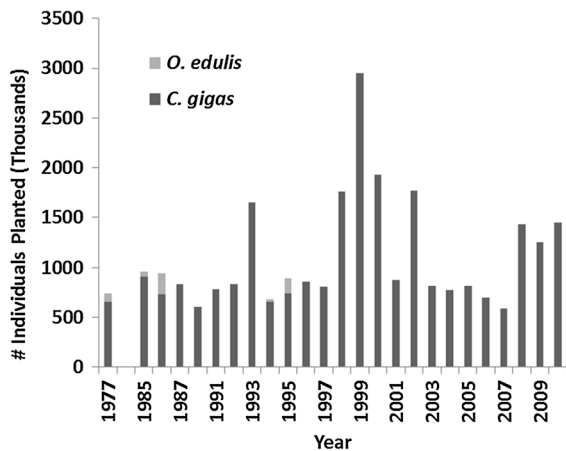


placed in California either historically or currently. However, we were able to gather enough information from specific leases in targeted areas over sufficient time periods to act as ‘case studies’ with which to identify trends in California aquaculture. By example, we found Proof of Use records for Tomales Bay lease allotments from the late 1970s which were typical of several other bays where similar lease data were available (e.g. Morro Bay and Santa Barbara in southern CA). Within Tomales Bay, allotment M-430-05 has the most consistent set of records showing the volume of oysters planted over the time period 1977, 1983, and 1985–2010 by species (Fig. 4). Tomales Bay has been the recipient of many NIS including Pacific oysters (*Crassostrea*

*gigas*), European flat oysters (*Ostrea edulis*), Eastern oysters (*Crassostrea virginica*), Manila clams (*Venerupis philippinarum*), and others (Online Resource 2). The overall pattern over time, which again was representative of other bays, showed a decrease in the number of sources, now primarily Washington and Hawaii. However, there has been a recent increase over the past several years in the numbers of Pacific oysters planted into Tomales Bay (Fig. 4).

#### Private stocking permits

We found 38 records related to the private stocking of species in California marine habitats during this time



**Fig. 4** Time series of aquaculture plantings of seed oysters in Tomales Bay allotment M-430-05 based on Proof of Use Permits (source California Dept. of Fish and Wildlife). Missing years represent missing data rather than no activity and data for 1977 and 1983 represent fiscal year July–June of following year. Not shown are data for two single plantings: *C. gigas* Kumamoto in 1985 and *C. virginica* in 1977

period (1989–2011). While many species planted under private stocking permits are native to California, both *C. gigas* and *M. galloprovincialis* were imported under these permits: therefore, this category of plantings represent potential opportunities for non-indigenous species introductions (Online Resource 3).

#### Temporal and spatial patterns of introduction

Our data compiled from NEMESIS and other data bases (see Methods) indicate that 126 NIS reported from California waters were associated with aquaculture imports (Online Resource 4) and 106 of these have become established in at least one location. Of these 126 reported species, 14 of these were intentionally placed into state waters in at least one location and, thus, represent intentional introductions. Most were raised commercially, but at least two, the clam *Corbicula fluminea* and the mitten crab *Erocheir sinensis*, are believed to have been planted unofficially to start commercial fisheries. Nearly all of these intentional introductions are bivalves, but other mollusc and algal species have also been used. Four of the 14 intentionally introduced species have become established in California: *Mya arenaria*, *Venerupis philippinarum*, *Mytilus galloprovincialis* (which hybridizes with native mussels) and *Mercenaria mercenaria*. *Crassostrea gigas*, which represents the

single greatest number of permits, has also been reported as naturalized at several sites in California, although not officially recognized as established (E. Grosholz, C. Zabin, and A. Chang, unpubl. data).

The remaining 112 NIS reported from California waters are believed to be accidental introductions or hitchhikers associated with aquaculture shipments. At least 97 of these hitchhikers have become established and include bivalve predators like the Atlantic (*Urosalpinx cinerea*) and Japanese oyster drills (*Ocenebra inornata*) and oyster pathogens (*Bonamia ostrea*), which are now among the most serious oyster pests. Relatively recent hitchhikers also include the sabellid polychaete parasite of abalone *Terebrasabella heterouncinata*, which infests and deforms abalone shells and has been a costly pest for the cultured abalone industry (Moore et al. 2007).

Overall there is a pattern of reduced numbers of species, although these data must be interpreted cautiously, since high numbers detected within a time period can reflect increased study as well as new introductions (Table 3). Of significance for assessing the future risk of aquaculture is the decline in number of new NIS introductions associated with aquaculture 1991–2000 (55 species) relative to 2000–2010 (39 species). However, we used one well studied site, Tomales Bay, where we had extensive import permit data to test the difference in the numbers of import permits before versus after 2000. We found no significant difference (*t* test;  $t_7 = -0.19$ ,  $p > 0.85$ ), which suggests that the quantity of imports of species in Tomales Bay and the opportunity for invasion has not declined.

Invasions linked to aquaculture are widespread throughout the state, although the vast majority are located in central and northern California (Table 3). The largest number of established NIS believed to be introduced via aquaculture is in San Francisco Bay: 30 are likely linked to aquaculture as the sole vector (only 29 with known date of introduction), and another 62 are linked to more than one vector (polyvectoric) with aquaculture as a possible vector. Elkhorn Slough, Tomales Bay and Humboldt Bay all have with a long history of aquaculture and also have high numbers of such NIS: Elkhorn Slough (14 sole, 37 poly), Tomales Bay (20 sole, 28 poly) and Humboldt (13 sole, 38 poly). Several other locations including Morro Bay, Drakes Estero and Bodega Bay are either currently or



**Table 3** The number of NIS linked to aquaculture from selected California bays by time period

Bay	1910	1911–1930	1931–1950	1951–1970	1971–1990	1991–2000	2001–2010	Total
Smith River		1		1	2		1	5
Mad/Redwood River	1	1	1		1			4
Humboldt Bay	2	1	4	7	10	15	6	45
Bodega Bay		1	4	2	9	6	5	27
Tomales Bay	1	3	11	15	3	6	9	48
Bays btw Tomales and Drakes		4	1	6	6	1		18
Drakes Estero		1	2	5	3	1	2	14
San Francisco Bay	15	9	22	21	12	4	8	91
Elkhorn Slough	2	4	5	10	13	14	3	51
Morro Bay		1	4	10	5	3	4	27
San Pedro Bay				3		2		5
Newport Bay			2			1		3
Mission Bay					1	1	1	3
San Diego Bay	1			1		1		3
Total	22	26	56	81	65	55	39	

Species include those attributed solely to aquaculture and those for which aquaculture is one of several possible vectors (data from CA NEMESIS). Note the last two time periods are shorter than earlier ones. Current aquaculture practices to reduce accidental introductions were being widely practiced by 2000

historically supported aquaculture and have high numbers of NIS.

#### *Impacts of NIS introduced via aquaculture*

We found that only a small percentage of peer-reviewed articles addressed the impacts of NIS in California. In our search, BIOSIS returned 2080 and 317 articles for molluscs and algae, respectively. As a result, we performed literature searches for impacts of 46 species of non-native algae and molluscs attributed to aquaculture introductions (Table 4).

For mollusc species entering California via aquaculture, we found that only a small percentage of peer-reviewed studies (3.4 %) quantified their impacts in the introduced range. We found a total of 61 peer-reviewed journal articles containing 122 cases that had impact data for nine of the 37 mollusc species introduced by aquaculture. However, only six species (*Crassostrea gigas*, *Crepidula fornicata*, *Littorina littorea*, *Musculista senhousia*, *Mytilus galloprovincialis* and *Venerupis philippinarum*) had five or more impact articles. Of these studies that measured impacts, 77 % reported an impact on native species or environments (positive or negative), while 23 %

reported no impact (Fig. 5a). The most common impacts were on abundance and demographic performance of native species and the majority of those biological impacts were negative or deleterious to the native community or species (Fig. 6a).

In comparison to the molluscs, a greater percentage (18.9 %) of studies of algae introduced by aquaculture contained data on impacts, although there were fewer peer-reviewed journal articles overall. We found impact data for only seven non-native algae species and only three species (*Codium fragile* ssp. *fragile*, *Gracilaria vermiculophylla* and *Sargassum muticum*) had more than five peer-reviewed journal articles reporting impacts. We found a total 49 peer-reviewed journal articles containing 210 studies that measured impacts of *Codium fragile* ssp. *fragile*, *Gracilaria vermiculophylla*, and *Sargassum muticum*. Similar to the results from non-native molluscs, 84 % of these studies reported significant impacts, while 16 % reported no impact on native species (Fig. 5b). Of these, the most common impacts were on the abundance of native species and similar to the impacts investigated for non-native molluscs, the majority of biological impacts were negative on the native community or species (Fig. 6b).

**Table 4** All algae and mollusc species imported into California via aquaculture for which we conducted a literature search on their impacts

Taxa	Species	Sole or polyvectic	CA status
Algae	<i>Ceramium kondoi</i>	Poly	Established
Algae	<i>Chondracanthus teedei</i>	Sole	Unknown
Algae	<i>Codium fragile</i> ssp. <i>fragile</i>	Poly	Established
Algae	<i>Gelidium vagum</i>	Sole	Established
Algae	<i>Gracilaria vermiculophylla</i>	Poly	Established
Algae	<i>Grateloupia lanceolata</i>	Poly	Established
Algae	<i>Lomentaria hakodatensis</i>	Poly	Established
Algae	<i>Sargassum muticum</i>	Poly	Established
Mollusc	<i>Anadara ovalis</i>	Sole	Failed
Mollusc	<i>Anadara transversa</i>	Sole	Failed
Mollusc	<i>Anomia simplex</i>	Sole	Failed
Mollusc	<i>Argopecten irradians</i>	Sole	Failed
Mollusc	<i>Batillaria attramentaria</i>	Poly	Established
Mollusc	<i>Boonea bisuturalis</i>	Poly	Established
Mollusc	<i>Busycotypus canaliculatus</i>	Poly	Established
Mollusc	<i>Corbicula fluminea</i> (I)	Poly	Established
Mollusc	<i>Crassostrea gigas</i> (I)	Poly	Unknown
Mollusc	<i>Crassostrea virginica</i> (I)	Sole	Failed
Mollusc	<i>Crepidula convexa</i>	Poly	Established
Mollusc	<i>Crepidula fornicata</i>	Sole	Failed
Mollusc	<i>Crepidula plana</i>	Poly	Established
Mollusc	<i>Eubranchus misakiensis</i>	Poly	Established
Mollusc	<i>Gemma gemma</i>	Sole	Established
Mollusc	<i>Geukensia demissa</i>	Poly	Established
Mollusc	<i>Haminoea japonica</i>	Poly	Established
Mollusc	<i>Ilyanassa obsoleta</i>	Poly	Established
Mollusc	<i>Littorina littorea</i>	Poly	Unknown
Mollusc	<i>Macoma petalum</i>	Poly	Established
Mollusc	<i>Mercenaria mercenaria</i> (I)	Poly	Established
Mollusc	<i>Meretrix lusoria</i>	Sole	Failed
Mollusc	<i>Musculista senhousi</i>	Poly	Established
Mollusc	<i>Mya arenaria</i> (I)	Sole	Established
Mollusc	<i>Myosotella myositis</i>	Poly	Established
Mollusc	<i>Mytilus galloprovincialis</i> (I)	Poly	Established
Mollusc	<i>Nuttallia obscurata</i>	Poly	Unknown
Mollusc	<i>Ocinebrellus inornatus</i>	Sole	Established
Mollusc	<i>Okenia plana</i>	Poly	Established
Mollusc	<i>Ostrea edulis</i> (I)	Sole	Failed
Mollusc	<i>Ostrea puelchana</i> (I)	Sole	Failed

**Table 4** continued

Taxa	Species	Sole or polyvectic	CA status
Mollusc	<i>Petricolaria pholadiformis</i>	Poly	Established
Mollusc	<i>Philine japonica</i>	Poly	Established
Mollusc	<i>Philine orientalis</i>	Poly	Established
Mollusc	<i>Sakuraeolis enosimensis</i>	Poly	Established
Mollusc	<i>Urosalpinx cinerea</i>	Sole	Established
Mollusc	<i>Venerupis philippinarum</i> (I)	Poly	Established

Species that were intentionally introduced for aquaculture purposes are indicated by (I); all others are unintentional introductions (hitchhikers)

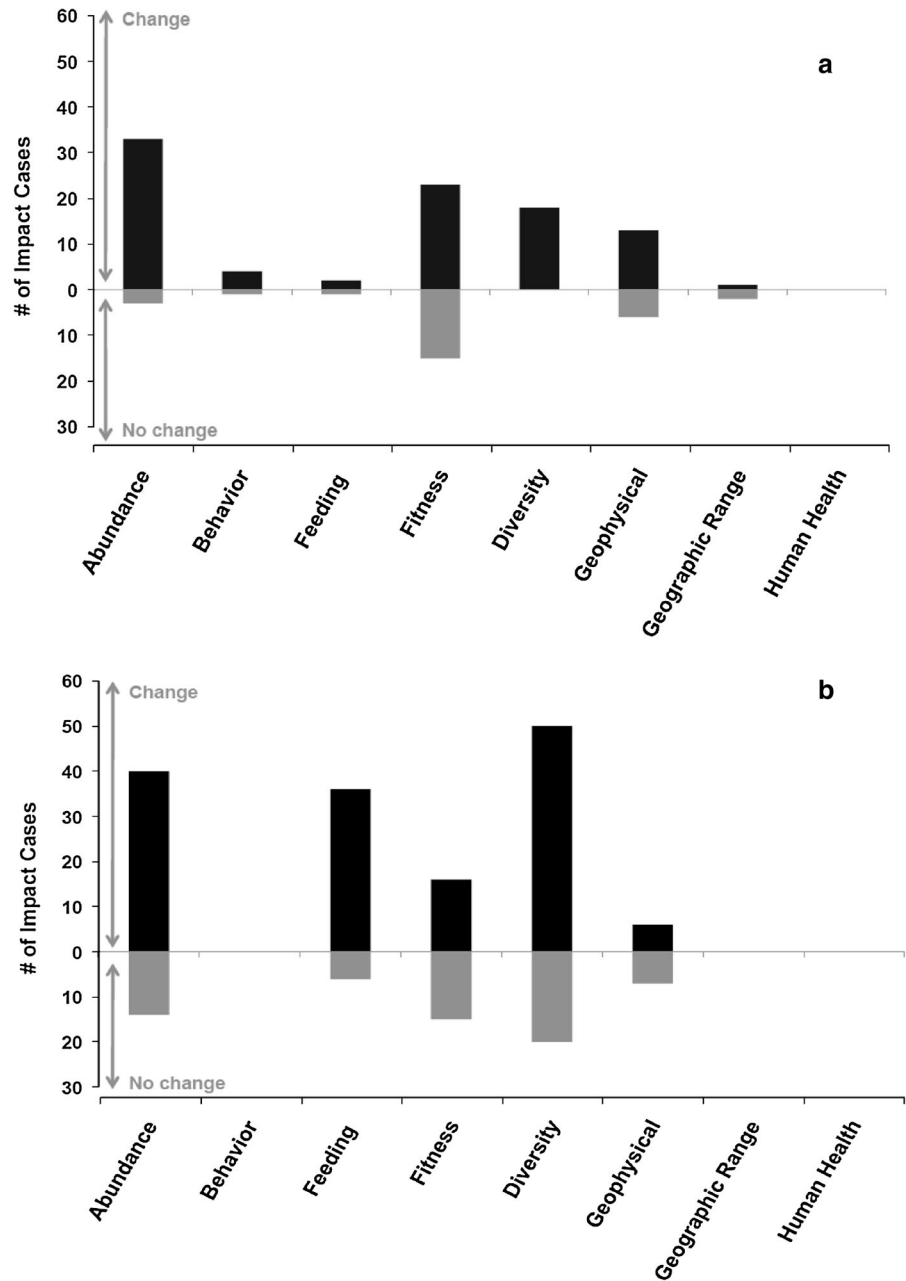
## Discussion

Our results suggest that, historically, aquaculture was a major vector of introduction of NIS into California with over 100 established species attributed either solely or in part to aquaculture importations (see Miller et al. 2007). We found that greater than 80 % of species likely associated with aquaculture and almost 50 % of species associated solely with aquaculture importation have become established in CA. Therefore, species introduced via aquaculture importations have a high likelihood of establishment.

Our data show the distribution of established NIS, either total number or first records, were disproportionately distributed in bays and estuaries where aquaculture has historically or continues to take place. The vast majority of these species were introduced initially into northern California. This is in agreement with previous studies showing California and San Francisco Bay in particular are ‘hotspots’ for invasions on the west coast (Ruiz et al. 2011). Although many species were introduced in the period prior to the period for which we have permit data, our results also make it clear that the primary sources for aquaculture invasions in the period for which we do have permits were from other western U.S. states including Hawaii, Washington and Oregon, but more local sources were not correlated with reduced risk.

Of importance for future vector management in CA is the changing nature of aquaculture importations. Our data show a modest decline in both the numbers of species imported into California as well as the number of established NIS associated with aquaculture. The

**Fig. 5** Summary of number of cases reported in the literature searched in which the presence of non-native mollusc species (a) or algal species (b) were associated with a change in a response variable (abundance, behavior, feeding, etc.) in surrounding native communities. ‘Change’ (upper black bars) includes a positive or negative difference in a response variable including non-directional responses such as a change in community structure. ‘No Change’ (lower gray bars) indicates no significant changes on surrounding native communities or environments. See Online Resource 5 for an explanation of data set and impact categories

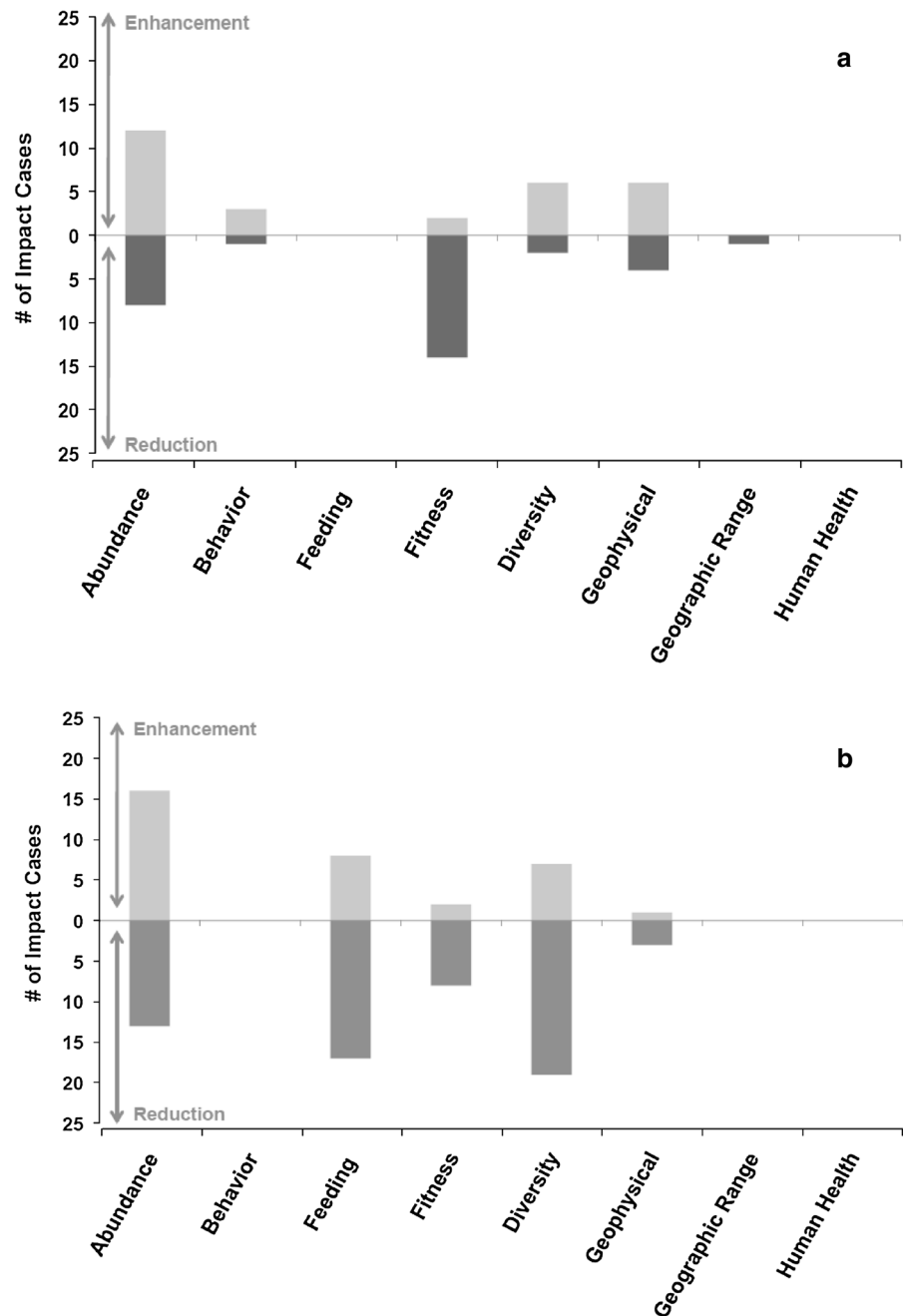


evidence suggests that changes in aquaculture industry practices including the importation of fewer species and aquaculture importation consisting primarily of larval and juvenile stages (for oysters) have reduced the potential for unintentional introductions. There is substantial uncertainty around this assumption given new introductions can require several years before they are detected. Therefore, changes in aquaculture practices and reduced opportunities for invasion may

require another decade of observation before a true decline can be determined.

This decline likely reflects qualitative changes in importation practices of the aquaculture industry from shipments of adult shellfish to mostly shipments of larvae or juvenile stages, thus reducing opportunities for hitch hikers. However, two opposing processes likely affect the modest trends in our data. First, the number of new NIS invasions associated with

**Fig. 6** The number of cases (within studies) for either non-native mollusc species (a) or algal species (b) introduced by aquaculture that show either a significant positive impact ('Enhancement', upper black bars) versus negative impact ('Reduction', lower gray bars) on response variables (abundance, behavior, feeding, etc.) in surrounding native communities. See Online Resource 5 for an explanation of data sets and impact categories



aquaculture reported between 1991–2000 are likely higher as the result of comprehensive surveys conducted in Humboldt Bay (Boyd et al. 2002) and Elkhorn Slough (Wasson et al. 2001). Second, the number of aquaculture-related NIS invasions reported 2000–2010 may be higher, and the post-2000 reduction more modest, as the result of time lags (often several years to a decade) associated with detecting

new species. Thus, the actual number of NIS introductions post-2000 may be smaller, but the reported numbers reflect NIS actually introduced prior to 2000.

We found evidence of both positive and negative impacts with negative impacts being generally more common. However, our data on impacts of NIS in California are clearly limited by the small number of available studies and there are obvious examples of

more extensive impacts for some species based on studies outside California. For example, Pacific oysters (*Crassostrea gigas*) have been shown to have significant negative impacts in locations around the world where feral populations have become established including Washington (Ruesink et al. 2005). Although *C. gigas* was not included among established species, populations have been tentatively identified in San Francisco Bay (Goodwin et al. 2010) and in San Pedro near the Port of LA and San Diego Bay (California Dept. of Fish and Wildlife), although their status is still uncertain.

Our results also highlight how few data are available documenting the importation of NIS into California via aquaculture. There are also no reasonable estimates of the flux or quantity of NIS imported into California via this vector due to gaps in the regulatory structure and reporting requirement. Even the identity of the species is uncertain in some cases, which is particularly unfortunate due to the high likelihood of establishment for intentional introductions.

Given this lack of information on aquaculture introductions, we make the following recommendations regarding permitting and reporting requirements for California and other states that have similar data gaps. Our recommendations echo similar points made in the ICES Codes of Practice (ICES 2005), and include additional points specific to aquaculture practices in California that can be applied elsewhere. First, even if importation permits contain information about numbers of individuals as well as species information, it is important for there to be subsequent reporting regarding how many and how often these shipments are outplanted into local waters. Second, for import permits, there needs to be information regarding not just the species, but the quantity, or at least volume, of individuals contained within the shipment. Third, other relevant information, such as the origin of the shipment, the ploidy of the organisms (e.g. oysters that are diploid vs. triploid, etc.) and life stage (larvae, juveniles, etc.) should also be included on import permits. Finally, we suggest that permitting and reporting data be centrally organized within a single agency, which would greatly facilitate the data analysis needed to accurately quantify the risks associated with aquaculture introduction.

In conclusion, it is widely acknowledged that the best strategy for reducing the risk of invasions into marine systems is to focus on the vectors of

introductions rather than on management options for individual species once they have become established. At present, we have limited information about ‘which vectors’ are the important ones to focus management attention. However, our data are among the first to shed light on the risk posed by current aquaculture practices by analyzing the rates and numbers of species associated with past and present aquaculture importation. Despite its historic importance as a vector, aquaculture-associated introductions of unintentional species have declined over time. The current risk of intentional introductions appears confined to *C. gigas* and similarly permitted species. Although other vectors in California such as the ornamental species trade are emerging as more risky in terms of high propagule supply (Williams et al. 2013), the steady number of import permits and the high establishment rate of aquaculture species remain potential risks to be evaluated seriously. We suggest that resource managers remain vigilant and maintain annual statewide surveys where possible to detect new introductions. Of most importance, and certainly contrary to most published recommendations (Williams and Grosholz 2008), we recommend that scarce management resources dedicated to NIS prevention not be spent on aquaculture importations. We strongly recommend that current industry practices of importing young life stages, which are currently voluntary, be maintained possibly by new regulations mandating these practices. The evidence emerging from many regions suggests that vectors such as hull fouling and the ornamental trade may potentially be much more important vectors for invasions in many regions including California (Williams et al. 2013). Given the scarcity of data, we also recommend considerably more resources invested in quantifying and understanding the risk posed by aquaculture and other invasion vectors such as hull fouling and the ornamental species trade.

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