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Research Article

Small boats provide connectivity for nonindigenous marine species between a highly invaded international port and nearby coastal harbors

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Abstract

While considerable variation exists in ecological and economic impacts among nonindigenous species (NIS), the potential magnitude of cumulative impacts for each species increases with increasing area occupied. In the marine environment, large commercial ships have often transferred NIS across ocean basins to new continents. However, following such initial invasions, small craft (recreational and fishing boats) likely play an important role in the secondary, coastwise spread of NIS, thus increasing the geographic range and potential magnitude of impact. In this study, we assess the connectivity among bays in terms of small vessel movement and associated biofouling organisms in central California (USA), examining flux between a heavily invaded international port, San Francisco Bay (SFB), and three small marinas on the adjacent coast. We estimated vessel flux among locations, using data from 405 boater questionnaires and 4,000 transient boat records, and found a strong bi-directional connection between SFB and the nearby coastal marinas. Video surveys of 36 boats that had recently traveled revealed macrofauna on the underwater surfaces on 80% of boats, and at least 27 taxa (including 7 NIS) were present on boats sampled by SCUBA. Importantly, while we provide evidence for strong connectivity, our data most certainly underestimate the flux of vessels and cumulative transfers of organisms among these locations during this short-term study, as vessel movement data are incomplete and surveys are limited even in this small region. This study underscores the opportunities for biofouling organisms, many with limited self-dispersal capacity, to spread via small boats and suggests that effective management strategies to minimize NIS spread and impacts must address the small-boat vector.

Key words: fishing boats, hulls, invasive species, recreational boats, secondary spread, vessel biofouling

Introduction

Nonindigenous species (NIS) are now found across multiple biomes from tropical rainforests to the Antarctic and coastal oceans worldwide (Carlton 1999; Ricciardi 2007). While some NIS may pose little or no threat, there are numerous examples of serious impacts on human health and economies, and on native species and ecosystems (Pimentel et al. 2005; Ehrenfeld 2010). The potential or cumulative magnitude of the impact that an NIS can have is related in part to how widely distributed it becomes as well as its abundance and per-capita effects (Parker et al. 1999; Ricciardi et al. 2011). Many risk-assessment models address explicitly the range of NIS, incorporating a term for the probability that a species, once introduced, becomes established and spreads in a new region (e.g., Leung et al. 2002; Cook et al. 2007).

In the marine environment, management of vessel-mediated invasions has focused primarily on the prevention of initial invasions rather than secondary spread along coastlines. This is exemplified by efforts to manage the ballast water of commercial ships, which is the marine invasion vector that has received most attention in recent decades, with regulations and agreements advancing at international, national, and sometimes state levels (Davidson and Simkanin 2012; USCG 2012; USEPA 2013). More recently, additional efforts have begun to include management of invasions associated with biofouling (the marine animals and algae that attach to the wetted surfaces of ships) on commercial ships and internationally traveling yachts (e.g. IMO 2011, 2012; DAFF 2011; MAFBNZ 2010). In contrast, relatively little regulatory attention has been given to secondary spread of NIS from their initial point of introduction within a region by boating activities, despite increasing numbers of studies that have documented rich fouling communities, including non-native species, on recreational and fishing boat hulls (Floerl 2002; Floerl and Inglis 2005; Ashton et al. 2006; Savini et al. 2006; Neves et al. 2007; Minchin et al. 2006; Mineur et al. 2008; Davidson et al. 2010). This has prompted calls for management of this vector (Kinloch et al. 2003; Piola and Forrest 2009; Clarke Murray et al. 2011) because it represents a major gap in the management of marine invasive species.

On the west coast of the United States, recreational and fishing boats (small boats) have been hypothesized to play a major role in the secondary spread of NIS (Wasson et al. 2001; Ruiz et al. 2011; Ashton et al. 2012; Davidson et al. 2012), although this has not been well quantified (but see Ashton et al. 2014; Davidson et al. 2010 for some examples from the US west coast). In contrast to large commercial ships, most small boats travel relatively short distances within large embayments or along a coast. Although smaller in size, such vessels appear to have significant potential for the secondary transfer of NIS associated with their underwater surfaces, due to the sheer number of vessels and vessel transits. More specifically, boaters living in coastal communities in Washington, Oregon and California own over one million boats (California Department of Boating and Waterways 2002; Oregon State Marine Board 2008; Responsive Management 2007). The number of days small vessels from these states spend underway each year is in the tens of millions; in Southern California alone, recreational vessels account for 11 million boater days (California Department of Boating and Waterways 2002).

San Francisco Bay, CA (SFB) is one of the most invaded estuaries in North America (Cohen and Carlton 1995), and is considered a likely source of invasions to smaller coastal harbors on the West Coast via small boat traffic. Support for this idea comes from the similarity of nonindigenous algae and invertebrates recorded in a nearby estuary without international shipping (Wasson et al. 2001) and the timing of subsequent invasions across California bays by species that were first recorded in SFB (Ruiz et al. 2011). Of the 151 nonindigenous invertebrate and algal species established in two or more bays in the state, 50% were reported first from SFB (Ruiz et al. 2011). SFB also appears to be an important invasion source more broadly across coastal North America; of the 290 established NIS in this region, 52% were first reported from SFB (Ruiz et al. 2011).

For many of the NIS in SFB, especially sessile forms with short larval durations, self-dispersal to other bays is unlikely, due to distances of tens of kilometers or more to suitable habitat in adjacent bays. Moreover, a large proportion of the marine NIS (both sessile and mobile species) in SFB, and North America more broadly, have some life stages that are associated with biofouling communities (Cohen and Carlton 1995; Ruiz et al. 2009). Thus, it appears that human-mediated dispersal by maritime vectors, such as recreational and fishing boats, is playing a role in the secondary spread of NIS.

To further evaluate the potential of small vessels to transfer species to and from a major commercial port, we reviewed the travel patterns and examined fouling on the hulls of boats that travel between SFB and three regional coastal marinas. Our goals were to quantify the connectedness of SFB and adjacent bays through boat movements (numbers of transits and travel patterns) and to begin to document the presence and extent of NIS on these boats. There is no requirement for small boats traveling within the US to report their arrivals to a central agency. While small boat arrivals from foreign countries report to Customs and Border Protection, these make up a small fraction of the state's boat movements (Ashton et al. 2012). Thus, data on vessel flux must be gathered directly from boaters or marinas, when available (as there is no requirement for marinas to keep such records). To this end, using focal marinas, we asked boaters about their travel patterns, collected marina arrivals data, used video to determine the extent of fouling on boats with a recent travel history, and collected and identified specimens from such boats. This study expands on the work of Davidson et al. (2010), which examined resident vessels within SFB, and we now evaluate the actual flux of vessels and associated biota between SFB and other adjacent bays.

Table 1. Data collected from study marinas.

Marina name	Bay	Transient boat data	Boater questionnaires returned	Video surveys of active boats	SCUBA surveys
Clipper Yacht Harbor	SF	N/A	56	10	
San Francisco Marina	SF	N/A	100	4	
South Beach Harbor Marina	SF	2 years	65	6	7
Spud Point Marina	Bodega	1 year	27	3	
Pillar Point Harbor	Half Moon	2 years	55	10	
Monterey Harbor	Monterey	2 years	102	3	7
Totals			405	36	14

Methods

Study sites

We conducted our research at three marinas in SFB and three marinas on the adjacent outer coast. Outer coast marinas represented the largest marinas in their respective bays: Spud Point Marina in Bodega Bay (~80 km north of San Francisco, 38°19'15"N, 123°03'30"W), Pillar Point Harbor in Half Moon Bay (~40 km south of San Francisco, 37°30'09"N, 122°28'55"W), and Monterey Harbor in Monterey Bay (~160 km south of San Francisco, 36°36'10"N, 121°53'35"W). The three marinas in SFB, Clipper Yacht Harbor (37°52'16"N, 122°29'55"W), San Francisco Marina (37°48'24"N, 122°26'28"W), and South Beach Harbor Marina (37°46'48"N, 122°23'15"W), were selected based on our earlier work (Davidson et al. 2010), which indicated that they had active sailing communities. An earlier survey of recreational boaters in SFB (Davidson et al. 2010) also indicated that the three nearby coastal harbors were among the top destinations for boats that traveled outside of SFB.

Transient boat data

We were able to obtain data on transient boats from four of our study marinas (Table 1). Transient boats are defined here as boats that stay at least one night in guest berths. Transient boat records are created by marina operators upon receiving fees for guest moorage and thus provide a highly reliable record of transient boat arrivals. In some marinas, boats that are actually residents are sometimes housed in guest berths or are otherwise designated as temporary due to a shortage of permanent slips. We worked with marina staff to eliminate as many of these “false-transients” as possible from the data.

Data collected by marina staff typically included the date of arrival, duration of visit, boat owner’s home town/zip code, vessel type, and vessel size. Across all marinas, data were missing for many records. Nonetheless, the volume of vessel records from each marina represented a large sample size, allowing us to begin to characterize travel patterns among bays, providing a minimum estimate of flux. In total, we collected data on transient boats over two years (2008–2009) from South Beach (1,208 records), Pillar Point (1,236 records) and Monterey Harbor (1,276 records); and for 2008 from Spud Point (884 records, marina staff were only able to provide one year of data).

Staff do not gather data on homeport or on previous or next port of call for a transient vessel at any of our study marinas. As a proxy for homeport, we determined the bay closest to the hometown of the registered boat owner. We excluded from our analysis cases where a boater’s hometown was approximately equidistant from separate bays or where a boat owner’s hometown was farther than 48 kilometers from a bay. For boaters with California home towns, we assigned likely home bay to 1,796 boater visits. We used these data to estimate the level of connectivity (= number of visits) between the visitors’ home bays and the destination marina (the source of the data).

Boater questionnaires

We used a questionnaire based on our previous work (Davidson et al. 2010, modified from Floerl and Inglis 2005) to gather additional data on travel and antifouling regimes. The questionnaire elicits information on vessel type, recent voyage history and hull husbandry. We sent 3,000 questionnaires to boaters renting slips in all six of our study marinas in February and March of 2009.

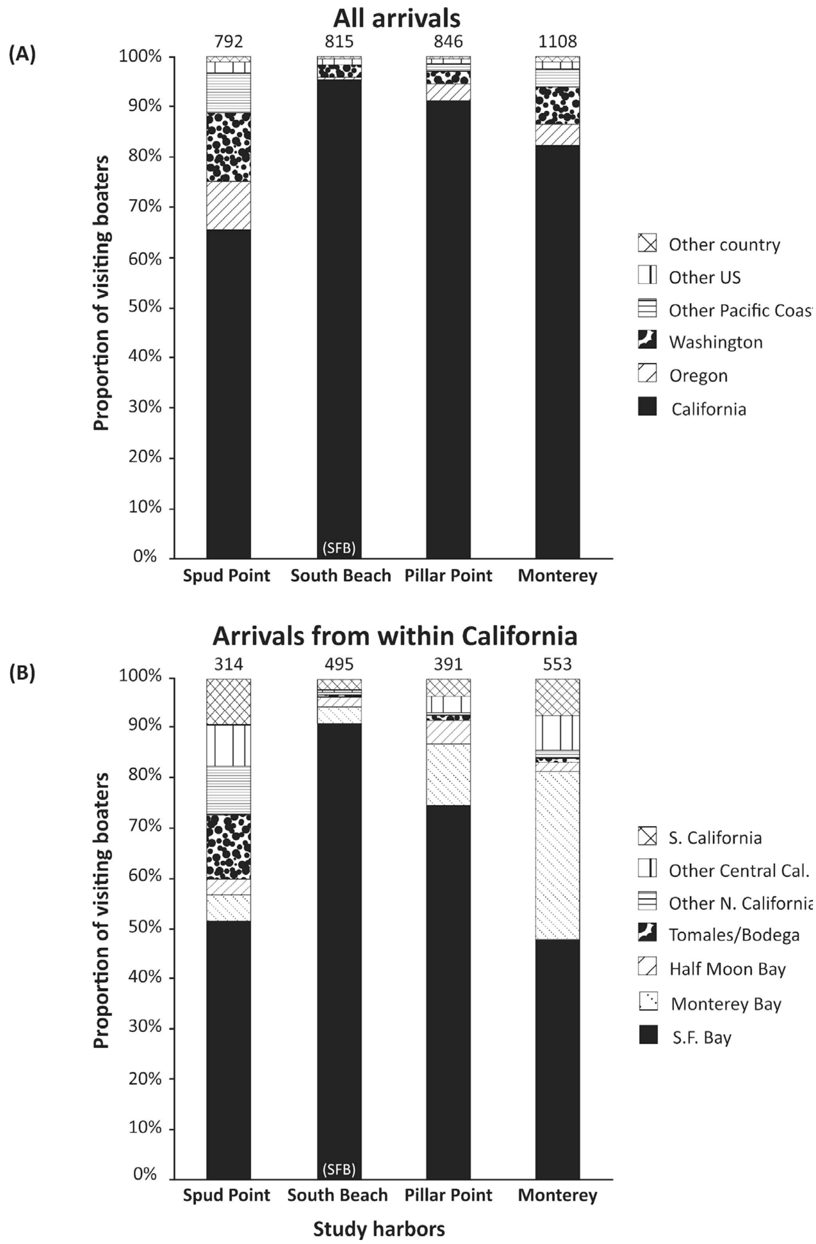

Figure 1. (A) Proportion of all visiting boaters by region for 2008–2009 (2008 only for Spud Point); **(B)** Proportion of visiting boaters from within California, by region or bay, in 2008–2009 (data from 2008 only for Spud Point).

Hull surveys: video analysis

Some respondents to questionnaires gave us permission to survey their boats using an underwater camera mounted on a pole (underwater pole-cam or UPC). The UPC is a video camera in a waterproof housing, attached to an extendable pole and connected via wiring to a battery box and monitor with a recording device. Across the study marinas, we used the UPC to sample 36 boats (Table 1) whose owners had indicated that they had stayed overnight outside of their home bay within the past 12 months (hereafter "active" boats). Twenty-six of the boats were recreational sail boats, four were recreational motor boats and six were commercial fishing vessels.

On each vessel, we took 16 8×12 cm photo-quadrats (still images) of hull surfaces. We stratified sampling by depth, taking eight photos haphazardly along a transect running from bow to stern just below the waterline and eight photos along a parallel transect at the bottom, as near to the keel line as possible. We downloaded photo-quadrats to a computer and generated percent cover data by projecting a grid of 100 points over each photograph and counting taxa under each point. We also used the UPC to record footage of the stern appendages (rudder, propeller, etc.) for comparison to hull transects. We did not determine percent cover on heterogeneous surfaces or appendages, but used this footage to make qualitative comparisons of taxonomic richness. In most cases, we could not resolve organisms in the photo-quadrats to species-level identifications. Instead, we calculated percent cover of coarse taxonomic groups (modified from Davidson et al. 2010). We used a least-squares regression to determine whether paint age (determined from boater questionnaires) was a good predictor of fouling extent.

From dockside, before photographing, we ranked the overall amount of fouling on each vessel using the level of fouling (LoF) ranking system developed by Floerl et al. (2005). The LoF ranks range from 0, which indicates no visible fouling, to 5, which indicates cover of macrofouling greater than 40%. Data generated from the videos (combining the two transects) were used to generate an underwater LoF rank based on percent cover estimates for comparison with the dockside LoF. We used a Pearson correlation to determine whether dockside and underwater LoF ranks were correlated.

Hull surveys: specimen collections

We used SCUBA to collect samples of biota from the undersides of boats at two marinas, one inside SFB (South Beach Harbor) and one on the outer coast (Monterey Harbor). We took samples from 14 active boats (Table 1), which included six of the vessels surveyed with video (above) as well as transient boats present on the days we carried out SCUBA surveys; we had detailed travel information from 10 of the 14 boats. Divers surveyed the full length of each vessel's hull and all "niche" areas (topographically complex areas such as propeller, rudder, keel and grates, which favor settlement by fouling species). In instances of relatively low biofouling cover, divers collected all organisms encountered. In instances of relatively high biofouling cover, divers collected examples of each morphologically distinct organism encountered. We vouchered specimens of each species and made identifications in the laboratory, with the help of taxonomic experts when necessary.

Results

Transient boat data

The overwhelming majority of transient boaters to each marina came from other harbors in California (Figure 1A), ranging from 65% to 95% of the totals. Nearly all of the out-of-state visitors were traveling along the coast from other US west coast states and British Columbia, Canada; overseas visitors accounted for less than <1% across all marinas. Boaters from Washington made up the second-largest proportion of visitors and Oregon boaters the third-largest proportion to Spud Point, South Beach, and Monterey. At Pillar Point, there were slightly more boaters from Oregon than from Washington. Visitors from outside the state made up larger proportions of transient boat traffic to Spud Point and Monterey Harbor than to Pillar Point and South Beach.

Of the California boaters visiting the study marinas, the majority came from the San Francisco Bay Area (Figure 1B). Most boaters (90%) visiting South Beach were from elsewhere in SFB. SFB boaters also contributed significantly to Pillar Point, Spud Point and Monterey transient boat visits (73%, 52% and 46%, respectively, Figure 1B). The outer coast bays were connected to one another as well, with visitors from all of these bays arriving at every study marina. Arrivals from Monterey Bay represented the second highest proportion of transient boaters at Pillar Point and Monterey Harbor (12% and 27% of visitors, respectively, Figure 1B). Visitors from Pillar Point and Spud Point made up small percentages of arrivals to the other marinas.

The relative flux of vessel transits reported from SFB to the three outer coast marinas and between the outer bays is more easily visualized in Figure 2, which shows the mean annual flux of vessels based on transient boat records kept by the outer coast marinas. It should be noted that the data indicate only the likely home bay of the boat owner, and do not include any stops that may have been made before a boat registered for an overnight berth at one of the outer coast study marinas. As we have transient boat data from only one SFB marina -- out of 85 in SFB -- mean annual traffic *into* SFB would be highly under-estimated and thus is not included in this figure.

Boater questionnaires

Three hundred eighty-five surveys were returned to us (a return rate of 12.8%) and an additional 20 surveys were carried out in person with

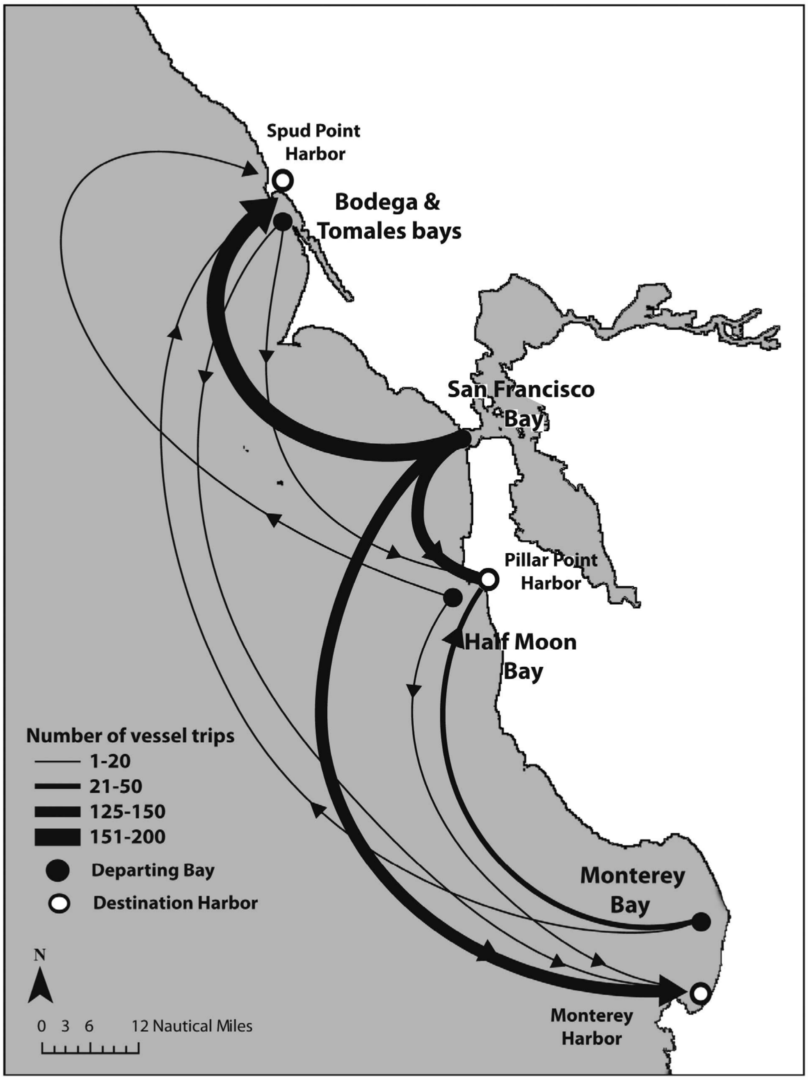

Figure 2. Arrivals of visiting boaters to the outer coast marinas from SFB and the outer coast bays as recorded in transient boat records. Arrivals were to specific marinas, but departures could only be determined at the level of bays (see Methods). Data were average annual visits for 2008–2009 for Monterey and Pillar Point, 2008 only for Spud Point. Thickness of lines corresponds to numbers of visits.

visiting boaters for a total of 405; 71% of the surveys were from owners of recreational sailboats and 29% from motorboat owners, which is fairly representative of the percentage of these boat types in our study marinas (Zabin et al. 2011). Eleven percent of respondents were owners of fishing vessels, but nearly all of these were from a single marina, Pillar Point.

Sixty-nine individuals (17%) reported travel outside of their home bay for overnight stays in the past year and provided some details of travel. We used these data to examine travel and antifouling regimes of these active boaters. As a group, these boaters reported 163 trips outside of their home bay in the past 12 months. On average, boaters made three trips per year (SE +/-0.41); however one recreational motorboat reported 36 trips and one fishing vessel reported 20. Boaters from marinas inside SFB made trips outside of their home bay slightly less frequently than those in the smaller outer coast bays (12% vs. 19%). Boaters from Spud Point had the highest proportion of active boats, with 33% of boaters reporting having traveled outside of Bodega Bay. Pillar Point boaters were second highest with 25% of boaters having made overnight stays outside of Half Moon Bay. Within SFB, Clipper Yacht Harbor was the most active, with 19% of boaters reporting trips outside the bay, and San Francisco Marina the least with only 8% active boaters. Monterey Harbor and South Beach had similar proportions, at 12% and 13% respectively.

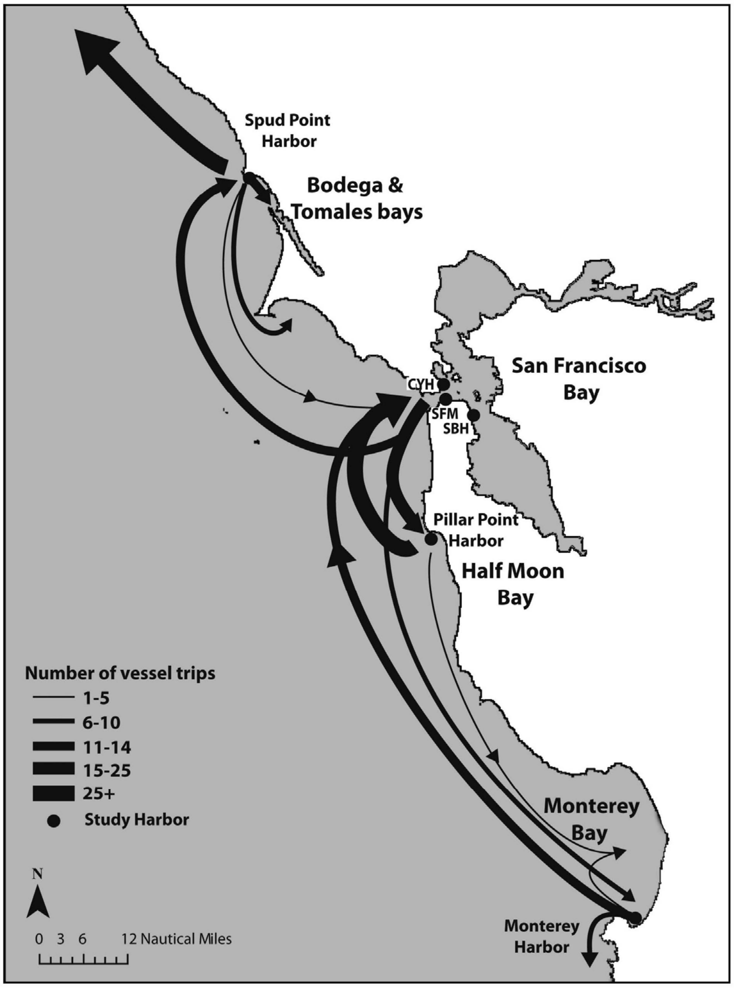

Figure 3. Connections between the six study marinas and points north and south in terms of number of trips as reported by boaters answering questionnaires. Boaters were asked to report trips made over the previous year. Thickness of lines corresponds to numbers of trips. Marinas in SFB abbreviated: CYH = Clipper Yacht Harbor; SFM = San Francisco Marina; SBH = South Beach Harbor.

In terms of travel destinations, the boater questionnaire data were largely congruent with the transient boat data collected at the study marinas, indicating strong linkages between SFB and Half Moon Bay (Pillar Point), and SFB and Monterey Bay (Figure 3). Half Moon Bay (Pillar Point) was the top overnight destination for SFB boaters, with Tomales/Bodega Bay and Monterey Bay second and third, respectively. SFB was the top destination for boaters from both Pillar Point and Monterey. The remainder of the Monterey Harbor respondents tended to travel south along the Central Coast and into Southern California. Pillar Point boaters also reported travels to Monterey Bay. Boaters from Spud Point (Bodega Bay) mostly traveled north to destinations along the California coast; nearby Tomales Bay and Drakes Bay ranked second and third, and boaters reported five visits to SFB.

All boaters except one who stored his boat out of water reported using antifouling paint. Mean paint age was 15 months (+/-1.1 SE). Thirty-six boats (52%) reported having cleaned at least once since the last application of antifouling paint, nearly all with a diver in-water, six (9%) had not cleaned and 27 (39%) did not answer this question. On average, it had been three months since the most recent cleaning (+/-0.3 SE). There was no correlation between fouling cover and paint age (R^2=0.6, p=0.12) however there were only 25 boats for which we had both video footage and information on antifouling paint.

Hull surveys: video analysis

The cover of fouling on the hulls of active boats varied widely (Figure 4). Two boats were completely clean and five were fouled only with

Table 2. Taxa collected from 14 active boats surveyed by SCUBA.

Boat number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total boats
Taxa															
*Bugula neritina**			x		x	x		x	x	x					6
Bugula californica										x					1
Bugula pacifica						x		x					x		3
*Bugula stolonifera**					x										1
Watersipora cf. *subtorquata**	x	x			x		x			x					5
Celleporaria brunnea	x	x			x										3
Tricelleria occidentalis									x	x	x				3
Obelia sp.													x		1
Bowerbankia sp.						x							x		2
Styela montereyensis						x									1
Molgula sp.						x									1
*Botrylloides violaceus**					x										1
*Botryllus schlosseri**						x							x		2
Diplosoma sp.			x		x										2
cf. *Euphysora*	x														1
Mytilus			x	x											2
Oyster (cf. *Pododesmus*)				x											1
*Ficopomatus enigmaticus**					x										1
Spirorbids			x												1
Sabellids		x													1
Other polychaetes					x										1
Balanus crenatus			x	x	x	x		x	x	x	x			x	9
Caprella sp.			x						x						1
*Caprella mutica**			x	x	x					x	x		x		6
Caprella californica				x	x		x								3
Gammarids	x	x	x	x			x		x	x					7
Algae												x			1
Total taxa	4	4	8	6	11	7	3	3	5	7	3	1	5	1	

*nonindigenous species

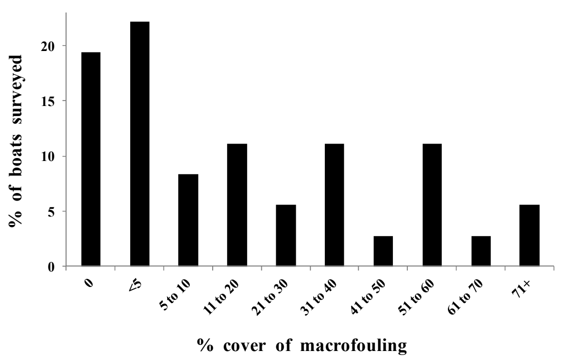

Figure 4. Macrofouling on boat hulls, calculated from the transect surveys made with the UPC. Bars represent the percentage of boats in each cover category.

a layer of biofilm; the remainder (29) had macrofouling cover ranging from <1% to 79.4% (mean 21.4%, +/-SE 4.0). Half of the boats surveyed with the UPC had less than 10% cover of macrofouling on their hulls, but 23% had fouling cover greater than 40%. On a per-boat basis, two taxa on average were recorded from hulls (+/-0.2 SE). Slightly more were carried on appendages (mean =2.8 taxa, +/-0.3 SE). Nearly all of the boats that had no macrofouling on hulls had some macrofouling on stern appendages (6 of 7).

Across all boats, we counted 16 taxa, five of which were found only on stern appendages (sponges, colonial diatoms, mussels, red coralline algae and foliose red algae). Eleven taxa were found on hulls. Most boats had amphipod tubes and biofilm (89% and 86%, respectively). Caprellids, filamentous green algae and foliose green algae were found on roughly 1/3 of boats,

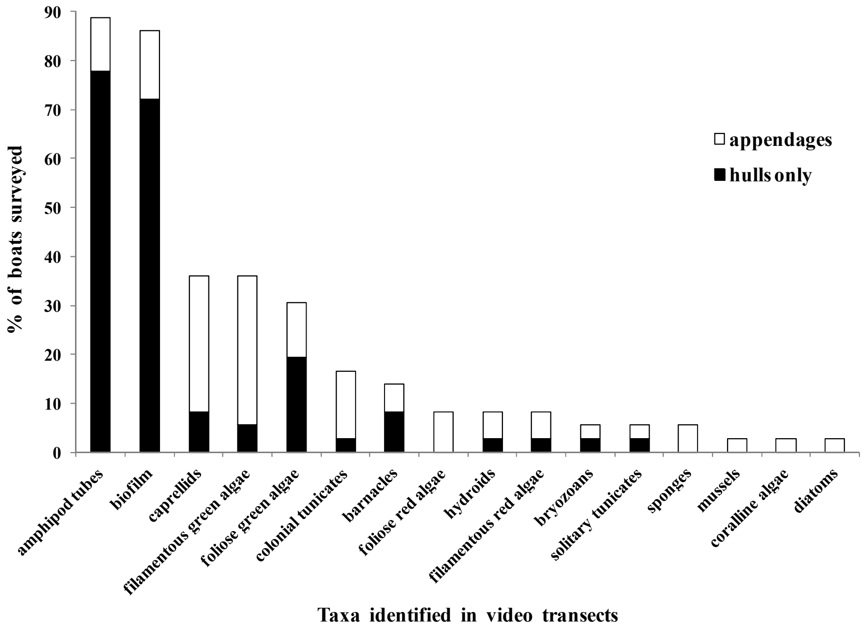

Figure 5. Taxonomic groups identified from boat hulls and appendages (i.e., keels, propellers, rudders, etc.), based on video surveys. Bars represent the percentage of boats on which each taxonomic group was found.

Table 3. Hull maintenance, travel information, and fouling on active boats surveyed using SCUBA.

Boat #	Marina	Status	Recent travel	# of taxa	Paint age (mos)	Last cleaned	LoF[a] rank
1	MH[b]	Resident	SFB[c]	4	6	N/A	2
2	MH	Resident	Capitola, Santa Cruz, (MB[d])	4	8	N/A	2
3	MH	Visitor	HI to SF to Monterey, next Mexico	8	36	1 week	3
4	MH	Visitor	From SFB	6	N/A	N/A	2
5	MH	Visitor	N/A	11	N/A	N/A	4
6	MH	Visitor	From SFB	7	6	N/A	3
7	MH	Visitor	N/A	3	N/A	1 day	2
8	SB[e]	Resident	To Santa Cruz, MB	3	14	N/A	2
9	SB	Resident	To Half Moon Bay	5	N/A	N/A	2
10	SB	Resident	To Half Moon Bay	7	21	2 mo	3
11	SB	Resident	Two locations outside SFB, no further info	3	5	3 mo	1
12	SB	Visitor	From Stockton, CA	1	24	Never	3
13	SB	Visitor	From Trinidad, CA: stops in SFB, Drakes Bay, MB	5	12	Never	4
14	SB	Visitor	N/A	1	N/A	N/A	2

[a]LoF: Level of fouling rank, assessed dockside: 0 = clean to 5 = >40% cover; [b]MH: Monterey Harbor; [c]SFB: San Francisco Bay;[d]MB: Monterey Bay;[e]SB: South Beach Marina, in SFB

and colonial tunicates and barnacles on 17% and 14% of boats, respectively (Figure 5).

Dockside LoF rankings and observed fouling ranks based on the video analysis were correlated, but boats were ranked the same by both methods only slightly better than half of the time (Pearson's correlation =0.556, p=0.001).

Hull surveys: specimen collections

Twenty-seven different taxa were identified from the 14 active vessels sampled using SCUBA. Bryozoans, tunicates, polychaetes and arthropods were the richest taxonomic groups on these vessels. We were able to identify 13 organisms to species level (Table 2). Seven of these are not native to Central California: the bryozoans *Bugula neritina* (a species complex), *Bugula stolonifera,* and *Watersipora subtorquata,* the tunicates *Botrylloides violaceus* and *Botryllus schlosseri*, the reef-building tube worm *Ficopomatus enigmaticus*, and the caprellid amphipod *Caprella mutica.* The native barnacle *Balanus crenatus* and gammarid amphipods were the most- and second-most commonly encountered taxa, found on nine and seven of the sampled boats, respectively. *Caprella mutica* and *B. neritina* were found on six of the vessels. *Watersipora subtorquata* was also common, found on five of the boats.

Overall fouling on boats was low whereby seven boats had an underwater LoF rank of 2 (1–5% cover of macrofouling) and one ranked 1 (biofilm only). Nonetheless, up to 11 taxa (mean 4.9, +/- SE 0.74) were detected on these vessels (Tables 2, 3). Although the two boats with the oldest anti-fouling paint had the highest species richness (eight taxa found on one vessel with 36-month-old paint and seven on another with 21-month-old paint, Table 4), the number of taxa varied greatly on boats with newer and intermediate paint ages (ranging from 5 to 14 months).

Of the 10 boats surveyed for which we also had detailed travel information, all but two had reported making only short trips within Central California, traveling between SFB and Half Moon Bay and/or Monterey Bay (Table 3). The exceptions were: boat no. 13, which had traveled from Trinidad in Northern California with stops in SFB and Monterey, with five taxa attached to the hull; and boat no. 3 on which we recorded seven taxa and which had arrived in Monterey after traveling from Hawaii with a stop in San Francisco and was heading to Mexico. Two NIS were detected on each of these boats (*Botryllus schlosseri* and *Caprella mutica* on boat no. 13, and *Bugula neritina* and *C. mutica* on boat no. 3).

Discussion

Movement of boats and species between SF Bay and adjacent bays

This study demonstrated a strong degree of connectivity between SFB and the three nearby coastal bays in terms of small boat traffic. Boaters from SFB dominated the arrivals at all of the study marinas for which we had transient boat data, which is not surprising, given the high number of boats with homeports in SFB. All three outer coast bays were also connected to one another via transient boats, according to marina records, and boaters from the outer bays visited the one SFB marina for which we had transient boat data. Data from boater questionnaires, although a smaller sample size (69 active boaters vs. thousands of arrival records), were largely consistent with these findings. Boaters from SFB marinas indicated that the coastal bays were their top three destinations for travel outside of SFB, and boaters from Monterey and Pillar Point harbors indicated that SFB was their top destination for trips outside of their home bays. Pillar Point boaters also reported travel to Monterey. Questionnaire data also highlighted the links between Spud Point and points north and between Monterey and Southern California.

In addition to demonstrating the connectivity provided by boat movements among bays, this study indicated through video and SCUBA surveys that fouling species were present on boats that traveled between bays. Our video surveys of 36 active boats found that while most had relatively low amounts of macrofouling, others were moderately to heavily fouled, and even among those with little to no fouling on hulls, many had organisms present on “niche” areas such as keels and rudders. As a result, 81% of these boats carried some degree of macrofouling. Despite our focus on active boats, our findings were similar to those of Davidson et al. (2010) who found macrofouling on 80% of boats at berth in SFB, most of which (77%) did not travel outside of SFB. Recent studies from Alaska (Ashton et al. 2014) and British Columbia (Clarke Murray et al. 2011) found far fewer fouled active boats (62% and 65%, respectively). The current study and Davidson et al. (2010) also found greater frequencies of boats in the higher LoF categories compared with studies in New Zealand (Floerl et al. 2005) and Scotland (Ashton et al. 2006).

Our SCUBA surveys of 14 active and transient boats found 27 distinct taxa, including at least seven NIS. While this limited survey of vessels highlights the capacity for species transfers, a larger sample size and greater taxonomic analysis of collected specimens would certainly increase overall species (and NIS) richness. Taken together with the volume of visits, small vessels such as these traveling between SFB and nearby coastal marinas have likely provided considerable opportunity for the transfer and introduction of numerous NIS among bays during the two-year study period, and certainly when scaled to longer timescales of vessel movements in the region.

The level of connectivity we have documented between SFB and its neighboring bays is certainly an underestimate. Between 600 and 800 visiting boats stayed overnight annually at each of the four marinas from which we were able to obtain data; with each recorded visit representing at least two opportunities to move species: on the outgoing and return trips. Given that there are three other marinas and a mooring area in Monterey Bay, a yacht club with guest berths in Half Moon Bay, two additional marinas in Bodega Bay, and more than 85 marinas in SFB, thousands of trips are likely made between marinas in the greater SFB region each year. We note here that although we are aware that the fishing fleet in Monterey travels to Southern California yearly, this was not reflected in the few questionnaires returned to us by owners of fishing vessels there, leading to an underestimate of the connectivity between Monterey and the southern portion of the state. This underscores the need to interpret data carefully and to attempt to gather information using several different approaches, such as a combination of boater questionnaires, commercial fishing data, and visiting boat information gathered by marinas.

All of the NIS identified by us from active boats at Monterey and South Beach marinas are already known from SFB and Monterey Bay (Fofonoff et al. 2010). Many are limited-dispersal species that have become widespread, such as *Caprella mutica* and the colonial tunicates, *Botrylloides violaceus* and *Botryllus schlosseri*, all of which may have initially come to North America in association with oyster culturing or on boat hulls (Fofonoff et al. 2010); the small boat vector may be particularly important to the secondary spread of such organisms. The potential impacts of *C. mutica* on native species in North America is unknown, but they are potentially significant given the caprellid's ability to achive high abundances and competitively displace congenors elsewhere (Ashton 2006; Shucksmith 2007). Botryllid tunicates can also attain high abundances on cultured shellfish, and thus are of economic consequence to the aquaculture industry (reviewed in Arens et al. 2011).

Other species found on the sampled boats are not yet known from all of the destinations to which boaters reported regular travel. An example of the latter, the tubeworm *Ficopomatus enigmaticus,* first reported from SFB, is known from only three other locations on the west coast of North America (Monterey Bay, Los Angeles-Long Beach Harbor, and San Diego Bay, Fofonoff et al. 2011). *Ficopomatus enigmaticus* can act as an ecosystem engineer, creating novel, large, three-dimensional structures in soft-sediment bays and estuaries. It has been shown to facilitate a suite of invertebrates (primarily NIS) that differ from those associated with another provider of hard three-dimensional structure, the native oyster *Ostrea lurida* (Heiman et al. 2008). Given the strong boating connections, we predict the tubeworm's eventual appearance in Half Moon Bay and Bodega Bay (if not already present).

Nearly all of the nonindigenous marine species reported from Bodega Bay (41 of 45) are also found in SFB. Half Moon Bay shares 8 of its 9 NIS with SFB, and Monterey Bay shares 71 of 77 with SFB (data for this comparison from NEMESIS, Fofonoff et al. 2011). Some of these similarities are due to other factors, such as similar habitat types and the shared history of aquaculture between bays (except for Half Moon Bay, which has higher wave exposure and no estuarine component), as discussed by Wasson et al. (2001). However, connections via boating traffic such as those demonstrated by this study have undoubtedly played a role in the spread of species among bays, particulary that of more recent invaders, as aquaculture has not been been practiced in SFB or Monterey Bay for nearly 30 years (Grosholz et al. 2012).

The Asian kelp *Undaria pinnatifida* is an example of a relatively new invader in the SFB area that is linked to recreational boat traffic. We did not find this kelp on the active boats sampled in this study, but we have previously noted its presence on boats at four of our six study marinas, Monterey, Pillar Point, San Francisco Marina and South Beach (Zabin et al. 2009), and have found it on boats moving between SFB marinas (CJZ personal observations) and on a transient boat in San Diego, where it is not yet established (Ashton et al. 2012). This high-profile invader is an example of a species with well-documented negative impacts worldwide (e.g., Curiel et al. 2001; ICES 2001; Casas et al. 2004; Farrell and Fletcher 2006; Raffo et al. 2009) that is clearly spreading along the west coast of North America through small-vessel traffic. It was first reported on this coast in 2000 from Los Angeles-Long Beach Harbor, several nearby small-craft harbors, and a kelp forest under a mooring used by recreational sailboats at Catalina Island (Silva et al. 2002). By 2001, it had been reported from Monterey Harbor (Silva et al. 2002) and in 2003 from the Todos Santos Islands in Baja California, Mexico (Aguilar-Rosas et al. 2004);

in 2009 it had reached Pillar Point (Half Moon Bay) and San Francisco Bay (Zabin et al. 2009).

While our study has focused on the connectivity among bays in central California, and on SFB as an important hub, the example of *U. pinnatifida* also illustrates the connectivity that exists with other bays within and outside California. The direct linkage to these regions is shown in Figures 1A and 3, when considering home ports of transient vessels, but these estimates do not capture longer transit histories (and ports of call) for arriving vessels or reflect all the voyage histories for small boats resident at the study marinas. Clearly, there is a broader network of connectivity that exists for small vessels on coastwise routes that is not yet characterized in our analysis, with relevance to the potential spread of NIS.

Data gaps for California

Major data gaps prevent a full assessment of the risk posed by the small-boat vector for the state of California. At this time, we do not have a complete picture of the degree to which various ports and marinas are connected, nor the full volume of boater traffic. Caution needs to be exercised in attempting to scale up from this study based on data such as numbers of guest berths or number of registered boats in the state. Data from this study and Davidson et al. 2010 indicate that only a small percentage of SFB boaters travel outside their home bays; more overnight stays were made at other marinas within SFB. This is perhaps less likely to be true in smaller bays, indeed Pillar Point (Half Moon Bay) and Spud Point (Bodega Bay) boaters reported more trips away from home than those in the larger San Francisco and Monterey bays. Greater movement among bays can be expected in the warmer climate of Southern California, which is also highly populated, than in Central or Northern California, where sailing conditions can be rough and distances between coastal marinas becomes greater.

Additionally, our current study and previous work (Davidson et al. 2010; Zabin et al. 2011) have focused largely on recreational boats. Owners of fishing vessels made up only 11% of survey respondents in the current study, only six allowed us to photograph their boats with the UPC, and none allowed SCUBA surveys. For the current study, which focuses on small boats as a group, we did not distinguish between recreational and fishing vessels in our analyses of fouling and travel patterns. Separate studies of the fishing fleet are warranted. Travel patterns are likely to be different, as they are motivated by fishing seasons and other business considerations, and it is not clear whether fouling extent is similar to that on recreational vessels (Davidson et al. 2012). Elsewhere, the fishing fleet has been found to present a higher risk than recreational vessels for the spread of NIS (Kinloch et al. 2003).

Also poorly characterized for our study region is the extent of fouling and travel patterns of vessels arriving from overseas, which can transport species across ocean basins. While these made up a small percentage of the transient traffic to our study marinas, and represent less than 1% of foreign flagged boaters entering the state (Ashton et al. 2012) they may represent an important vector of new (initial) introductions as well as secondary spread, as reported elsewhere in the world (Floerl 2002; Floerl et al. 2005; Minchin et al. 2006). Data on numbers of such vessels entering the US are kept by Customs and Border Protection, but only indicate ports of departure (the last foreign port of call) and port of arrival (port where boats registered with Customs) rather than the full itinerary of stops a boat might make along a coast.

Other assessments of the small-boat vector

Two recent studies (Ashton et al. 2014; Clarke Murray et al. 2011) contribute further to our understanding of boat activity and biota associated with small boats on the west coast of North America. These studies found that small boats made hundreds of trips annually outside of their home bays and carried NIS, thus providing a mechanism for intra-regional spread. In Ketchikan, Alaska, nearly 700 non-resident small-craft (fishing and recreational) arrivals were reported in 2009 (Ashton et al. 2014). Of the 50 recreational boats sampled by Ashton et al. (2014) within 24 hours of arrival in Ketchikan, 38% were found to have no macrofouling. Macrofouling on the remainder of vessels (62%) ranged widely, with 14% of boats carrying tens (or fewer) individuals, but 16% carrying thousands. Ashton et al. (2014) documented at least 55 taxa on the vessels, including several NIS not yet established in the state.

In British Columbia, Canada, a survey of 616 boaters indicated that most were active: 83% reported mooring outside of their home marina, traveling on average to eight distinct destinations in a year, and nearly 21% had traveled between the US and BC (Clarke Murray et al. 2011). Of surveyed boats, 65% had macrofouling, and although overall fouling cover was low (mean = 6%), 25% of boats carried NIS. Clarke Murray et al. (2011) surveyed for species on a list of 12 NIS known from BC waters, rather than carrying out surveys of all taxa. They recorded 9 from their list, and many of these were found on boats that were active travelers.

Dozens of studies from around the world have documented the presence of fouling species on small boats kept in saltwater (e.g. Floerl 2002; Godwin et al. 2004; Floerl and Inglis 2005; Ashton et al. 2006; Savini et al. 2006; Neves et al. 2007; Mineur et al. 2008; Leonard 2009). However, because data on small-boat travel are generally lacking, few have attempted to quantify patterns of connectivity (exceptions include Floerl et al. 2009). Nonetheless, sufficient data exist to support a role of small vessels in NIS spread for some species. We suggest that busy commercial shipping ports in North America and elsewhere around the world likely play a similar role to that of SFB, serving as source of NIS populations that are spread along coasts to harbors and marinas via small vessels (Floerl et al. 2009). There is considerable variation among and within continental margins in the magnitude of flux, distances, seasonality, and hull husbandry (including antifouling treatment, haul out, and cleaning) that can affect the diversity and quantity of associated biota moving within any region. Although current data underscore a role of small vessels in NIS spread, further data on traffic patterns and associated biota are needed to estimate the full scale of biota moved by these boats. Ideally, such measures would be compared to flux by other vectors and used to evaluate the risk (likelihood) of establishment (Williams et al. 2013).

Management of the small-boat vector

While management efforts to reduce biotic transfers by commercial ships can decrease new invasions at commercial hubs, it is evident that other vectors contribute to (and may even dominate) secondary spread. Thus, even if completely effective, vector management for commercial ships will not stop the continuing secondary spread and human-aided range expansion for many species.

Management of recreational and regional fishing boats themselves poses a significant challenge. Owners of these smaller boats are more numerous and widely distributed than owners of commercial vessels. In terms of hull-maintenance and travel patterns, they are motivated by a wider variety of factors that are more difficult to predict than those for commercial operators, and they are not regulated by a single authority. The IMO (2012) has issued guidelines for the prevention of species transfers via biofouling on small vessels, but we know of only two countries, Australia and New Zealand, that currently enforce any such regulations on small vessels arriving from foreign ports (DAFF 2011; MAFBNZ 2010). In both countries vessels must present documentation of their antifouling programs ahead of arrival, may be required to undergo visual inspections, and are expected to arrive with little to no fouling. The adoption of a similar practice in the US could be implemented to reduce primary introductions from overseas vessels.

New Zealand is also promoting a "clean before you go" ethic to boaters preparing to travel between ports within New Zealand (http://www.biosecurity.govt.nz/files/pests/salt-freshwater/boaties-guide-to-marine-biosecurity.pdf), but as far as we are able to determine, with the exception of regulations on the movement of targeted species such as zebra mussels on boats traveling over land between freshwater bodies, no jurisdiction has attempted to regulate fouling on small vessels travelling locally.

We know of only one study that has assessed the potential management options for both foreign and local recreational vessels for a region, a study of recreational boats in Nelson Harbor, New Zealand (Piola and Forrest 2009). The report recommended a combination of approaches such as a required antifouling regime that includes application of antifouling paint every 12 months, regular inspections at surface and in water, and the provision of adequate local facilities for cleaning vessels.

Previous studies have found paint age to be correlated with extent of hull fouling (Floerl and Inglis 2005; Ashton et al. 2012; Clarke Murray et al. 2013), although this isn't always the case (Ashton et al. 2014; Davidson et al. 2010). In the current study, the lack of a clear relationship between paint age and extent of fouling may be due to a small sample size, or it may be that multiple factors are important in fouling extent (i.e. Floerl and Inglis 2003), obscuring the effect of antifouling paint on our sample vessels. The effectiveness of dockside inspections of boat hulls has been investigated in several locations, with mixed results. In New Zealand, Floerl et al. (2005) sampled 189 boats and found that dockside rankings reliably distinguished fouled from non-fouled boats, and Davidson et al. (2010) found good correlation between dockside and underwater rankings (R^2=0.742, p<0.001), but Clarke Murray et al. (2013) in a survey of 430 boats in British Columbia found that dockside LoFs had a low level of accuracy in terms of distinguishing fouled and non-fouled boats, and generally did not match underwater rankings. While our sample size is small, an earlier, larger study across our six study marinas, which compared video and dockside LoF rankings for 122 boats (Zabin et al. 2011) supports the findings of the present study. Zabin et al. (2011) found the while dockside LoF rankings were not good predictors of underwater LoF (R^2=0.50, p<0.0005), they were reliable in accurately identifying clean vessels (ranks 0 and 1).

Given the lack of proven models for management of the local small boat vector, which makes up the bulk of the traffic in California (Ashton et al. 2012), we believe that the state could benefit from a coordinated, scientific approach to risk assessment and management. To advance our understanding of the vector, we recommend the creation of a centralized resource to collect data concerning recreational and fishing vessel habits, travel, and associated biota. This would help to close data gaps, advance our understanding of the broader network of small boat connections along the coast, and inform risk assessment and management. The development and implementation of a management strategy for small boats in California would also be improved by the designation of a single agency with the authority and funding to do so; authority for vessels is currently divided across multiple agencies, and no funding has been designated for the small-boat vector (Ashton et al. 2012). Among the first activities of such an agency should be an evaluation of available management options, including the costs and benefits of these within the context of California's jurisdictions. A logical first step would be an analysis by social scientists to consider opportunities and potential strategies to advance voluntary guidelines and boater-education campaigns aimed at promoting a clean-boat ethic. Any adopted management strategies also need to be evaluated for efficacy, and should take an adaptive management approach. Efforts to detect and understand the impacts of NIS, particularly at locations deemed to be high risk, also need to be sustained to better guide future management resource decisions.

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References

Aguilar-Rosas R, Aguilar-Rosas LE, Avila-Serrano G, Marcos-Ramirez R (2004) First record of *Undaria pinnatifida* (Harvey) Suringar (Laminariales, Phaeophyta) on the Pacific Coast of Mexico. *Botanica Marina* 47: 255–258, http://dx.doi.org/10.1515/BOT.2004.028

Arens CJ, Paetzold SC, Ramsay A, Davidson J (2011) Pressurized seawater as an antifouling treatment against the colonial tunicates *Botrylloides violaceus* and *Botryllus schlosseri* in mussel aquaculture. *Aquatic Invasions* 6: 465–476, http://dx.doi.org/10.3391/ai.2011.6.4.12

Ashton GV (2006) Distribution and dispersal of the non-native caprellid amphipod, *Caprella mutica* Schurin, 1935. PhD thesis, University of Aberdeen, Scotland, 180 pp

Ashton GV, Boos K, Shucksmith R, Cook E (2006) Risk assessment of hull fouling as a vector for marine non-natives in Scotland. *Aquatic Invasions* 1: 214–218, http://dx.doi.org/10.3391/ai.2006.1.4.4

Ashton G, Davidson I, Ruiz GM (2014) Transient small boats as a long-distance coastal vector for dispersal of biofouling organisms. Estuaries and Coasts published online 08 March 2014, http://dx.doi.org/10.1007/s12237-014-9782-9

Ashton GV, Zabin CJ, Davidson I, Ruiz GM (2012) Aquatic Invasive Species Vector Assessments: Recreational vessels as vectors for non-native marine species in California. Ocean Sciences Trust, 58 pp

California Department of Boating and Waterways (2002) Boating Facilities Needs Assessment: Volume 2, Regional boaters and boating facilities, 132 pp

Carlton JT (1999) The scale and ecological consequences of biological invasions in the world's oceans. In: Sandlund OT, Schei JJ, Viken Å (eds), Invasive species and biodiversity management. Kluwer Academic, Dordrecht, Netherlands, pp 195–212, http://dx.doi.org/10.1007/978-94-011-4523-7_13

Casas G, Scrosati R, Piriz ML (2004) The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). *Biological Invasions* 6: 411–416, http://dx.doi.org/10.1023/B:BINV.0000041555.29305.41

Clarke Murray C, Pakhomov EA, Therriault TW (2011) Recreational boating: a largely unregulated vector transporting marine invasive species. *Diversity and Distributions* 17: 1161–1172, http://dx.doi.org/10.1111/j.1472-4642.2011.00798.x

Clarke Murray C, Therriault TW, Pakhomov EA (2013) What lies beneath? An evaluation of rapid assessment tools for management of hull fouling. *Environmental Management* 52: 374–384, http://dx.doi.org/10.1007/s00267-013-0085-x

Cohen AN, Carlton JT (1995) Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. NTIS Report Number

PB96-1666525. United States Fish and Wildlife Service, and the National Sea Grant College Program, Connecticut Sea Grant, 246 pp

Cook DC, Thomas MB, Cunningham SA, Anderson DL, Barro PJ (2007) Predicting the economic impact of an invasive species on an ecosystem service. *Ecological Applications* 17: 1832–1840, http://dx.doi.org/10.1890/06-1632.1

Curiel D, Guidetti P, Bellemo G, Scattolin M, Marzocchi M (2001) The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the Lagoon of Venice. *Hydrobiologia* 477: 209–219, http://dx.doi.org/10.1023/A:102 1094008569

DAFF (Department of Agriculture, Fisheries and Forestry) (2011) Proposed Australian Biofouling Management Strategies Factsheet for Recreational Vessels. Prepared by the Australian Government, Department of Agriculture, Fisheries and Forestry. http://www.daff.gov.au/animal-plant-health/pests-diseases-weeds/marine-pests/biofouling/recreational-vessels (Accessed Feb 2014)

Davidson I, Ashton G, Zabin C, Ruiz G (2012) Aquatic invasive species risk assessments: the role of fishing vessels as vectors for marine and estuarine species in California. Ocean Sciences Trust, 57 pp

Davidson IC, Zabin CJ, Chang AL, Brown CW, Sytsma MD, Ruiz GM (2010) Recreational boats as potential vectors of marine organisms at an invasion hotspot. *Aquatic Biology* 11: 179–191, http://dx.doi.org/10.3354/ab00302

Davidson IC, Simkanin C (2012) The biology of ballast water 25 years later. *Biological Invasions* 14: 9–13, http://dx.doi.org/10.1007/s10530-011-0056-1

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution and Systematics* 41: 59–80, http://dx.doi.org/10.1146/annurev-ecolsys-102209-144650

Farrell P, Fletcher RL (2006) An investigation of the introduced brown alga *Undaria pinnatifida* (Harvey) and its competition with some species on the man-made structures of Torquay Marina (Devon, UK). *Journal of Experimental Marine Biology and Ecology* 334: 236–243, http://dx.doi.org/10.1016/j.jembe.2006.02.006

Floerl O (2002) Intracoastal spread of fouling organisms by recreational vessels. PhD thesis, James Cook University, Townsville, Australia, 287 pp

Floerl O, Inglis GJ (2003) Boat harbour design can exacerbate hull fouling. *Austral Ecology* 28: 116–127, http://dx.doi.org/10.1046/j.1442-9993.2003.01254.x

Floerl O, Inglis GJ (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biological Invasions* 7: 589–606, http://dx.doi.org/10.1007/s10530-004-0952-8

Floerl O, Inglis GJ, Dey K, Smith A (2009) The importance of transport hubs in stepping-stone invasions. *Journal of Applied Ecology* 46: 37–45, http://dx.doi.org/10.1111/j.1365-2664.2008.01540.x

Floerl O, Inglis GJ, Hayden BJ (2005) A risk-based predictive tool to prevent accidental introductions of nonindigenous marine species. *Environmental Management* 35: 765–788, http://dx.doi.org/10.1007/s00267-004-0193-8

Fofonoff PW, Ruiz GM, Steves B, Carlton JT (2011) National Exotic Marine and Estuarine Species Information System, http://invasions.si.edu/nemesis/index.html (Accessed March 2011)

Grosholz ED, Crafton RE, Fontana RE, Pasari J, Williams S, Zabin C (2012) An analysis of aquaculture as a vector for introduced marine and estuarine species in California. Ocean Sciences Trust, 77 pp

Godwin LS, Eldredge LG, Gaut K (2004) The assessment of hull fouling as a mechanism for the introduction and dispersal of marine alien species in the main Hawaiian Islands. Bishop Museum Technical Report No. 28, Honolulu, 122 pp

Heiman KW, Vidargas N, Micheli F (2008) Non-native habitat as home for non-native species: comparison of communities associated with invasive tubeworm and native oyster reef. *Aquatic Biology* 2: 47–56, http://dx.doi.org/10.3354/ab00034

ICES (International Council for the Exploration of the Sea) (2001) Report of the Working Group on Introductions and Transfers of Marine Organisms, International Council for the Exploration of the Sea, Barcelona, Spain, 11 pp

IMO (International Maritime Organization) (2011) Resolution MEPC.207(62), adopted 15 July 2011. 2011 Guidelines for the Control and Management of Ships' Biofouling to Minimize the Transfer of Invasive Aquatic Species. London, 25 pp

IMO (International Maritime Organization) (2012) MEPC 64/23 (paragraph 11.8), approved Oct 2012. Guidance for Minimizing the Transfer of Invasive Aquatic Species as Biofouling (Hull Fouling) for Recreational Craft. London, 7 pp

Kinloch M, Summerson R, Curran D (2003) Domestic vessel movements and the spread of marine pests: risks and management approaches. Report to the Department of Agriculture, Fisheries and Industry, Canberra, 168 pp

Leonard J (2009) Hull fouling surveys of recreational boats in Hawaii. Division of Aquatic Resources, Honolulu, 32 pp

Leung B, Lodge, DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London B* 269: 2407–2413, http://dx.doi.org/10.1098/rspb.2002.2179

MAFBNZ (Ministry of Agriculture and Forestry, Biosecurity New Zealand) (2010) Requirements for Vessels Arriving in New Zealand; A MAF Biosecurity New Zealand (MAFBNZ) Standard prepared by the Biosecurity Standards Group, 17 pp

Minchin D, Floerl O, Savini D, Occhipinti-Ambrogi A (2006) Small craft and the spread of exotic species. In: Davenport J, Davenport JL (eds), The ecology of transportation: managing mobility for the environment. Springer, Dordrecht, pp 99–118, http://dx.doi.org/10.1007/1-4020-4504-2_6

Mineur F, Johnson MP, Maggs CA (2008) Macroalgal introductions by hull fouling on recreational vessels: Seaweeds and sailors. *Environmental Management* 42: 667–676, http://dx.doi.org/10.1007/s00267-008-9185-4

Neves CS, Rocha RM, Bettini-Pitombo F, Roper JJ (2007) Use of artificial substrata by introduced and cryptogenic marine species in Paranagua Bay, southern Brazil. *Biofouling* 23: 319–330, http://dx.doi.org/10.1080/08927010701399174

Oregon State Marine Board (2008) Boating in Oregon: Triennial survey results, 118 pp

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19, http://dx.doi.org/10.1023/A:1010034312781

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288, http://dx.doi.org/10.1016/j.ecolecon.2004.10.002

Piola R, Forrest B (2009) Options for Managing Biosecurity Risks from Recreational Vessel Hubs. Prepared for Nelson City Council. Cawthron Report No. 1591, 45 pp

Raffo MP, Eyras MC, Iribarne OO (2009) The invasion of *Undaria pinnatifida* to a *Macrocystis pyrifera* kelp in Patagonia (Argentina, south-west Atlantic). *Journal of the Marine Biological Associations of the UK* 89: 1571–1580, http://dx.doi.org/10.1017/S002531540900071X

Responsive Management (2007) Washington boater needs assessment: An independent assessment of Washington State boaters' needs submitted to the Washington State Recreation and Conservation Office, 44 pp

Ricciardi A (2007) Are modern biological invasions an unprecedented form of global change? *Conservation Biology* 21: 329–336, http://dx.doi.org/10.1111/j.1523-1739.2006.00615.x

Ricciardi A, Jones L, Kestrup A, Ward J (2011) Expanding the propagule pressure concept to understand the impact of biological invasions. In: Richardson D (ed), Fifty Years of Invasion Ecology: The Legacy of Charles Elton. Blackwell Publishing Ltd., Chichester, pp 225–235

Ruiz GM, Freestone AL, Fofonoff PW, Simkanin C (2009) Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. In: Wahl M (ed), Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Springer, Dordrecht, Netherlands, pp 321–332, http://dx.doi.org/10.1007/b76710_23

Ruiz GM, Fofonoff PW, Steves B, Foss SF, Shiba SN (2011) Marine invasion history and vector analysis of California: a hotspot for Western North America. *Diversity and Distributions* 17: 362–373, http://dx.doi.org/10.1111/j.1472-4642.2011.00742.x

Savini D, Marchini A, Forni G, Castellazzi M (2006) Touristic harbours and secondary spread of alien species. *Biologia Marina Mediterranea* (1): 760–763

Shucksmith R (2007) Biological invasions: the role of biodiversity in determining community susceptibility to invasion. PhD thesis, University of Aberdeen, 402 pp

Silva PC, Woodfield RA, Cohen AN, Harris LH, Goddard JHR (2002) First report of the Asian kelp *Undaria pinnatifida* in the northeastern Pacific Ocean. *Biological Invasions* 4: 333–338, http://dx.doi.org/10.1023/A:1020991726710

USCG (United States Coast Guard) (2012) Final Rule. Federal Register, vol. 77, no 57, March 23, 2012, Washington, DC

USEPA (United States Environmental Protection Agency) (2013) Vessel General Permit for Discharges Incidental to the Normal Operation of Vessels (VGP), Washington, DC

Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biological Conservation* 102: 143–153, http://dx.doi.org/10.1016/S0006-3207(01)00098-2

Williams SL, Davidson IC, Pasari JR, Ashton GV, Crafton RE, Fontana RE, Grosholz, ED, Miller AW, Ruiz GM, Zabin CJ (2013) Managing multiple vectors for marine invasions in an increasingly connected world. *BioScience* 63: 952–966, http://dx.doi.org/10.1525/bio.2013.63.12.8

Zabin CJ, Ashton GV, Brown CW, Ruiz GM (2009) Northern range expansion of the Asian kelp *Undaria pinnatifida* (Harvey) Suringar (Laminariales, Phaeophyceae) in Western North America. *Aquatic Invasions* 4: 429–434, http://dx.doi.org/10.3391/ai.2009.4.3.1

Zabin CJ, Ashton GV, Brown CW, Davidson I, Chestnut T, Draheim R, Sytsma MD, Ruiz GM (2011) Hull fouling: characterizing magnitude and risk of species transfers by recreational and fishing vessels. Report to the Pacific States Marine Fisheries, 105 pp, http://dx.doi.org/10.2478/v10043-008-0002-3