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Factors influencing densities of non-indigenous species in the ballast water of ships arriving at ports in Puget Sound, Washington, United States

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ABSTRACT

1. Oceanographic characteristics and the presence of international shipping in Puget Sound, Washington, USA contribute to its vulnerability to non-indigenous species (NIS) invasions. To evaluate NIS arriving in ballast water, zooplankton was sampled in 380 ballast tanks of ships after they entered Puget Sound.
2. Taxa were classified into a higher risk group of coastal organisms (including known NIS), and a lower risk group of largely oceanic species. Most ships reported conducting mid-ocean ballast water exchange (BWE). However, despite state regulations requiring BWE, and apparent compliance by ship operators, most sampled tanks from both transpacific and coastal routes had coastal zooplankton densities exceeding internationally proposed discharge standards.
3. BWE efficiency models and controlled before-and-after BWE experiments indicate that BWE consistently removes most coastal zooplankton. However, this study found that although the empty–refill method of BWE significantly reduced coastal plankton compared with un-exchanged tanks, the flow-through method did not, and in either case remaining coastal plankton densities presented appreciable risks of introducing NIS.
4. Densities of high risk taxa were consistently and significantly higher from US domestic trips dominated by tank ships carrying ballast water from California, and lower in samples from trans-Pacific trips dominated by container ships and bulk carriers with ballast from Asia. These findings are probably a result of the dense and diverse NIS assemblages present in California and other US west coast estuaries and the comparatively short transit times between them and Puget Sound.
5. While it appears that BWE can effectively replace NIS with less risky ocean species, new reporting, verification, and operational procedures may be necessary to enhance BWE efficacy. In the long-term, the introduction of ballast water treatment technologies may be required to significantly reduce the discharge of risky organisms from commercial ships if BWE practices do not become more effective.

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KEY WORDS: Puget Sound; zooplankton; non-indigenous species; shipping; mid-ocean exchange; introduction risk; ballast water

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INTRODUCTION

Along with worldwide growth in shipping commerce, increasing ship speeds and ballast capacities have increased the risk of introductions of non-indigenous aquatic species to coastal ports. In the North American Great Lakes there are 90 known introductions between 1810 and 1959, 43 known introductions between 1960 and 1990, and even higher discovery rates since 1990 (Mills *et al*., 1993; Holeck *et al*., 2004). A similar but more pronounced pattern occurred in the San Francisco estuary on the west coast of North America, where the rate of new species introductions increased from about one every 55 weeks before 1960 to one every 14 weeks after 1960, for a total of over 200 species (Cohen and Carlton, 1998). The Puget Sound region in the northwest USA experienced a similar cumulative increase in successful marine/estuarine non-indigenous species invasions, with a documented total of 76 introduced species (Wonham and Carlton, 2005). Compared with other locations in the region, Puget Sound and the adjacent Straits of Juan de Fuca have fewer ballast-mediated introductions and more introductions associated with aquaculture imports of the Pacific oyster *Crassostrea gigas*. However, oyster imports to the Puget Sound region peaked in the 1950s and are now rare, and introductions in the region after the 1980s are thought to be mostly from ballast water (Wonham and Carlton, 2005).

Puget Sound, located in Washington State, is a fjord-like estuary comprising four major sub-basins connected to the Pacific Ocean by the Straits of Juan de Fuca (Figure 1). The main sub-basin covers about 45% of the area, contains about 60% of the water, and is the location of the major shipping ports of Seattle and Tacoma. In 1991, these ports together ranked 6th among 17 United States ports in the volume of ballast water discharged, receiving an estimated 2.69×10^6 metric tons (Carlton *et al*., 1995; Gramling, 2000). In Washington State as a whole, ships discharge an average of 9.5×10^6 cubic metres of ballast water per year (A. Pleus, Washington Department of Fish and Wildlife, personal communication). Ballast water arriving at other locations on the Pacific coast of North America has been shown to contain dense and diverse assemblages of organisms (Carlton and Geller, 1993; Levings *et al*., 2004; Choi *et al*., 2005) and is currently the most frequently cited method for transfer of non-native organisms worldwide.

Puget Sound is characterized by having several relatively deep basins separated from each other and from the Straits of Juan de Fuca by shallow sills (Figure 1). These and other factors (e.g. drought, Newton *et al*., 2003) may limit exchange both among basins and bays in Puget Sound and between Puget Sound and the ocean. Residence times of water can be quite long in some parts of Puget Sound (up to 2 months in the southern sub-basin, Albertson *et al*., 2002). These oceanographic factors and the large ballast volumes and frequency of possible non-indigenous species inoculations may enhance the risk of further invasions in Puget Sound.

There is a poor record of eliminating introduced species once they are established so it is preferable to prevent introductions through management actions. Oceanic ballast water exchange (BWE) is currently the only widely approved method for reducing the transfer of invasive aquatic species in ballast water. Ballast taken on in coastal ports and containing risky coastal species is exchanged with oceanic water that contains low risk species. Ships primarily conduct two types of BWE: flow-through exchange, in which ocean water is pumped continuously through a ballast tank to flush out coastal water from the ballast source port, and empty–refill exchange, in which a ballast tank is first emptied of coastal water and then refilled with ocean water. Flow-through exchange usually involves exchange of at least three times the volume of the ballast tank. When properly practised, BWE can replace 95% to 100% of the original source water (Hay and Tanis, 1998; Rigby *et al*., 1999). In theory, the process of exchange should significantly reduce the number of non-indigenous species introductions. However, in practice, organism removal is a complex issue that can vary among particular ships, voyages, seasons, type of BWE conducted, and types of organisms (Dickman and Zhang, 1999; Rigby *et al*., 1999; Zhang and Dickman, 1999; Wonham *et al*., 2005).

In the USA, federal law requires ballast exchange to be conducted a minimum of 200 nautical miles from shore for international voyages. Coastal voyages are exempt from the federal law, but the states of Washington, Oregon, and California require ships on coastal voyages to exchange their ballast a minimum of 50 nautical miles from shore. The requirement is that ships conduct a single empty–refill exchange or a three times flow-through exchange (300% volumetric exchange). At present, BWE verification at state and federal levels mostly consists of asking ship operators if they complied with the law. Federal inspectors may board a ship and measure the salinity of ballast water. If the salinity is lower than found in the ocean, then the conclusion is that the ship failed to perform a BWE. Salinity measurements may be useful for ships ballasting in ports with low salinity waters, but many ports in western North America or Asia have high salinities. In addition, there is no clear understanding of how much reduction in undesirable organisms is achieved by currently practised BWE techniques, either on individual ship or aggregated bases. Washington Department of Fish and Wildlife (WDFW) was given authority to implement the Washington State ballast management law, and in 2004 began a systematic collection of ballast exchange data and zooplankton samples from ships arriving in Puget Sound. This study examined exchange data and zooplankton from

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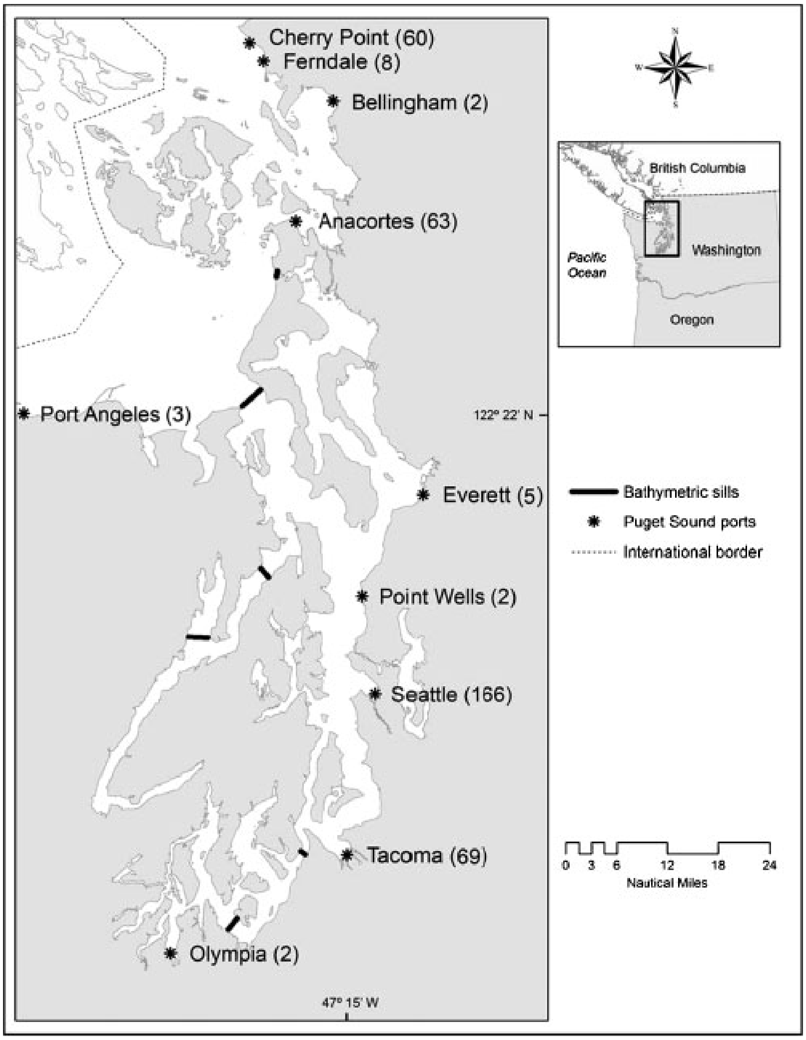

Figure 1. Location of Puget Sound, Washington State and its shallow sills, and ports where ballast water zooplankton sampling was conducted. Numbers in parentheses indicate total number of ballast tanks sampled at each port.

these collections and from previous samples collected by the University of Washington (UW) beginning in 2001. The goals of this study were to (1) document the sources and exchange locations of ballast water entering Puget Sound, as reported on ships' ballast water reporting forms; (2) compare zooplankton faunas of those ships that recorded BWE vs. those that did not; and (3) explore relationships between zooplankton assemblage structure and density and factors such as ballast source, ship route, and ship type. The intent was to better understand the effectiveness of BWE in reducing the risk of new invasions in Puget Sound and the Pacific Northwest.

METHODS

Ship sampling

The UW began sampling ship ballast water on 28 May 2001. Sampling was conducted on ships entering the ports of Seattle and Tacoma, Washington. On 22 June 2004, WDFW assumed the ship sampling in conjunction with ship inspections conducted as part of implementing ballast water regulations. On a given day, if a ship from a potentially high-risk domestic port was available (e.g. San Francisco Bay), it was sampled. Also, if a ship was previously sampled and was found to

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contain high proportions of coastal or non-indigenous organisms, it was sampled when it returned to Puget Sound. Otherwise, ships were sampled randomly as they arrived. Most of the samples taken by WDFW were in the ports of Seattle and Tacoma, but several other smaller ports in the Puget Sound region were occasionally sampled (Figure 1).

In general, zooplankton were collected from a single ballast tank per ship, although occasionally up to three tanks were sampled. Tanks were chosen in the following order of priority: (1) tanks that had undergone a reported BWE; (2) fullest tanks; (3) easiest tanks to access via manways (wing tanks were preferred, as they generally had easiest access and most unobstructed water columns); and (4) arbitrary choice by master or chief mate of the ship.

We obtained the following information from each ship's Ballast Water Reporting Form (BWRF): ship name, IMO number, owner, ship type, last port, total ballast capacity, water volume of the sampled tank, total discharge of the ship, exchange status, exchange method, date source water was ballasted, exchange date, and exchange location.

Sampling and laboratory methods

Zooplankton were sampled with a conical 30 cm diameter 73 μm mesh plankton net. Three replicate plankton samples were taken in each ballast tank. Depth was measured with a 30 m weighted measuring tape, from tank bottom to the top of the water column. The net was then lowered to the bottom, and after approximately 15 s, it was pulled to the surface at a rate of approximately $30\,\mathrm{cm\,s^{-1}}$. The water depth sampled averaged 3.85 ± 3.23 (SD) m. Occasionally, the internal structure of the ballast tank prevented the net from reaching the tank bottom. Those cases were noted by the inspector during sampling. Zooplankton was washed from the cod-end of the net into plastic sample jars and fixed in 10% buffered formalin. In each tank near-surface salinity and temperature were measured with a YSI model 33 salinity–temperature meter (YSI Incorporated, Yellow Springs, Ohio) or with a handheld refractometer and thermometer.

In the laboratory, each zooplankton sample was filtered through a 30 μm mesh screen and placed into a plankton counting tray. Zooplankton taxa were counted under a microscope at 25× magnification, except for some taxa, which were removed and identified using a compound microscope. Larval forms of invertebrates were generally identified to higher taxonomic levels such as order (e.g. Calanoida), suborder (e.g. Balanomorpha), or class (e.g. Bivalvia). Adults were identified to species in most cases. Based on published taxonomic and distributional literature (available from the corresponding author), each species or group was assigned to one of the following categories: (1) coastal taxa, which included meroplankton such as larvae of shallow water invertebrates, plus holoplankton species, such as copepods not native to the north-east Pacific; and (2) oceanic taxa, plus those that are cosmopolitan or of uncertain origin (this category is henceforth referred to as oceanic). Organisms in the first category were assumed to represent source port or nearshore ballast water, and those in the second category represented oceanic (exchanged) ballast water. It was also noted if a species was known to be non-indigenous and invasive on the west coast of North America. Copepoda nauplii were counted but were not included when calculating zooplankton density since in most cases they could not be accurately assigned as coastal or oceanic species.

Data analyses

Among the goals of this study was to understand how zooplankton densities varied according the following categorical factors: trip type (transpacific vs. coastal voyages), exchange method (empty–refill vs. flow-through vs. no exchange), ship type, and ballast water source. To test the effect of ballast water age on zooplankton density, age bins (1–5 days old, 6–10 days old, etc.) were used, and average densities of zooplankton in each bin were compared. In many cases factors were partially confounded, making it difficult to assess the effect of each factor on coastal and oceanic zooplankton density independently. For example, most of the tanker samples contained California source water, while most of the bulk carrier samples contained source water from Japan (Table 1). Confounded variables affected the assumption of statistical tests that the explanatory variables be independent of one another.

To reduce problems associated with confounding factors, a composite factor called 'trip type' was created that separated the data into two groups: (1) ships making transpacific voyages to Puget Sound that typically contained ballast water from Asia, and (2) ships travelling to Washington State from other ports on the west coast of North America. Vessels from the second category typically contained ballast water from California, Oregon, and British Columbia. These two groups correspond to major risk factors from coastal organisms from Asian sources and NIS already established in west coast ports. Relationships between zooplankton densities and continuous variables including temperature and salinity were also examined.

When testing for the effect of BWE on zooplankton density, any ship whose ballast water source was oceanic (i.e. taken up in mid-ocean as opposed to in port) was excluded, because the primary interest of the study was to determine the effectiveness of exchange in replacing coastal/nearshore organisms with oceanic ones.

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Table 1. Categorical factors used in analyses. Samples with unknown or oceanic source water were excluded from the exchange method analyses; trip type for samples with an 'unknown' ballast source was determined from exchange coordinates

Categorical factor	Categories	Transpacific	West Coast
Trip type		239	141
Year	2001–2002	9	3
	2003	15	—
	2004	75	19
	2005	57	45
	2006	36	32
	2007	47	42
BW age (days)	1–5	17	96
	6–10	80	26
	11–15	85	9
	16–20	37	5
	21–25	5	2
	26–30	4	2
	> 30	9	1
	Unknown	2	—
Exchange method	Exchanged — empty–refill	86	47
	Exchanged — flow-through	115	51
	No exchange	5	28
	Unknown or oceanic source water	33	15
Ship type	Bulk Carrier	177	13
	Container	48	4
	General cargo	6	—
	Gas carrier	3	—
	Product tanker	1	10
	Oil tanker	4	38
	Integrated Tug/Barge	—	30
	Articulated Tug/Barge	—	46
Ballast source	China	49	—
	Japan	124	—
	Korea	24	—
	Pacific	18	—
	Sri Lanka	1	—
	Taiwan	3	—
	Thailand	2	—
	Hawaii	4	—
	Western Pacific	4	—
	Alaska	—	1
	California	—	104
	Canada	—	2
	Oregon	—	10
	Washington	—	9
	West Coast of US	—	12
	Unknown	10	3

Statistical methods

Zooplankton densities from ballast samples were positively skewed (most of the values were low with relatively few extremely large outliers) and sample sizes and variances of the data were heterogeneous across factor levels. In an effort to normalize the data, equalize variances, and enhance the power of statistical tests, all zooplankton densities were log $(x+1)$ transformed before statistical analyses. This reduced skewness, although it often did not completely homogenize variances.

The main factors of interest (exchange method, ship type, and ballast water source) were sampled unequally because WDFW targeted certain ship types and ballast sources, and because certain ship types visit Puget Sound more frequently than others. Thus, samples sizes for comparing the main effects were often unbalanced, especially when looking at interactions of these factors. This non-factorial design reduced the power of the study and the overall ability to analyse the data statistically. Owing to these limitations and basic differences in characteristics of the two major voyage types (including

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differences in ballast water age, exchange location, ship type, and ballast water source, Tables 1 and 2) transpacific and west coast samples were for the most part analysed separately.

One-way ANOVAs were used to test for differences in total, coastal, or oceanic zooplankton density based on ballast water age, exchange method, vessel type, and ballast water source. It was assumed that an effect of any test was significant using an a priori α level of 0.05. If a main effect was significant, the Tukey–Kramer *post hoc* test was used to determine which factor levels (categories) were different. All statistical tests were conducted in NCSS (2001 version).

In most cases average zooplankton densities are reported as geometric rather than arithmetic means because of the largely skewed data set, and the tendency for arithmetic means to be greatly influenced by a few large outliers.

RESULTS

Ballast water sources and characteristics

Transpacific voyages

WDFW and UW sampled 239 ballast tanks from ships on transpacific voyages, beginning 28 May 2001 and ending 20 December 2007. The majority of the transpacific samples came from bulk carriers (74%) and container ships (20%). General cargo ships, gas carriers, product tankers, and oil tankers were also sampled (Table 1). Japan was the largest source of ballast water (52%) for transpacific ships, followed by China (21%), and Korea (10%). Transpacific ships also contained ballast from Taiwan, Thailand, Sri Lanka, Hawaii, and the mid or western Pacific Ocean. Ballast water in transpacific samples was on average 12 days old, and the majority of samples (85%) had ballast aged from 6 to 20 days old. An average of 9 days elapsed from the time a transpacific tank was ballasted to when it completed BWE.

Of the samples from transpacific ships, 98% were taken from exchanged tanks. Of those tanks, 42% were exchanged using the empty–refill method, while 58% employed the flow-through method. The location of reported BWE ranged widely throughout the north Pacific for these ships (Figure 2). Densities of coastal zooplankton in exchanged ballast water had a large range, spanning five orders of magnitude (Figure 2). However, 92% of the transpacific ballast samples had coastal zooplankton densities less than 1000 individuals m^{-3}, and 15% of the samples contained no coastal zooplankton. Only one transpacific ballast sample had a coastal zooplankton density exceeding 10000 individuals m^{-3} (density = 13 974 individuals m^{-3}).

The salinity in exchanged transpacific tanks averaged 34 ± 3 (SD) PSU. The salinity in unexchanged tanks was lower, averaging 25 ± 13 (SD) PSU. Water temperatures ranged from 4.7–35.0°C (mean 13.0 ± 4.4 (SD)°C) in exchanged tanks and from 3.7–16.2 °C (mean 9.9 ± 5.2 (SD)°C) in unexchanged tanks. Ballast water age ranged from 4 to 377 days for exchanged ships (measured from date of exchange), averaging 14 ± 26 (SD) days. Unexchanged ships contained ballast water 17–181 days old, averaging 73 ± 75 (SD) days (measured from date of ballasting). Transpacific container ships had much older ballast water compared with other transpacific ship types (average ballast water age 45 days vs. 14 days or less for other ship types, Table 2).

West Coast voyages

For ships on west coast voyages, 141 ballast tanks were sampled between 20 June 2001 and 28 December 2007 (Table 1). The majority of the west coast samples came from tank ships that included articulated tug/barges (33%), oil tankers (27%), integrated tug/barges (21%), and product tankers (7%). Thirteen bulk carriers and four container ships were also sampled from west coast voyages. California was the largest ballast water source for west coast samples (74%). Ships also contained ballast water from waters immediately offshore of the US west coast (9%), Oregon (6%), Washington (6%), Alaska (1%), and Canada (1%). The ballast water in west coast samples was on average 6 days old, where the majority of the samples had ballast aged from 1 to 10 days (87% of the samples). On average, 3 days elapsed from the time a west coast tank was ballasted to when it completed BWE.

Of the samples from west coast trips, 77% were from exchanged tanks. Of those samples, 48% were exchanged using the empty–refill method, while 52% used the flow-through method. Ships on west coast voyages generally exchanged their ballast just over 50 nautical miles offshore (Figure 3). Of the west coast ballast samples, 72% had coastal zooplankton densities less than 1000 individuals m^{-3} (Figure 3); 21% of the samples contained 1000–10 000 coastal zooplankton m^{-3}. Eight exchanged west coast samples (7.5%) contained greater than 10 000 coastal zooplankton m^{-3}. All of the samples taken from ships travelling along the west coast had at least one coastal zooplankton m^{-3}.

Salinity in exchanged tanks from west coast voyages averaged 35 ± 2 (SD) PSU. The salinity in unexchanged tanks was lower, averaging 20 ± 14 (SD) PSU. Water temperatures ranged from 6.9–20.9 °C (mean 12.9 ± 3.3 (SD)°C) in exchanged ships and from 7.8–19.9°C (mean 15.0 ± 4.0 (SD)°C) in unexchanged ships. Ballast water age ranged from 1–38 days for exchanged ships (measured from date of exchange), averaging 5 ± 5 (SD) days. Unexchanged ships had ballast water 2–21 days old, averaging 7 ± 5 (SD) days (measured from date of ballasting).

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Table 2. Ballast water age, source, discharge and exchange characteristics from sampled tanks, for main transpacific and west coast ship types

Ship type	Average ballast water age (days)	Dominant ballast water source (> 10% of samples)	If discharging, average discharge volume (m^3)	Maximum discharge (m^3)	Percentage of ships discharging	Exchange method (%)	
						Empty–refill	Flow-through
Transpacific							
Container	45	China, Japan, mid-Pacific	4021	12 802	48	89	11
Bulk Carrier	14	China, Japan, Korea	18 156	35 051	99	36	64
General Cargo	9	China, mid-Pacific, western Pacific	2210	5001	64	83	17
Oil Tanker	11	Hawaii	14 401	30 321	100	0	100
West Coast							
Container	12	California, Washington, US coastal water	7975	9400	50	100	0
Bulk Carrier	6	California	13 226	21 337	91	38	63
Oil Tanker	4	California	11 048	20 402	92	44	56
Product Tanker	7	California	8510	19 740	63	100	0
Integrated Tug/Barge	7	California, US coastal water	12 598	18 581	92	75	25
Articulated Tug/Barge	6	California, Oregon	6685	10 008	93	16	84

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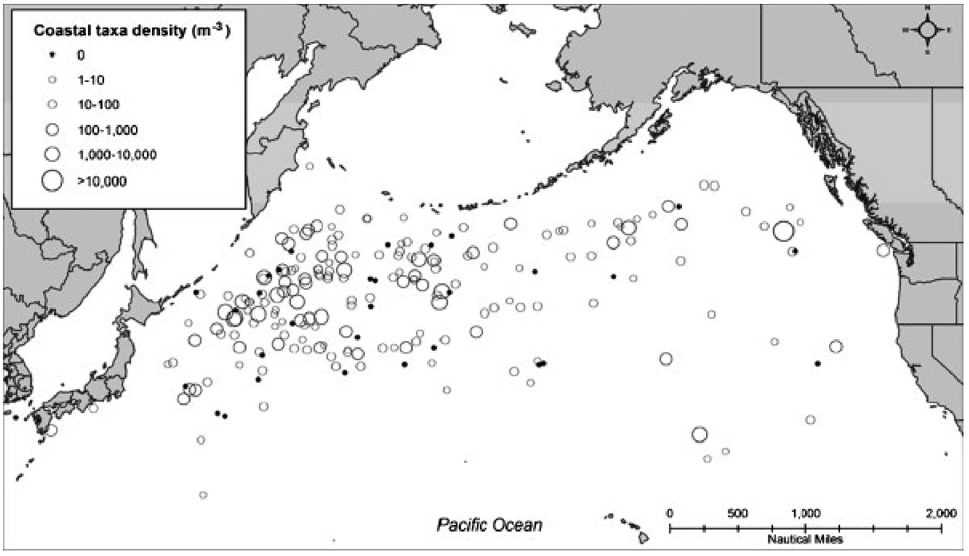

Figure 2. Locations of reported mid-ocean ballast water exchange (end of exchange event) for transpacific trips. Symbols indicate exchange locations and densities of coastal zooplankton taxa.

Zooplankton assemblages

In total, 124 coastal zooplankton taxa were identified from transpacific and west coast ballast water samples (Table 4). The most common coastal taxa in transpacific samples included bivalve larvae (49.8% of the samples); the calanoid copepod *Acartia* (*Acartiura*) sp. (32.6%); the cyclopoid copepod *Oithona davisae* (31.8%); and barnacle cyprid and nauplii larvae (25.9% and 21.3%, respectively). Of these, bivalve larvae and *O. davisae* also had high average densities.

Common coastal taxa found in west coast trips included bivalve larvae (72.3% of the samples); the cyclopoid copepods *O. davisae* (70.2%) and *Dioithona oculata* (33.3%); barnacle nauplii and cyprid larvae (46.8% and 42.6%, respectively); the harpacticoid *Euterpina acutifrons* (46.8%); the calanoid copepods *Acartia* (*Acartiura*) sp. (43.3%), *Acartia californiensis* (29.1%), and *Pseudodiaptomus marinus* (33.3%); and spionid polychaete larvae (27.7%). *O. davisae* was the most abundant coastal taxon in west coast ballast.

Ballast samples had 165 taxa classified as oceanic, cosmopolitan, or of unknown origin (referred to as 'oceanic', Table 5). Common oceanic taxa in transpacific ballast included copepod nauplii (88.7%); the cyclopoid copepods *Oithona similis* (83.3%), *Oncaea* sp. (59.4%), and *Corycaeus anglicus* (25.1%); the calanoid copepods *Pseudocalanus* sp. (59.4%); *Paracalanus* sp. (41.0%), *Metridia* sp. (32.2%), and *Calanus pacificus* (26.8%); gastropod larvae (38.5%), and the harpacticoid copepod *Microsetella norvegica* (25.9%). Copepod nauplii and *O. similis* had the highest oceanic densities in transpacific samples.

Dominant oceanic taxa in ships performing coastal voyages included copepod nauplii (100%), the cyclopoid copepods *O. similis* (86.5%), *C. anglicus* (73.8%), *Oncaea* sp. (63.1%), and unidentified Cyclopoida (36.9%); the calanoid copepods *Paracalanus* sp. (74.5%), *Clausocalanus* sp. (66.7%), *Acartia* sp. (63.8%), *Acartia tonsa* (59.6%), *C. pacificus* (53.2%), *Pseudocalanus* sp. (46.1%), *Ctenocalanus vanus* (29.8%), and *Metridia* sp. (27.7%); Gastropoda larvae (71.6%), unidentified polychaete larvae (52.5%), the harpacticoid *M. norvegica* (48.9%), unidentified Euphausiacea (41.8%); hydrozoans (35.5%); *Sagitta* sp. (32.6%); *Oikopleura* sp. (29.1%); and Turbellaria (28.4%). Copepoda nauplii and *O. similis* had the highest mean densities of oceanic taxa in west coast ballast.

Ballast in ships from west coast trips had more coastal taxa than ships on transpacific voyages (107 vs. 75 taxa), and 59 of the coastal taxa occurred in samples from both trip types. Transpacific samples had 16 species not found in west coast ballast, and west coast samples had 49 taxa not found in transpacific ships. For the dominant coastal taxa that occurred in both trip types, west coast samples usually had higher mean and maximum densities than the same taxon in transpacific ballast (e.g. *Oithona davisae*, Table 4).

The number of oceanic species present in transpacific and west coast trip types was similar (137 and 138 taxa, respectively). Transpacific samples had 27 oceanic species not found in west coast ballast, and west coast samples had 23 species not found in transpacific tanks. Mean and maximum

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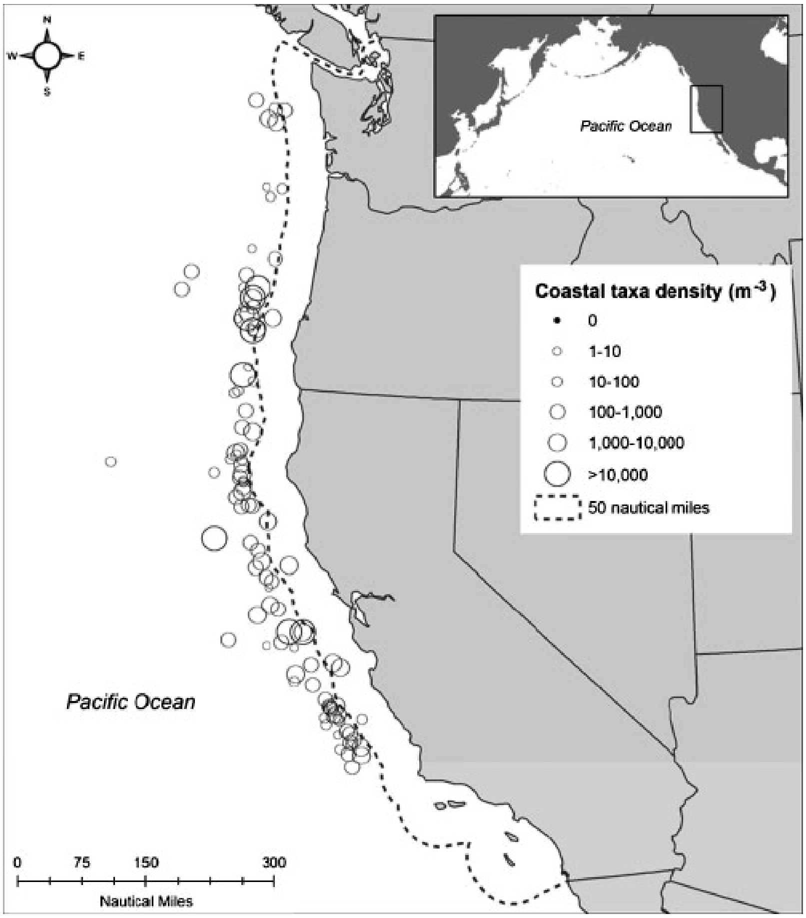

Figure 3. Locations of reported mid-ocean ballast water exchange (end of exchange event) for west coast trips. Symbols indicate exchange locations and densities of coastal zooplankton taxa. Inset shows region of exchange locations.

densities were generally similar for many common oceanic taxa found in transpacific and west coast ballast (e.g. *O. similis*), although not always (e.g. copepod nauplii, Table 5).

Coastal and oceanic zooplankton densities

Temperature and salinity

Coastal and oceanic zooplankton densities were not significantly related to either ballast water temperature or salinity (linear regression, data not shown).

Trip type

Mean densities of coastal zooplankton were significantly greater in samples from west coast trip types (geometric mean = 364 individuals m^{-3}: 95% CL = 245 to 542) than in those from transpacific trips (geometric mean = 24 individuals m^{-3}: 95% CL = 18 to 33, Table 3, Figure 4). Oceanic zooplankton densities were also higher in west coast (geometric mean = 2092 individuals m^{-3}: 95% CL = 1562 to 2801) compared with transpacific voyages (geometric mean = 296 individuals m^{-3}: 95% CL = 221 to 395).

Ballast water age

Total zooplankton densities were significantly different based on ballast water age: abundances declined with ballast age for both transpacific and west coast trip types (Table 3, Figure 5). For transpacific ships, ballast water between 1 and 5 days old had a geometric mean of 1266 total zooplankton m^{-3} (95% CL = 576 to 2786), while 26 to 30 day-old ballast had a geometric mean of 44 total zooplankton m^{-3} (95% CL = 17 to

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Table 3. Results of ANOVA testing main factor effects on total, coastal, or oceanic zooplankton categories. Numbers in bold type indicate — values ≤ 0.05

Main factor	Dependent variable	*P*-value	
Trip type	Coastal zooplankton	**0.000**	
	Oceanic zooplankton	**0.000**	
		Transpacific	West Coast
Ballast water age	Total zooplankton	**0.000**	**0.000**
	Coastal zooplankton	0.379	**0.037**
	Oceanic zooplankton	**0.000**	**0.004**
Exchange method	Coastal zooplankton	0.208	**0.019**
	Oceanic zooplankton	**0.001**	**0.000**
Ship type	Coastal zooplankton	0.111	0.171
	Oceanic zooplankton	**0.006**	0.319
Ballast water source	Coastal zooplankton	**0.001**	**0.046**
	Oceanic zooplankton	0.188	**0.000**

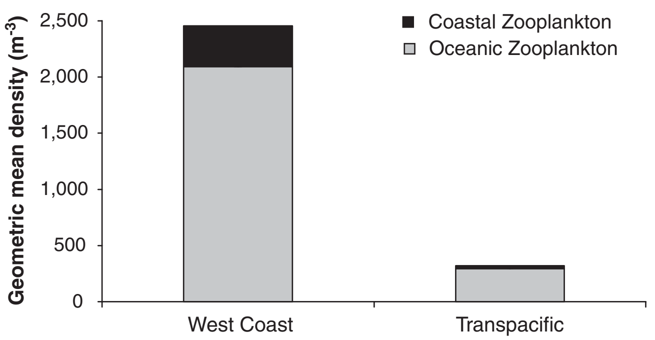

Figure 4. Geometric mean densities of coastal and oceanic zooplankton in west coast and transpacific trip types.

117). West coast samples with ballast between 1 and 5 days old had a geometric mean of 4529 total zooplankton m^{-3} (95% CL = 3508 to 5849), compared with 116 total zooplankton m^{-3} (95% CL = 89 to 152) for ballast water between 26 and 30 days old. For each ballast water age group (1–5 days, 6–10 days, etc.), total zooplankton densities were higher in west coast trip type samples than in transpacific trip type samples (Figure 5).

Mid-ocean exchange

There was no significant difference in coastal zooplankton density between transpacific ships that performed an exchange and those that did not (Table 3, Figure 6). Transpacific ships that conducted empty–refill BWE had a geometric mean of 28 coastal zooplankton m^{-3} (95% CL = 16 to 47). Those that performed a flow-through BWE had a geometric mean of 29 coastal zooplankton m^{-3} (95% CL = 19 to 44). Unexchanged transpacific ships had a geometric mean of 4 coastal zooplankton m^{-3} (95% CL = 0 to 36).

For ships on coastal voyages, tanks exchanged using empty–refill BWE contained significantly lower densities of coastal organisms (geometric mean = 227 individuals m^{-3}: 95% CL = 119 to 432) than unexchanged tanks (geometric mean = 1150 individuals m^{-3}: 95% CL = 442 to 2986; Table 3, Figure 6). Densities of coastal zooplankton in west coast ships that conducted flow-through BWE (geometric mean = 421 individuals m^{-3}: 95% CL = 220 to 803) were not significantly different from ships that did not exchange their ballast water (*post hoc* analysis).

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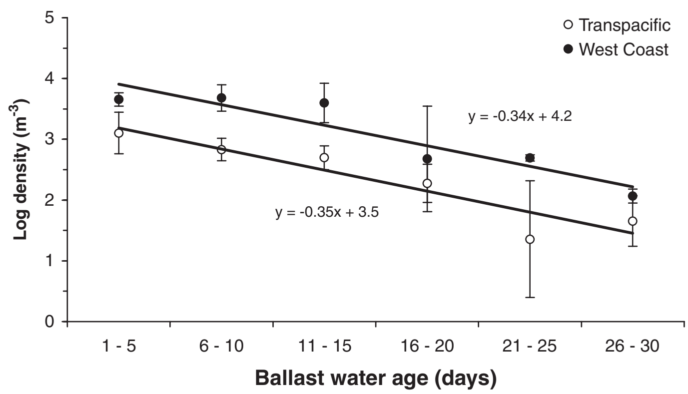

Figure 5. Mean densities of total zooplankton by ballast water age for transpacific and west coast trip types; error bars indicate 95% confidence intervals.

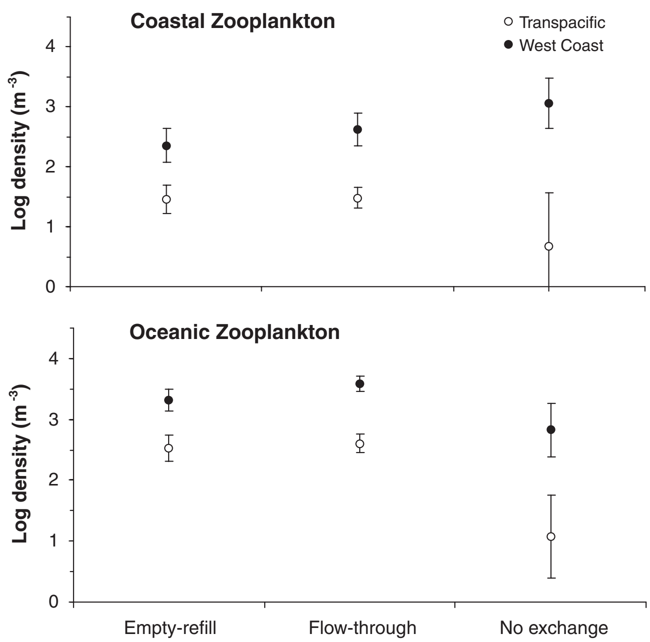

Figure 6. Mean densities of coastal and oceanic zooplankton by trip type and ballast water exchange method; error bars indicate 95% confidence intervals.

For both transpacific and west coast trips, exchanged ballast tanks had significantly higher densities of oceanic zooplankton than unexchanged tanks. In transpacific ships, tanks that underwent empty–refill and flow-through exchanges had similar numbers of oceanic zooplankton, with geometric means of 337 individuals m^{-3} (95% CL = 207 to 549) and 402 individuals m^{-3} (95% CL = 282 to 572), respectively. Unexchanged transpacific tanks contained a geometric mean of 11 oceanic zooplankton m^{-3} (95% CL = 2 to 56). For ships making a coastal voyage, tanks that underwent empty–refill and flow-through had a geometric mean of 2070 oceanic zooplankton m^{-3} (95% CL = 1375 to 3118) and 3855 oceanic zooplankton m^{-3} (95% CL = 2866 to 5185), respectively. Unexchanged tanks in coastal ships had a geometric mean of 673 oceanic zooplankton m^{-3} (95% CL = 243 to 1859).

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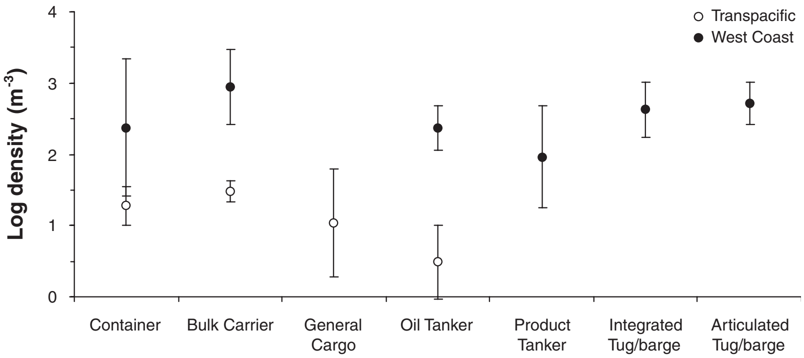

Figure 7. Mean densities of coastal zooplankton by trip type and vessel type; error bars indicate 95% confidence intervals.

Ship type

There was no significant difference in the density of coastal zooplankton found among samples from the different transpacific ship types, or for those among west coast ship types (Table 3, Figure 7).

For ship types common to both trip types, those on west coast voyages had much higher coastal zooplankton densities. West coast bulk carriers had a geometric mean of 892 coastal zooplankton m^{-3} (95% CL = 266 to 2985) compared with 29 coastal zooplankton m^{-3} (95% CL = 20 to 42) in transpacific bulk carriers. West coast container ships had a geometric mean of 238 coastal zooplankton m^{-3} (95% CL = 25 to 2,192), while transpacific container ships had 18 coastal zooplankton m^{-3} (95% CL = 9 to 34) on average. A similar pattern was observed for oil tankers on transpacific voyages compared with west coast voyages. Transpacific oil tankers had a geometric mean of 2 coastal zooplankton m^{-3} (95% CL = 0 to 9) compared with 232 coastal zooplankton m^{-3} (95% CL = 112 to 480) in west coast oil tankers. Differences in coastal zooplankton densities between transpacific and west coast bulk carriers, container ships, and oil tankers were statistically significant (*t*-tests, container ships $t = -1.7$, $P = 0.048$; bulk carriers, $t = -5.09$, $P < 0.000001$; oil tankers, $t = -3.72$, $P = 0.003$).

Oceanic zooplankton densities significantly differed among the transpacific ship types (Table 3). Bulk carriers had higher densities of oceanic zooplankton than container ships (geometric mean = 395 individuals m^{-3} and 136 individuals m^{-3}, respectively). Oceanic zooplankton densities were similar among all west coast ship types (Table 3).

Ballast source region

Coastal zooplankton densities were significantly different depending on the ballast water source for transpacific voyages (Table 3, Figure 8). However, the only significant difference identified via *post hoc* analysis was that Japan had significantly higher coastal organism densities than China, with geometric means of 44 individuals m^{-3} (95% CL = 29 to 65) and 10 individuals m^{-3} (95% CL = 6 to 19), respectively.

Within the west coast trip type samples, ballast water sources had similar densities of coastal zooplankton (Figure 8). Although a marginally significant difference in coastal zooplankton densities was found among the west coast sources when compared using a one way ANOVA ($P = 0.046$, Table 3), a *post hoc* test contrasting these sources with each other did not identify any significant differences.

Ballast water from California contained significantly higher densities of taxa known to be non-indigenous to the west coast of North America ($P < 0.0001$, Figure 8) when compared with other west coast sources. Ships carrying California water as ballast contained a geometric mean of 112 non-indigenous zooplankton m^{-3} (95% CL = 63 to 197), while ships that ballasted in Oregon, Washington, or off the west coast of the USA contained non-indigenous zooplankton abundances ranging from 4 to 9 individuals m^{-3} (95% CL = 0 to 70). This difference was statistically significant when comparing California with ballast sources from Oregon and the coastal Pacific Ocean (*post hoc* analysis).

Coastal zooplankton densities varied significantly when comparing all ballast water sources simultaneously (i.e. all transpacific and west coast sources, $P < 0.0001$). California-sourced ballast water had significantly higher coastal zooplankton densities than ballast from the Pacific Ocean, China, Korea, and Japan. For taxa known to be non-indigenous to the west coast of North America, California had higher densities than ballast from the mid-Pacific Ocean, China, Korea, Japan, Oregon, and the Pacific Ocean near the North American west coast (Figure 8).

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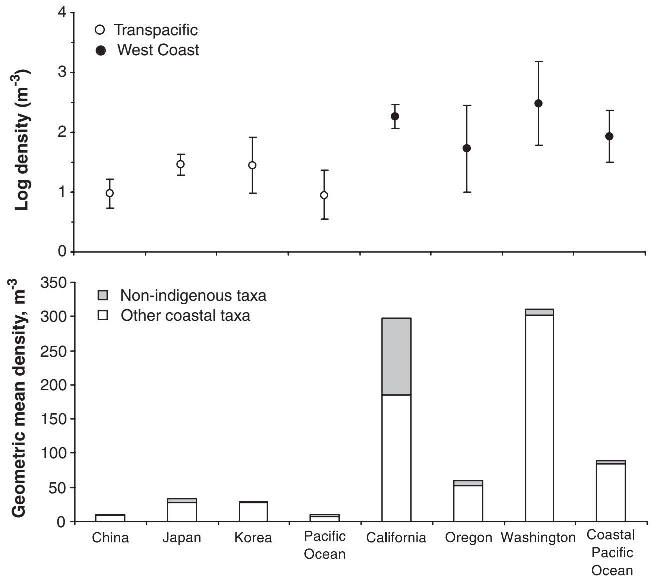

Figure 8. Mean densities of coastal zooplankton by ballast water source (top) and geometric mean densities of coastal zooplankton separated into taxa known to be non-indigenous to the west coast of North America and other coastal taxa (bottom); error bars indicate 95% confidence intervals.

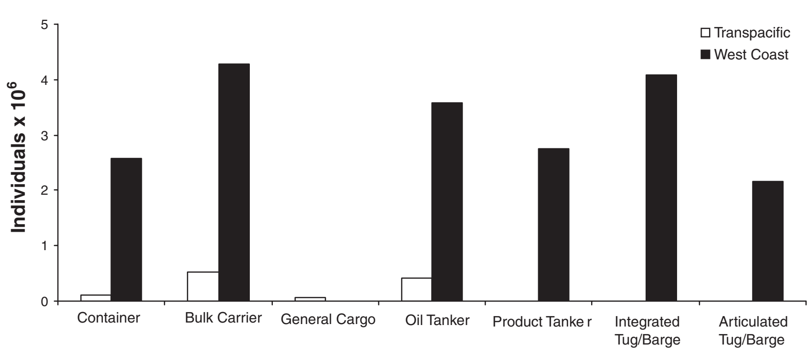

Figure 9. Estimated number of coastal organisms discharged per deballasting event for each ship type.

Ballast discharge

For ships conducting transpacific trips, bulk carriers and oil tankers had much higher average and maximum ballast discharge volumes into Puget Sound than container and general cargo ships (Table 2). Similarly, for ships travelling on coastal trips, bulk carriers, oil tankers, and integrated tug/barges had higher average ballast discharge volumes than other ship types.

To estimate roughly the number of coastal organisms discharged by each ship type, the average density of coastal organisms (individuals m^{-3}) for a given ship type was multiplied by each ship type's average discharge (m^3). Based on this calculation it appears ships conducting west coast voyages discharged many more coastal zooplankton per deballasting event than did transpacific ships (Figure 9). For example, although transpacific bulk carriers discharged similar or greater ballast water volumes to bulk carriers on west coast trips (Table 2), the number of coastal organisms discharged during deballasting was an order of magnitude greater for the west coast ships.

DISCUSSION

This study indicates that BWE significantly reduces the density of coastal taxa that pose invasion risk, while increasing the density of less risky oceanic taxa in ships that enter Puget Sound ports. In particular, for west coast trip types, for which there were adequate sample sizes of exchanged and unexchanged tanks, ships that had undergone empty–refill exchange had significantly lower coastal taxa abundances than those that did not conduct BWE. For transpacific trip types, there was no significant difference in coastal plankton densities between exchanged and unexchanged ships. However, the sample size of unexchanged transpacific ships was very low ($n = 5$), and tanks from these samples had a mean ballast age of 73 days, probably causing the low observed densities. Additional sampling of unexchanged tanks from transpacific trips will be required to understand how they compare with exchanged tanks.

Despite apparent compliance by ship operators with regulations requiring BWE (i.e. indicating BWE on reporting forms), ships entering Puget Sound continue to pose a large risk of introducing non-indigenous organisms. There were many cases in both transpacific and west coast trip types in which ships reported BWE, but still had relatively high densities of coastal taxa (Figures 2 and 3). Although densities of these organisms were lower in ships that conducted BWE, the differences were not statistically significant in some cases (e.g. for west coast trip types, densities in flow-through exchanged tanks were not significantly different from those in unexchanged tanks). Also, most sampled tanks had densities of coastal plankton (a subset of total zooplankton) that were well above proposed discharge standards for total zooplankton. For example, the International Ballast Water Convention, adopted by member countries of the International Maritime Organization (IMO), proposes a ballast discharge standard of less than 10 viable organisms greater than or equal to 50 μm in minimum dimension, per cubic metre of water (IMO standards summarized in Gollasch *et al.*, 2007). If this standard is applied to the study results to read 'less than 10 *coastal* organisms per cubic metre remaining after BWE', then only 70 of the 201 transpacific ballast samples and 9 of the 98 west coast ballast samples that recorded BWE would have passed the standard. This is a conservative application of the standard, as the net mesh used in this study was 73 μm.

Ballast exchange efficiency models suggest that exchange can be quite effective at eliminating organism-bearing water (Armstrong *et al.*, 1999). Furthermore, when conducted under controlled experimental conditions, with before-and-after exchange sampling, BWE is consistently effective in reducing the density of coastal zooplankton (summarized in Ruiz and Reid, 2007). For example, Wonham *et al.* (2001) found in an experimental test of mid-ocean exchange 93 to 100% of the coastal water and 80 to 100% of the coastal organisms were removed; Ruiz *et al.* (2005) found that BWE conducted on tankers resulted in reduction of non-indigenous organisms of 70 and 90% for the flow-through and empty–refill exchange methods, respectively; and Ruiz and Reid (2007) described removal efficiencies of zooplankton by empty–refill exchanges of 80%, 90%, and 95% for container ships, oil tankers and a bulk carrier, respectively. Although this study did not have before-and-after BWE results and single-voyage BWE efficacies could not be measured, the aggregate findings presented here suggest that BWE did not consistently reduce risk (i.e. the number of coastal organisms) to the degree predicted by BWE efficacy experiments. There are several explanations for this: one possibility is that in some cases BWE was reported by ship operators, but not conducted, or incompletely conducted (Harkless, 2003). If this was the case, it points to the need for enforcement and verification of existing ballast exchange regulations. A second reason for relatively abundant coastal assemblages in exchanged ships is the possibility that open-ocean waters may contain coastal organisms transported offshore by ocean conditions. Taylor *et al.* (2007) found when ships conducted their oceanic exchanges in the vicinity of coastal river plumes, BWE appears to replenish tanks with coastal zooplankton taxa such as bivalve and Cirripedia larvae. A third possibility is that BWE is less efficient in certain types of ships (Verling *et al.*, 2005). While some ship types had higher densities of high-risk taxa (e.g. tug/barges, tankers), confounding of these results with trip type and ballast age (e.g. most tankers were from domestic routes which had lower ballast water ages) makes it impossible to pinpoint riskier ship types with the present data. Controlled before-and-after BWE experiments on several ship types conducting similar voyages would help to answer this question, and provide information to the shipping industry on ship design components that increase the efficiency of exchange. Ship owners and operators would like to transport as little ballast as possible because it does not directly contribute to revenue. Recently proposed alternative ship designs could decrease the risk of introductions by limiting the amount of ballast needed, retaining more ballast on board, or changing ballast tank internal structure to facilitate drainage (National Research Council, 1996). Also, ballast water treatment systems (e.g. chemical biocides, physical separation, deoxygenation, ultraviolet light) are currently being developed as an alternative to BWE (summarized in Matheickal and Raaymakers, 2004). Some of these systems have been tested and show promise in reducing organisms in ships' ballast (Rigby *et al.*, 1999; Tamburri *et al.*,

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2002; Sutherland *et al.*, 2003; Waite *et al.*, 2003; Herwig *et al.*, 2006).

This study found that densities of high-risk coastal taxa were significantly higher from west coast trips, which were dominated by tank ships that obtained ballast water in California. Furthermore, estimates of the number of coastal plankton released per discharge suggest that west coast-sourced ballast contributes far more invasion risk to Puget Sound than transpacific-sourced ballast. It should be pointed out, however, that the ships sampled may not reflect the actual aggregate ship arrivals and discharge routines of ships visiting Puget Sound, and additional research to integrate shipping patterns and ballast discharges is needed.

Coastal zooplankton densities and discharges were lower in samples from transpacific voyages with ballast sources in Japan, China, and South Korea. From the results of this study, it is not possible to determine whether the higher densities of coastal taxa in west coast ships are due to differences in ballast source, transit times, or the ship types on these routes, compared with transpacific ships. However, a likely explanation is a combination of the dense and diverse NIS assemblages present in California estuaries and comparatively short transit times from California to Puget Sound. San Francisco Bay appears to be a particularly important source of NIS, with at least 212 introduced taxa, many of which dominate their invaded habitats (Cohen and Carlton, 1995, 1998). It is notable that for planktonic copepods alone, much of San Francisco Bay is now dominated by an East Asian fauna (Orsi and Ohtsuka, 1999). Three of these copepod species have recently been found in the Columbia River estuary, 1000 km north of San Francisco Bay, but do not occur in other west coast US estuaries (Cordell *et al.*, 2008). While they may have been introduced to the Columbia River via shipping from Asia, this study suggests that San Francisco Bay and other California ports were more likely sources: the data showed much higher abundances of species known to be non-indigenous in ballast from California than from any other source region (Figure 8). Higher densities of zooplankton in west coast trips are also likely related to transit time. The findings of this study that transpacific trips were much longer than west coast trips and that zooplankton density declined as a function of ballast age coincide with experimental results showing that most zooplankton taxa decline in ballast tanks over time, sometimes greatly (Lavoie *et al.*, 1999; Gollasch *et al.*, 2000; Wonham *et al.*, 2001). It is interesting that given the same ballast water age, transpacific plankton densities are lower than west coast densities (Figure 5). This suggests that it is not ballast age alone that contributes to overall lower plankton densities from transpacific trips. One explanation for this is that ships on west coast trip types conduct their BWE closer to shore than transpacific ships. Most BWE on west coast trips is conducted close to the required 50 nautical mile distance (Figure 3), and local ocean conditions (e.g. onshore–offshore flow, river plumes, natural plankton distribution) may result in coastal zooplankton occurring beyond 50 nautical miles. In contrast, BWE conducted on transpacific trips is mandated to occur at least 200 nautical miles offshore (Figure 2). Another factor that could contribute to higher plankton densities in west coast trip types is related to the amount of time elapsed before exchange was completed: transpacific trips averaged 9 days before completing their exchange. Ships on west coast voyages typically initiate their exchange immediately upon reaching the 50 nautical mile line, especially if they are conducting the more time-intensive flow-through exchange, and on average complete their exchange 3 days after ballasting. For transpacific trips, the longer time lag between originally taking on ballast and the time when the exchange occurs may result in plankton die-off, lowering the densities of 'residual' zooplankton after BWE.

The lower average coastal plankton densities in longer transpacific trips does not mean that NIS introduction risk from that source is insignificant: coastal taxa often numbered in the thousands per cubic metre in transpacific samples, well above proposed and current discharge standards (see discussion above). Many invasive taxa in US west coast estuaries are thought to have been originally introduced via this pathway (Wonham and Carlton, 2005). Thus, transpacific trips pose the risk of introduction of new non-indigenous taxa while US west coast trips pose a risk of spreading already established invasive taxa from highly invaded estuaries (e.g. San Francisco Bay) to new coastal locations. This is analogous to what happened in the Caspian Sea after construction of the Volga-Don canal. Subsequent to its construction in 1952, several invasive species (including the notorious comb jelly *Mnemiopsis leidyi* and the crab *Rhithropanopeus harrisii*) first introduced in the western Atlantic to the Black and Azov Seas, appeared in the Caspian Sea. These species were presumably moved there via shipping in the canal (Ivanov *et al.*, 2000; Grigorovich *et al.*, 2003).

In a recent comparison of the Puget Sound region (including northern Washington State and southern British Columbia province) with three other north-eastern Pacific coastal embayments (not including San Francisco Bay), Wonham and Carlton (2005) found that the Puget Sound region had the highest number of known NIS. They found that most of these introductions were invertebrates likely introduced with oyster seed from the Atlantic and north-west Pacific, but suggested that this pathway has peaked and that ballast water discharge is an increasing source of introductions to the region. Similar to the findings presented here for Puget Sound, Levings *et al.* (2004) documented a number of potential planktonic

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colonizers arriving at Vancouver, British Columbia in ships' ballast. In particular, several planktonic copepods found by Levings *et al*. (2004) and also in this study are known NIS invaders in the region, and are hypothesized (based on physiological tolerances and native distributions) to be successful colonizers in the region (Levings *et al*., 2004). Two of these species, the calanoid *Pseudodiaptomus marinus* and the cyclopoid *Oithona davisae* were among the most common in terms of frequency of occurrence and/or abundance in ballast samples from this study (see Table 4). Despite this high relative propagule pressure, neither of these species is known to have successfully established in Puget Sound or other coastal estuaries of the north-east Pacific (J. Cordell, unpublished data). Additional autecological case studies of species like these will help to understand why some species that are abundant in ballast water discharge become invasive and others do not.

In addition to copepods, a number of other potentially invasive coastal invertebrate larvae (e.g. barnacles, bivalves, polychaetes) were abundant in the ballast samples. Although little studied, the ecological effects of both planktonic and benthic invaders can be large in the north-eastern Pacific (summarized by Wonham and Carlton, 2005). Puget Sound may be at particular risk of continued ballast-mediated invasions because of its physical geography and continued ballast discharges.

RECOMMENDATIONS

Ultimately, for BWE or any other ballast water treatment method to significantly reduce the risk of new invasions, viable propagules of non-indigenous taxa must be reduced below a critical threshold (Choi *et al*., 2005; Wonham *et al*., 2005). In both models and controlled experiments, it has been shown that BWE can be very effective in replacing potential invaders with less risky oceanic species (Wonham *et al*., 2001; Ruiz *et al*., 2005; Ruiz and Reid, 2007), and in theory, BWE can be conducted in ways that significantly reduce propagule pressure (Wonham *et al*., 2005). In this study, a number of ships that conducted BWE had no detectable coastal organisms (Figure 2). Although it is suggested that ballast water treatment should eventually replace BWE as a ballast water management practice, at this time technologies are in the development stage, and their efficacy, reliability, and costs are still being evaluated. Thus, it is recommended that BWE be retained for the time being in the ballast water management 'toolbox'. However, a caveat to this recommendation is that in order to be effective, BWE will require more regulatory oversight and compliance verification than is currently practised. Current BWE verification methods such as ballast exchange reporting by ship operators and measuring ballast salinity are problematic: in the first case, ballast exchange records can be manipulated or poorly kept, and in the second case, salinity is a poor predictor of BWE because some ballast source ports are located in high salinity waters (Murphy *et al*., 2004). One verification method that shows potential is the use of chemical tracers indicative of coastal vs. oceanic waters (Murphy *et al*., 2004). Another possible verification method is to examine water to be discharged for indicator taxa known to occur only in coastal habitats. As Murphy *et al*. (2004) suggest, downsides of a taxonomic verification method include the expertise required and extremely high temporal variation in abundances at a given source. However, this method bears more consideration, and studies should be conducted to determine (1) whether there are easily identified taxa that can be reliable indicators of coastal waters, and (2) how seasonal variability in these taxa affects one's ability to determine whether or not BWE was conducted.

At state, federal, and international levels, the importance of ballast water regulation and management is increasingly recognized. In Washington State, regulatory activity and scrutiny has increased in the form of additional ship inspections, review of ballasting records, and collecting samples from ballast tanks for zooplankton analysis. Ship ballast sampling in Puget Sound and elsewhere should be continued to help understand the effects of ballast management efforts. For example, some ships may need to make changes in their ballast pump capacity, intake and discharge locations within a tank, or modify tanks in other ways to achieve greater exchange efficiency. Data from this study comprise a useful baseline for evaluating the effectiveness of ballast tank design modifications, new exchange practices, or treatment technologies in removing coastal species.

To understand if any NIS interdiction effort significantly reduces invasion risk, much more needs to be known about what constitutes 'invasibility' for a given organism or receiving ecosystem. While the results of this and similar studies can offer valuable information (e.g. on ballast management effects on propagule pressure), such data will be much more useful for predicting and understanding future invasions when integrated with information such as physiological requirements of species of concern, disturbance regimes of receiving locations, and native ranges of NIS. Although propagule pressure is an important predictor of invasion success (Lockwood *et al*., 2005), models that merge propagule pressure and invasibility measures may be even more useful (Leung and Mandrak, 2007). Results of additional research to measure invasibility metrics and join them with propagule pressure data will be invaluable to resource managers and other stakeholders concerned with managing NIS and preserving the ecological functions of coastal ecosystems.

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Table 4. Taxa that were considered to be of coastal origin from ballast of 380 ballast tanks sampled in Puget Sound, 2001–2007. The frequency of occurrence, mean and maximum density of each species is reported according to trip type (Transpacific or West Coast). Asterisk denotes species that have been introduced to the Pacific coast of North America; †denotes fresh water taxa.

Taxon	Transpacific			West Coast		
	Frequency of occurrence (%)	Mean density (m^{-3})	Maximum density (m^{-3})	Frequency of occurrence (%)	Mean density (m^{-3})	Maximum density (m^{-3})
Class Branchiopoda, Suborder Cladocera						
Bosmina longirostris (O.F. Müller, 1776)†	1.7	2.6	4.2	5.7	1120.4	4030.3
Ceriodaphnia sp. †				2.1	3.0	3.7
Chydoridae†				2.1	5.8	8.3
Cladocera	0.4	0.7	0.7	1.4	2.7	4.1
Daphnia sp. †	1.3	7.7	19.5	5.7	198.8	886.5
Daphniidae†				0.7	7.1	7.1
Diaphanosoma sp†.	0.4	1.5	1.5	1.4	2.6	3.5
Leptodora kindtii (Focke, 1844)†				2.1	11.0	20.1
Moina sp. †				1.4	1.8	1.8
Penilia avirostris Dana, 1849				0.7	11.8	11.8
Podon schmackeri Poppe, 1889	0.4	3.4	3.4			
Sida sp. †				0.7	4.8	4.8
Class Maxillopoda, Infraclass Cirripedia						
Suborder Balanomorpha, cypris	25.9	67.4	1320.4	42.6	61.0	1218.2
Suborder Balanomorpha, nauplii	21.3	24.3	214.2	46.8	195.5	3556.1
Subclass Copepoda, Order Calanoida						
Acartia (*Acanthacartia*) *californiensis* Trinast, 1976				29.1	810.3	22 972.2
Acartia (*Acartiura*) spp., includes *A. hudsonica* Pinhey, 1926 and *A. omorii* Bradford, 1976	32.6	104.8	2775.2	43.3	534.4	17 796.6
Acartia (*Odontacartia*) *pacifica* Steuer, 1915	0.4	1.4	1.4	0.7	84.0	84.0
Acartia (*Acanthacartia*) *steueri* Smirnov, 1936				0.7	6.7	6.7
Acartiella sinensis Shen and Lee, 1963*	0.4	4.2	4.2	2.8	4.1	14.1
Acartiella sp.	0.4	5.9	5.9	0.7	5.6	5.6
Calanus sinicus Brodsky, 1965	11.3	23.1	284.8			
Diaptomidae†	1.3	14.2	39.6	2.8	28.8	47.2
Epischura sp. †				1.4	1.8	1.8
Eurytemora affinis (Poppe, 1880)*	0.4	1.7	1.7	5.0	84.0	292.5
Eurytemora pacifica Sato, 1913	7.5	39.6	511.7	9.2	6.3	20.2
Eurytemora sp.	2.5	11.0	52.5	8.5	170.9	1244.4
Labidocera euchaeta Giesbrecht, 1889	2.5	30.8	164.6			
Labidocera kröyeri (Brady, 1883)	0.4	1.9	1.9			
Labidocera rotunda Mori, 1929	1.3	11.7	30.5			
Leptodiaptomus ashlandi (Marsh, 1893)†				0.7	8.3	8.3
Leptodiaptomus novamexicanus (Herrick, 1895)†				1.4	37.2	72.5
Parvocalanus crassirostris (F .Dahl, 1894)	3.3	7.7	19.8	12.1	321.4	3481.8
Pseudodiaptomus euryhalinus M. W. Johnson, 1939				0.7	0.3	0.3
Pseudodiaptomus forbesi (Poppe and Richard, 1890)*				5.0	678.9	4365.6
Pseudodiaptomus inopinus Burckhardt, 1913*	1.3	12.7	17.7			
Pseudodiaptomus marinus Sato, 1913*	10.5	53.5	375.0	33.3	184.1	4325.7
Pseudodiaptomus sp.	3.3	4.4	14.1	12.1	21.0	194.8
Sinocalanus doerrii (Brehm, 1909)*	0.4	61.4	61.4	0.7	39.4	39.4
Sinocalanus sinensis (Poppe, 1889)	0.4	0.3	0.3			
Sinocalanus sp.				0.7	4.4	4.4
Skistodiaptomus pallidus (Herrick, 1879)†				1.4	7.0	10.4
Skistodiaptomus reighardi (Marsh, 1895)†				1.4	3.6	5.5

Table 4 (*continued*)

Taxon	Transpacific			West Coast		
	Frequency of occurrence (%)	Mean density (m^{-3})	Maximum density (m^{-3})	Frequency of occurrence (%)	Mean density (m^{-3})	Maximum density (m^{-3})
Tortanus (*Eutortanus*) *dextrilobatus* Chen and Zhang, 1965*				11.3	9.7	78.9
Subclass Copepoda, Order Cyclopoida						
Acanthocyclops robustus (G.O. Sars, 1863)†				1.4	2.3	2.8
Acanthocyclops sp.†	0.4	13.5	13.5	1.4	3.6	4.4
Clausidiidae	18.0	14.9	123.8	23.4	43.6	567.2
Cyclopinidae	2.9	11.0	34.3	5.7	161.1	640.5
Diacyclops thomasi (S.A. Forbes, 1882)†	0.4	227.6	227.6	5.0	72.4	252.2
Dioithona oculata (Farran, 1913)	1.7	167.0	624.8	33.3	133.5	3004.6
Ergasilidae	0.4	7.9	7.9	2.8	3.7	6.4
Hemicyclops sp.	10.0	10.9	72.8	7.1	3.3	8.0
Limnoithona tetraspina Zhang and Li, 1976*†	0.4	5.2	5.2	13.5	370.7	4715.7
Limnoithona sp.†	0.4	1.6	1.6	1.4	5.6	8.7
Mesocyclops sp.†	0.4	2.1	2.1	0.7	1.1	1.1
Oithona brevicornis Giesbrecht, 1891	0.4	14.2	14.2			
Oithona davisae Ferrari and Orsi, 1984*	31.8	273.6	7083.1	70.2	3226.1	117 113.2
Subclass Copepoda, Order Harpacticoida						
Ameira sp.				0.7	2.5	2.5
Amphiascopsis cinctus (Claus, 1866)				0.7	3.8	3.8
Amphiascopsis sp.	0.4	1.9	1.9			
Coullana canadensis (Willey, 1934)	0.8	10.2	15.7	14.2	6.1	27.5
Dactylopusia sp.	0.4	0.9	0.9			
Diathrodes sp.	0.4	9.0	9.0	0.7	1.9	1.9
Diosaccidae	0.4	3.9	3.9	0.7	0.6	0.6
Diosaccus spinatus Campbell, 1929	0.4	4.5	4.5			
Diossacus sp.	0.4	5.8	5.8			
Ectinosomatidae	1.7	1.5	1.8	2.1	43.7	129.7
Ectinosoma melaniceps Boeck, 1865				0.7	0.6	0.6
Enhydrosoma sp.	0.4	1.0	1.0			
Euterpina acutifrons Dana, (1848)	3.3	62.8	466.7	46.8	529.4	14 188.1
Harpacticoida (unidentified)	22.2	15.2	497.1	23.4	44.1	865.2
Harpacticus uniremis Kröyer, 1842	0.8	1.4	1.4			
Harpacticus sp.	1.3	8.3	13.3	2.1	45.8	135.0
Idomene purpurocincta (Norman and T Scott, 1905)				0.7	1.3	1.3
Laophontidae	0.4	1.3	1.3			
Leimia vaga Willey, 1923				0.7	0.6	0.6
Longipedia sp.	1.7	5.3	9.2	1.4	512.9	1025.2
Mesochra pygmaea (Claus, 1863)	0.4	9.0	9.0	0.7	2.5	2.5
Mesochra rapiens (Schmeil, 1894)				0.7	5.2	5.2
Metis sp.	0.4	2.9	2.9			
Microarthridion sp.				1.4	236.1	471.6
Neotachidius triangularis (Shen and Tai, 1963)				0.7	8.7	8.7
Paradactylopodia sp.				0.7	0.6	0.6
Pseudobradya sp.	1.3	3.3	4.7	14.9	25.4	168.9
Rhynchothalestris helgolandica (Claus, 1863)				0.7	4.2	4.2
Rhynchothalestris sp.				0.4	5.8	5.8
Schizopera sp.	1.7	1.6	2.0	0.7	2.6	2.6
Tisbe sp.	7.9	317.4	2116.2	14.2	20.6	125.3
Tisbidae	0.4	2.4	2.4	1.4	33.2	61.9
Zaus sp.				0.7	0.7	0.7

Table 4 (*continued*)

Taxon	Transpacific			West Coast		
	Frequency of occurrence (%)	Mean density (m^{-3})	Maximum density (m^{-3})	Frequency of occurrence (%)	Mean density (m^{-3})	Maximum density (m^{-3})
Class Malacostraca, Order Amphipoda						
Anisogammaridae				1.4	3.6	6.3
Caprellidae	0.8	1.6	2.6	0.7	1.3	1.3
Corophium sp.	0.4	5.9	5.9	0.7	0.7	0.7
Eochelidium sp.*	0.4	1.7	1.7	1.4	1.4	1.5
Gammaridea, unidentified	1.3	1.9	2.9	2.1	315.3	943.1
Class Malacostraca, Order Cumacea						
Cumacea, unidentified	0.8	4.0	5.5	3.5	2.3	4.2
Nippoleucon hinumensis (Gamô, 1967)*				6.4	5.9	34.7
Class Malacostraca, Order Decapoda						
Blepharipoda				0.7	0.8	0.8
Callianassidae				0.7	5.1	5.1
Hemigrapsus sp.	0.4	1.4	1.4			
Lophopanopeus bellus (Stimpson, 1860)				1.4	3.9	6.2
Neotrypaea californiensis (Dana, 1854)	0.4	4.2	4.2	1.4	0.8	1.0
Pachygrapsus sp.				0.7	17.5	17.5
Paguridae				1.4	4.7	7.5
Pugettia sp.	0.4	3.1	3.1	2.1	1.6	2.2
Pyromaia tuberculata (Lockington, 1877)				2.1	2.0	4.1
Class Malacostraca, Order Isopoda						
Epicaridea microniscid and cryptoniscid stages	1.7	4.3	11.6	4.3	5.5	13.5
Gnorimosphaeroma oregonense (Dana, 1853)	0.4	1.6	1.6	2.1	0.6	0.7
Gnorimosphaeroma sp.				0.7	0.6	0.6
Idotea sp.				0.7	0.2	0.2
Isopoda, unidentified	6.7	3.5	12.2	19.1	4.7	38.6
Class Malacostraca, Order Mysida						
Acanthomysis aspera Ii, 1964*	0.4	7.8	7.8	1.4	0.5	0.7
Acanthomysis bowmani Modlin and Orsi, 1997*				0.7	0.6	0.6
Alienacanthomysis macropsis W. Tattersall, 1932				6.4	1.7	7.3
Neomysis kadiakensis Ortmann, 1908				2.1	4.2	11.3
Class Arachnida						
Acarina	0.8	1.8	1.9	1.4	1.8	1.8
Phylum Annelida, Class Polychaeta						
Harmothoe imbricata (Linnaeus, 1769)	0.4	9.9	9.9	0.7	58.2	58.2
Spionidae larvae	15.9	454.3	12 072.2	27.7	573.2	18 054.4
Phylum Bryozoa	2.9	2.9	8.9	24.8	27.8	215.6
Phylum Ciliophora, Order Tintinnida	1.3	36.0	93.3	9.2	984.7	11 132.4
Phylum Mollusca, Class Bivalvia	49.8	163.4	9013.5	72.3	605.9	18 940.1
Phylum Rotifera						
Asplanchna spp.†				1.4	20.2	22.2
Brachionus spp.†				0.7	1414.7	1414.7
Kellicottia spp.†				0.7	16.6	16.6
Keratella spp.†				0.7	430.0	430.0
Synchaeta spp.†				0.7	939.5	939.5
Total number of taxa/groups		75			107	

*Denotes species that have been introduced to the Pacific coast of North America.
†Denotes fresh water taxa.

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Table 5. Taxa that were considered to be oceanic, cosmopolitan, or of unknown origin from of 380 ballast tanks sampled in Puget Sound, 2001–2007. The frequency of occurrence, mean and maximum density of each species is reported according to trip type (Transpacific or West Coast)

Taxon	Transpacific			West Coast		
	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})
Class Branchiopoda, Suborder Cladocera						
Evadne sp.	0.8	3.8	4.9	5.7	19.1	135.0
Podon sp.	2.5	51.5	231.1	2.1	26.9	49.3
Class Maxillopoda, Subclass Copepoda						
Copepoda eggs	2.9	1754.4	12 142.9	1.4	688.0	1334.8
Copepoda nauplii	88.7	1588.6	20 641.3	100.0	11 023.4	118 565.9
Subclass Copepoda, Order Calanoida						
Acartia (*Acartia*) *danae* Giesbrecht, 1889	0.4	1.6	1.6	11.3	5.2	29.2
Acartia (*Acartiura*) *longiremis* (Lilljeborg, 1853)	20.5	33.5	508.0	22.7	128.9	2829.4
Acartia (*Acanthacartia*) *tonsa* Dana, 1849	4.2	185.0	1788.6	59.6	208.6	8218.8
Acartia spp.	19.2	37.6	929.7	63.8	409.8	8825.1
Aetideus armatus (Boeck, 1872)				1.4	5.0	9.4
Aetideus pacificus Brodsky, 1950	0.4	4.3	4.3			
Aetideus sp.	0.4	1.4	1.4			
Augaptilidae	0.4	3.3	3.3			
Calanoida (unidentified)	9.2	95.2	1303.6	17.7	220.4	830.0
Calanidae	17.6	20.6	177.1	21.3	624.2	14 335.2
Calanus jashnovi Hulsemann, 1994	2.5	1173.9	6936.4	0.7	9.6	9.6
Calanus marshallae Frost, 1974	1.3	17.6	42.9			
Calanus pacificus Brodsky, 1948	26.8	26.2	377.3	53.2	122.0	1469.7
Calanus spp.	15.5	35.2	615.9	19.9	68.0	437.3
Calocalanus styliremis Giesbrecht, 1888	3.3	7.7	17.4	19.1	24.5	138.9
Calocalanus tenuis Farran, 1926	0.8	1.0	1.4	2.8	5.4	9.4
Calocalanus sp.	2.9	21.0	107.9	12.1	20.3	106.6
Candacia bipinnata (Giesbrecht, 1889)				1.4	2.6	4.3
Candacia sp.				2.8	4.3	11.9
Centropages abdominalis Sato, 1913	13.0	19.0	117.5	10.6	14.9	146.5
Centropages bradyi Wheeler, 1901	1.3	8.5	19.8	4.3	1.5	2.1
Centropages elongatus Giesbrecht, 1896	0.4	1.7	1.7	0.7	0.9	0.9
Centropages sp.	1.3	14.7	39.3	6.4	1.6	6.2
Clausocalanidae	0.4	88.7	88.7			
Clausocalanus arcuicornis (Dana, 1849)	0.4	1.5	1.5	1.4	20.0	30.0
Clausocalanus furcatus (Brady, 1883)	2.1	7.1	10.5	24.8	47.6	462.3
Clausocalanus lividus Frost and Fleminger, 1968	3.3	2.9	12.4	19.1	19.7	280.9
Clausocalanus minor Sewell, 1929	0.4	2.0	2.0	0.7	8.3	8.3
Clausocalanus paululus Farran, 1926	0.4	61.6	61.6			
Clausocalanus pergens Farran, 1926	2.1	6.2	19.1	5.7	29.4	135.9
Clausocalanus sp.	20.1	22.0	135.0	66.7	212.8	3080.9
Ctenocalanus vanus Giesbrecht, 1888	4.2	8.2	31.4	29.8	14.4	110.6
Ctenocalanus sp.	3.8	11.5	24.8	20.6	37.7	285.4
Epilabidocera longipedata (Sato, 1913)				7.1	1.3	4.1
Epilabidocera sp.	0.4	0.7	0.7	5.0	1.9	6.2
Eucalanus sp.	2.1	2.3	6.2	7.8	59.8	483.1
Euchaeta spinosa Giesbrecht, 1893	0.8	1.4	1.4	0.7	1.4	1.4
Euchirella rostrata (Claus, 1866)	0.4	1.5	1.5	1.4	1.0	1.2
Euchirella sp.				0.7	0.3	0.3
Gaetanus sp.	0.4	2.6	2.6			

Table 5 (*continued*)

Taxon	Transpacific			West Coast		
	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})
Ischnocalanus tenuis Farran, 1926	1.7	3.8	6.6	22.7	5.2	27.4
Labidocera jollae Esterly, 1906				0.7	1.8	1.8
Labidocera trispinosa Esterly, 1905				14.9	112.9	2112.6
Labidocera sp.	0.4	42.7	42.7	0.7	0.5	0.5
Lucicutia flavicornis (Claus, 1863)	0.4	2.0	2.0			
Lucicutia gaussae Grice, 1963	0.4	4.3	4.3			
Lucicutia sp.	1.3	1.0	1.9			
Mecynocera clausi Thompson, 1888	1.7	8.7	11.2	5.7	3.4	10.0
Mesocalanus tenuicornis (Dana, 1849)	3.8	5.9	12.4	5.0	5.6	24.9
Mesocalanus sp.	2.5	3.8	9.5	5.7	3.7	12.2
Metridia lucens Boeck, 1865	2.9	13.9	63.7	3.5	11.8	19.1
Metridia okhotensis Brodsky, 1950				0.7	0.4	0.4
Metridia pacifica Brodsky, 1950	12.1	13.2	134.1	18.4	7.0	70.8
Metridia sp.	32.2	19.3	229.0	27.7	20.3	190.4
Microcalanus pusillus G. O. Sars, 1903	5.4	12.0	64.7	2.8	3.3	6.3
Microcalanus sp.	1.3	5.1	10.6	0.7	358.4	358.4
Neocalanus plumchrus (Marukawa, 1921)	6.3	54.9	466.9			
Neocalanus robustior (Giesbrecht, 1888)	3.8	17.1	88.8	12.1	583.6	3720.0
Neocalanus sp.	13.8	26.9	221.4	9.9	14.5	46.8
Paracalanidae	2.1	43.0	98.0	12.8	971.2	4495.3
Paracalanus aculeatus Giesbrecht, 1888	0.8	3.2	3.3			
Paracalanus denudatus Sewell, 1929	0.4	3.5	3.5			
Paracalanus cf. *quasimodo* Bowman, 1971	1.3	244.4	686.6	2.1	1049.3	2878.8
Paracalanus sp.	41.0	64.3	1118.3	74.5	1049.6	13 267.7
Paraeuchaeta concinna (Dana, 1849)	0.4	7.5	7.5			
Paraeuchaeta sp.	0.4	1.5	1.5	1.4	1.2	1.9
Phaenna spinifera Claus, 1863	0.4	1.4	1.4			
Pleuromamma abdominalis (Lubbock, 1856)	0.4	2.7	2.7	2.1	2.2	3.7
Pleuromamma borealis (F. Dahl, 1893)	0.4	1.9	1.9	6.4	4.5	16.5
Pleuromamma gracilis (Claus, 1863)	1.3	0.9	1.5	0.7	3.7	3.7
Pleuromamma xiphias (Giesbrecht, 1889)	0.4	0.7	0.7			
Pleuromamma sp.	1.3	8.2	21.3	2.8	1.0	1.6
Pontellidae	0.8	9.4	13.1	9.9	138.1	705.2
Pontellopsis sp.				4.3	45.3	137.4
Pseudocalanus mimus Frost, 1989	5.9	59.4	287.0	22.7	715.5	5946.4
Pseudocalanus newmani Frost, 1989	16.7	232.7	6507.4	9.2	17.1	105.1
Pseudocalanus sp.	55.2	181.8	2086.7	46.1	214.0	2785.5
Rhincalanus nasutus Giesbrecht, 1888	0.8	510.4	1019.6	0.7	0.8	0.8
Rhincalanus sp.	1.3	6.5	16.4	2.1	11.7	33.1
Scolecithricella dentata (Giesbrecht, 1893)	0.4	1.1	1.1			
Scolecithricella minor (Brady, 1883)	6.7	23.4	263.5	3.5	1.3	3.2
Scolecithricella sp.	0.4	0.5	0.5			
Scolecithrix bradyi (Giesbrecht, 1888)				0.7	0.8	0.8
Scolecithrix danae (Lubbock, 1856)	0.8	30.8	60.4	1.4	1.6	2.4
Subeucalanus crassus (Giesbrecht, 1888)				0.7	0.6	0.6
Temora turbinata (Dana, 1849)	0.4	3.8	3.8			
Temorites sp.	0.4	2.5	2.5			
Tortanus (*Boreotortanus*) *discaudatus* (Thompson and Scott, 1897)	0.8	4.0	4.7	16.3	7.6	39.3

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Table 5 (*continued*)

Taxon	Transpacific			West Coast		
	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})
Tortanus sp.	1.3	3.2	4.7	9.9	10.2	71.4
Subclass Copepoda, Order Caligoida	2.5	10.0	14.7	8.5	47.7	369.1
Subclass Copepoda, Order Cyclopoida						
Cyclopoida (unidentified)	10.0	21.7	266.1	36.9	183.0	3525.2
Corycaeus (*Ditrichocorycaeus*) *amazonicus* (F. Dahl, 1894)				2.1	3.5	7.2
Corycaeus (*Ditrichocorycaeus*) *anglicus* Lubbock, 1857	25.1	22.8	336.8	73.8	147.9	2594.9
Corycaeus (*Onychocorycaeus*) *catus* (F. Dahl, 1894)	0.4	7.0	7.0	0.7	1.7	1.7
Corycaeus sp.	13.4	9.5	79.9	5.0	154.6	1014.7
Farranula curta (Farran, 1911)				0.7	0.8	0.8
Farranula sp.	0.4	0.2	0.2	0.7	0.8	0.8
Oithona atlantica Farran, 1908	10.0	3.7	16.8	10.6	2.5	13.3
Oithona nana Giesbrecht, 1892	0.4	10.1	10.1	0.7	2.7	2.7
Oithona similis Claus, 1866	83.3	1017.7	18 957.1	86.5	1965.9	15 700.1
Oithona sp.	7.1	60.8	772.3	5.7	45.1	314.4
Oncaea clevei Früchtl, 1923	0.4	1.7	1.7			
Oncaea conifera Giesbrecht, 1891	0.8	2.7	2.8			
Oncaea dentipes Giesbrecht, 1891	1.7	49.4	184.0	0.7	7.1	7.1
Oncaea media Giesbrecht, 1891	1.3	9.3	16.5			
Oncaea mediterranea (Claus, 1863)	0.8	22.7	34.9			
Oncaea scottodicarloi Heron and Bradford-Grieve, 1995	0.8	6.3	10.5			
Oncaea subtilis Giesbrecht, 1892	2.1	44.5	101.5	8.5	94.0	597.3
Oncaea venusta Philippi, 1843	2.5	5.7	11.5			
Oncaea zernovi Shmeleva, 1966	2.5	42.5	157.2	0.7	6.1	6.1
Oncaea sp.	59.4	169.1	5133.5	63.1	142.3	6754.7
Sapphirina gemma Dana, 1849				1.4	1.8	2.7
Sapphirina sp.	2.1	6.5	15.3	2.8	4.8	10.9
Subclass Copepoda, Order Harpacticoida						
Clytemnestra scutellata Dana, 1848	2.9	7.2	32.6	2.8	2.6	6.1
Goniopsyllus rostratus Brady, 1883	0.8	15.8	30.3	3.5	5.7	22.6
Macrosetella gracilis (Dana, 1847)	1.3	5.9	13.2			
Microsetella norvegica (Boeck, 1865)	25.9	34.8	1069.6	48.9	57.4	922.6
Microsetella rosea (Dana, 1848)	2.1	4.3	7.1	6.4	4.6	18.9
Microsetella sp.	4.2	6.3	21.0	2.8	12.6	44.0
Miraciidae				0.7	2.5	2.5
Class Malacostraca, Order Amphipoda						
Amphipoda (unidentified)				3.5	1.9	3.9
Hyperiidea	10.9	17.3	331.4	11.3	3.3	15.6
Parathemisto sp.	4.2	4.9	27.6	2.1	1.6	1.9
Class Malacostraca, Order Decapoda						
Cancridae	0.4	1.0	1.0	1.4	1.5	2.7
Caridea	0.4	1.8	1.8	0.7	1.6	1.6
Crangonidae				2.8	3.3	8.7
Decapoda (unidentified)	2.1	2.4	3.7	7.1	1.4	3.3
Hippolytidae	0.4	0.3	0.3	2.1	2.2	4.4
Majidae	0.8	2.0	2.6	6.4	1.0	1.6
Pandalidae	0.4	3.1	3.1	2.1	2.1	4.7
Pinnotheridae	1.7	4.2	9.8	15.6	15.4	186.6
Sergestidae				1.4	1.0	1.3
Class Malacostraca, Order Euphausiacea						

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Table 5 (*continued*)

Taxon	Transpacific			West Coast		
	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})	Frequency of Occurrence (%)	Mean density (m^{-3})	Maximum Density (m^{-3})
Euphausia pacifica Hansen, 1911				1.4	43.5	84.3
Euphausia sp.				0.7	0.6	0.6
Euphausiacea (unidentified)	4.6	2.9	9.4	41.8	34.1	725.7
Class Malacostraca, Order Mysida	0.4	1.0	1.0	7.1	4.9	28.4
Class Malacostraca, Order Tanaidacea				0.7	1.0	1.0
Class Ostracoda	4.2	13.7	81.7	6.4	2.3	8.6
Phylum Annelida, Class Oligochaeta	1.3	44.9	55.9	0.7	11.5	11.5
Phylum Annelida, Class Polychaeta						
Autolytus sp.				0.7	0.6	0.6
Tomopteris sp.				1.4	0.8	1.4
Polychaeta (unidentified)	20.9	42.1	530.1	52.5	343.7	5658.8
Phylum Chaetognatha	8.8	38.6	420.6	17.7	11.2	105.6
Sagitta sp.	16.3	7.1	43.7	32.6	20.5	258.2
Phylum Chordata, Class Cephalochordata				3.5	1.9	4.1
Phylum Chordata, Infraclass Teleosti				4.3	1.8	4.1
Phylum Chordata, Class Larvacea	1.3	52.7	154.7	2.1	10.1	14.6
Phylum Chordata, Class Ascidiacea				0.7	4.0	4.0
Phylum Chordata, Order Copelata						
Oikopleura sp.	2.1	6.2	13.2	29.1	216.0	2169.2
Phylum Cnidaria	0.4	1.1	1.1	2.8	31.6	119.0
Phylum Cnidaria, Class Anthozoa	0.4	1.4	1.4	0.7	47.8	47.8
Phylum Cnidaria, Class Hydrozoa	6.7	3.8	23.6	35.5	23.5	219.6
Phylum Ctenophora				0.7	0.6	0.6
Phylum Echinodermata	7.5	5.0	40.3	18.4	4.0	47.2
Phylum Mollusca, Class Gastropoda	38.5	11.4	275.1	71.6	40.7	1050.9
Phylum Nematoda	3.8	2.0	3.5	7.8	6.0	44.0
Phylum Phoronida	1.7	4.1	8.0	7.1	5.9	30.0
Phylum Playthelminthes, Class Turbellaria	7.9	4.0	28.3	28.4	7.6	100.5
Phylum Rotifera				0.7	507.6	507.6
Phylum Sarcomastigophora, Order Foraminiferida	2.9	406.7	2751.9	20.6	990.2	15 229.4
Phylum Sarcomastigophora, Class Radiolaria	2.5	2.8	5.3	5.0	114.9	785.9
Unidentified Larvae	2.1	4.8	12.7	10.6	20.4	209.1
Total number of taxa/groups		137			138	

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