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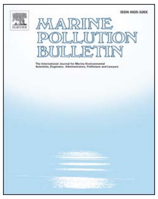

Trait-based characterization of species transported on Japanese tsunami marine debris: Effect of prior invasion history on trait distribution☆

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ABSTRACT

Nearly 300 coastal marine species collected from > 630 debris items from the 2011 Great East Japan earthquake and tsunami have landed alive along the North American Pacific coast and the Hawaiian Archipelago. We synthesized life history, environmental, and distributional traits for 103 of these species and compared species with ($n = 30$) and without ($n = 62$) known invasion histories. The species represent 12 phyla, and Mollusca, Crustacea, and Bryozoa accounted for 71 of the 103 species. The majority are native to the Northwest Pacific and the Central Indo-Pacific. Species with known invasion history were more common on artificial and hardpan substrates, in temperate reef, fouling, and flotsam habitats, at subtropical and tropical temperatures, and exhibited greater salinity tolerance than species with no prior invasion history. Thirty-five Japanese tsunami marine species without prior invasion history overlapped in ordination trait space with known invaders, indicating a subset of species in this novel assemblage that possess traits similar to species with known invasion history.

1. Introduction

In the years since the devastating 2011 Great East Japan earthquake and tsunami, it has become evident that hundreds of coastal species from Japan have crossed the Pacific Ocean in association with tsunami debris, including species known previously to be invasive and cause ecosystem and economic impacts elsewhere (Choong et al., 2012; Calder et al., 2014; Carlton et al., 2017). As of January 2017, we documented the arrival of > 630 debris items with living organisms. These items span a wide spectrum and include docks, buoys, boats, pallets, and wooden structures. All of these items were identified as having originated in Japan and being associated with the tsunami based on evidence as presented in Carlton et al. (2017).

A monumental effort by many researchers and taxonomists generated a comprehensive list of species associated with Japanese Tsunami Marine Debris (JTMD). Although taxonomic identification and genetic verification is ongoing, nearly 300 taxa of invertebrates and protists have been documented on JTMD collected along the Pacific coast of North America and the Hawaiian Archipelago since 2012 (Choong et al., 2012; Calder et al., 2014; Carlton et al., 2017). While the movement of marine species around the globe through anthropogenic activities, such as ships' ballast water and hull fouling, has been a concern for some time (Carlton and Geller, 1993; Carlton, 1996; Ruiz et al., 1997; Callaway et al., 2006), the transport of such large numbers of marine species across an ocean basin on debris appears to be a new phenomenon that has not been documented previously. Furthermore, while similar in some respects to hull fouling, JTMD has some distinct characteristics when compared with other known marine vectors (Sylvester et al., 2011; Clarke Murray et al., 2012; Lo et al., 2012). The transport pathways and landing locations are much less predictable for marine debris than other vectors, and the travel speed is substantially slower than ships. Additionally, JTMD and marine debris in general

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transport adult stages more often than larval stages, which are commonly transported in ballast water (Ruiz and Carlton, 2003).

At this time, we do not know if any of the JTMD species will become established outside of their current distributional range as a result of tsunami debris transport and landing. There are some JTMD species with known prior invasion histories, such as the mussel *Mytilus galloprovincialis* and tunicate *Didemnum vexillum* that, solely due to their prior history, warrant attention in monitoring efforts. However, the identification of species for monitoring from the pool of remaining JTMD species, which do not have a prior invasion history and often have not been previously documented as rafters (Carlton et al., 2017), poses more of a challenge.

The ability to predict biological invasions has been notoriously difficult (Nentwig, 2007). Some approaches to understanding invasion success focus on aspects of the novel environment that can facilitate or dampen invasion propensity, such as the empty niche and biotic resistance hypotheses (Elton, 1958; Levine et al., 2004). Others adopt more of an organismal approach and determine if there are certain biological or ecological species traits, which reflect physiology, morphology, and life history, related to invasion propensity. For example, Van Kleunen et al. (2010) identified traits related to performance, including growth rate and size, which were positively related to invasion propensity in plants. Kolar and Lodge (2002) determined that successful fish invaders in the Great Lakes of North America grew relatively faster, had greater temperature and salinity tolerance, and were more likely to have a prior invasion history than species that had been introduced to the region but did not become invasive. Romanuk et al. (2009) developed a general food web model and determined that feeding mode and trophic position were the most consistent predictors of invasion success. Sol et al. (2012) determined that clutch size was negatively associated and propagule pressure positively associated with invasion propensity in birds and highlighted a potential interaction between propagule pressure and population growth rate. Despite reasonable success identifying traits associated with invasion propensity in terrestrial and freshwater taxa, similar analyses in the marine realm lag behind (Bremner, 2008; Verberk et al., 2013), potentially due, at least in part, to more limited trait information for many marine species (but see Devin and Beisel, 2007; Grabowski et al., 2007).

As part of an international effort to evaluate the risks related to JTMD and its associated species, a database of distributional, environmental, and life history traits of JTMD taxa that were identified to the species level was developed for reference and analysis and is publically-accessible (invasions.si.edu/nemesis/jtmd/index.jsp). A qualitative risk assessment tool, the Canadian Marine Invasive Screening Tool (available at www.bio.gc.ca/science/monitoring-monitorage/cmist/usage-en.php) was used in conjunction with the database to evaluate JTMD species (Therriault et al., in press, this issue). This tool scores both the probability and potential impacts of a species invasion for receiving ecosystems, requires assessors with good general knowledge of invasive species and the assessment area, and is strongly influenced by prior invasion history.

Japanese tsunami marine debris is arguably a novel transport vector and, given that many of the species have not been previously documented as invasive or as long-distance rafters (Carlton et al., 2017), diverse approaches to evaluate their propensity to invade non-native habitats are warranted. Here we present an approach for identifying JTMD species with no prior invasion history that may have a greater propensity to invade based on quantitative analysis of distributional, environmental, and life history information. We defined "invasion history" as documented evidence of establishment and negative impact in areas outside of a species' native range. We used the publically-available JTMD database and focused on traits with broad coverage across species in order to: 1) quantify variability in species' traits along statistically independent gradients; 2) test the hypothesis that certain traits differentiate species with prior invasion history from those without any known invasion history; and 3) identify species without invasion history that have traits similar to those with invasion history and, therefore, may have a propensity for invasion.

2. Methods

2.1. Species associated with Japanese Tsunami Marine Debris (JTMD)

We considered a debris item as JTMD if it had: 1) clear identification such as a serial or registration number that was linked to an object lost during the tsunami of 2011; 2) clear evidence of associated biota originating primarily from the Tōhoku coast of Japan, which is where the greatest impacts from the tsunami occurred; or 3) a combination of these factors (Carlton et al., 2017). JTMD biofouled items landing along the Pacific coast of North America (British Columbia, Canada and Alaska, Washington, Oregon, and California, U.S.A.) and the Hawaiian Archipelago were opportunistically sampled for invertebrates, algae, and fish between June 2012 and July 2016. Associated biota were collected, preserved, and identified to the lowest taxonomic level by experienced systematists. We used the publically-accessible database of life history, distributional, and environmental traits of JTMD taxa that were identified to the species level (invasions.si.edu/nemesis/jtmd/index.jsp). The information came from a variety of sources, including primary publications, reports, databases, and internet searches in both international and Japanese literature.

For this analysis, we used the subset of invertebrate species for which there was adequate information for qualitative synthesis (Table A1; $n = 103$) and quantitative analysis ($n = 92$). Although 51 species (out of 154 species included in the database as of June 2016) were removed due to inadequate information, there was no difference in the proportion of species per phyla between the reduced ($n = 103$) and the larger ($n = 154$) database ($\chi^2 = 9.56$, df = 11, $P > 0.80$). In only two instances, we included a species complex (*Jassa marmorata*-complex and *Stenothoe crenulata*-complex).

We assigned each species to one of the three following invasion history categories: 1) clear invasion history outside of native range with documented establishment in non-native areas; 2) not known outside of its native range; or 3) cryptogenic, i.e., unknown or unclear origin. For 29 of the 30 species included in our analysis as having clear invasion history (Table A1), there is documentation of negative impacts on a novel environment outside of the species' native distribution. The history of one species, *Lyrodus takanoshimensis*, a wood boring bivalve, was somewhat ambiguous. It was identified as invasive by Carlton (1992) and as a probable invasive in Fofonoff et al. (2016). Therefore, given the available information, we included it as a species with known invasion history in our analysis.

2.2. Qualitative synthesis

We compiled summaries of JTMD species across various categories of interest, including phyla, native range, and invasion history, to provide some synthesis of the 103 species included in our analysis. Given that JTMD is arguably a newly documented species transport vector (Carlton et al., 2017), we also summarized the available information on prior, reported transport history for these 103 species. Potential vectors included hull fouling, aquaculture and fisheries, ballast water, natural dispersal, recreation, moveable structures, solid ballast, and other (primarily natural dispersal). Given that we did not have robust estimates of species abundance or a comprehensive evaluation of which individuals were reproductive across debris items, we did not include any measure of abundance or propagule pressure. The number of species included in each qualitative summary varied depending on the availability of information.

2.3. Quantitative analysis

Given our objective was to quantitatively compare species with and