Exploring potential establishment of marine rafting species after transoceanic long-distance dispersal

Christina Simkanin [1*], James T. Carlton[2], Brian Steves[1], Paul Fofonoff[1], Jocelyn C. Nelson[3,4], Cathryn Clarke Murray[3,5], Gregory M. Ruiz[1]

[1] Smithsonian Environmental Research Center, Edgewater, MD, USA

[2] Williams College - Mystic Seaport, Mystic, CT, USA

[3] North Pacific Marine Science Organization (PICES), Sidney, BC, Canada

[4] Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC, Canada

[5] Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, BC, Canada

* Corresponding author - 647 Contees Wharf Rd, Edgewater, MD 21037-0028; csimkanin@gmail.com; simkanic@si.edu

Acknowledgements

We are grateful to the large team of collaborators and taxonomists who contributed enormous time and expertise to collecting tsunami-related debris and identifying organisms. We also gratefully acknowledge those who assisted in the literature review and compilation of relevant references: Meagan Abele, Reva Gillman, Shigeo Kawaguchi, Lauran Liggan, Kiyotaka Matsumura, Hiroshi Ogawa, Michio Otani, Masaki Sakaguchi, Danielle Scriven, and Janson Wong. Research support was provided by the Ministry of Environment of Japan through the North Pacific Marine Science Organization (PICES); National Science Foundation (Division of Ocean Science, Biological Oceanography), NSF-OCE-1266417, 1266234, 12667, and 1266406; and the Smithsonian Institution.

Biosketch

Christina Simkanin is a marine ecologist interested in biogeography, conservation biology, and nearshore ecosystems. The research team includes scientists from the United States and Canada who work on the ecology of non-native species and the role of marine debris in species transport.

Short running title: Modelling establishment of marine rafting species

Abstract

Aim On March 11, 2011, the Great East Japan Earthquake triggered a massive tsunami that resulted in the largest known rafting event in recorded history. By spring 2012, marine debris began washing ashore along the Pacific Coast of the U.S. and Canada with a wide-range of Asian coastal species attached. We used this unique dataset, where the source region, date of dislodgment, and landing location are known, to assess the potential for species invasions by transoceanic rafting on marine debris.

Location Northeast Pacific from 20 to 60°N

Time period Current

Major taxa studied Forty-eight invertebrate and algal species recorded on Japanese tsunami marine debris.

Methods We developed Maximum Entropy (MaxEnt) species distribution models for 48 species recorded on Japanese tsunami marine debris to predict establishment potential along the Pacific Coast from 20-60°N. Models were compared within the context of historical marine introductions from Japan to this region to validate the emergence of marine debris as a novel vector for species transfer.

Results Overall, 27% (13 species) landed with debris at locations with suitable environmental conditions for establishment and survival, indicating that these species may be able to establish new populations or introduce greater genetic diversity to already established non-native populations. A further 22 species have environmental match in areas where tsunami debris likely landed, but was not extensively sampled. Nearly 100 Japanese marine species previously invaded the northeastern Pacific, demonstrating this region's environmental suitability for rafting Japanese biota. Historical invasions from Asia are highest in California and largely known from bays and harbors.

Main conclusions Marine debris is a novel and growing vector for non-native species introduction. By utilizing a unique dataset of Japanese tsunami marine debris species, our predictive models show capacity for new transoceanic invasions and can focus monitoring priorities to detect successful long-distance dispersal across the world's oceans.

Keywords: biological invasions, introduced species, Japanese tsunami, long-distance dispersal, marine debris, marine rafting, MaxEnt, species distribution modelling

1. Introduction

Accidental and episodic long-distance dispersal is considered a critical process for population expansion (Darwin, 1859; Carlquist, 1981). However, the unpredictable and random nature of its occurrence poses a challenge for quantifying its role in shaping species distributions (Nathan, 2006; Gillespie *et al.*, 2012). In some cases, extreme or catastrophic events may trigger long-distance dispersal, as was shown for the 2011 Great Japan Tsunami (Carlton *et al.*, 2017). On March 11, 2011 the Great East Japan Earthquake, with a magnitude of 9.0, struck the Tōhoku region and triggered a massive tsunami. Waves up to 40.5 m high inundated more than 550 km^2 of land, causing large-scale devastation and washing immense amounts of material and debris into the ocean. While non-buoyant materials sank close to shore, buoyant material created a massive, floating debris field (Goto & Shibata, 2015). The dominant currents in the region, the Kuroshio and Oyashio, converge off the coast of Tōhoku and curve eastward to join the North Pacific Current. This predominantly eastward flow meant that by spring 2012, debris associated with the tsunami had transited the Pacific Ocean and started washing ashore on beaches along the United States (U.S.) and Canadian coasts (Carlton *et al.*, 2017). This debris harbored hundreds of living Japanese species, having survived the journey, with potential to establish populations in North America.

In the oceans, species have rafted long distances while attached to natural substrates, such as wood, for millennia. However, most contemporary floating debris has shifted to being anthropogenic in origin (Thiel & Gutow, 2005a). Since the 1950s, when reports of oceanic plastic pollution first appeared (Ryan, 2015), this non-biodegradable substrate has increased in prevalence throughout the world's seas (Thompson *et al.*, 2004; Law, 2017). Plastic, of all shapes and sizes, is now ubiquitous in marine environments and occurs as shoreline debris on all continents and islands (Barnes, 2002; Lavers & Bond, 2017). This debris can host and transport living marine species (Winston *et al.*, 1997; Thiel & Gutow, 2005b). Critically, plastic and other human-made debris persists much longer than natural materials (e.g., logs), such that previously rare transoceanic dispersal events may now be more common, but little is known about the likelihood or prevalence of species spread associated with this growing transport mechanism.

Biofouling, or the accumulation of sessile assemblages and associated mobile taxa on surfaces of solid substrates, is a well-known and potent vector for global species introductions (Hewitt & Campbell, 2010; Davidson *et al.*, 2018). Most examples of species introductions resulting from biofouling transfers are associated with commercial ships, recreational boats, or as epibionts on algae or shellfish associated with live bait and aquaculture shipments (Ruiz *et al.*, 2000; Cohen *et al.*, 2001; Floerl *et al.*, 2005). There are far fewer documented cases of species introductions through rafting on ocean debris (but see Censky *et al.,* 1998 for a documented example of a lizard introduction). The longevity of plastic and its growing ubiquity in marine environments (Cozar *et al.*, 2014; Jambeck *et al.*, 2015) suggests that marine debris may play an increasingly important role as a vector of potentially nuisance non-native species. Ship-based surveys of debris in the open ocean have found a diversity of coastal marine invertebrates including hydroids, barnacles, amphipods, bryozoans, echinoderms and bivalves (Goldstein *et al.*, 2014; Gil & Pfaller, 2016), which could establish new populations on arrival to foreign coastlines.

Quantifying invasion risks associated with species rafting on marine debris is challenging, as items are typically devoid of any identifying characteristics to determine origin or duration at sea, and the frequency of species arrivals on drift material is difficult to enumerate over large scales (Rech *et al.*, 2016). Furthermore, surviving the dispersal event is only the first step to population establishment (Blackburn *et al.*, 2011); upon arrival, species face varying abiotic and biotic conditions which can preclude survival and reproduction. Predictive models to investigate the suitability of a receiving environment for species persistence may help infer invasion risks. Specifically, species distribution models (also commonly known as Environmental Niche Models), which utilize global occurrence records and broad scale environmental data, can be used to predict species distributions in novel environments and conditions (Peterson & Vieglais, 2001; Guisan *et al.*, 2014) and can provide valuable information for targeted monitoring and surveillance efforts (Guisan *et al.*, 2013).

A large scale survey of the organisms found attached to debris associated with the 2011 Japanese tsunami identified over 289 species from 16 phyla of marine species on a variety of anthropogenic items (Carlton *et al.*, 2017). Here, we use this unique dataset, where the source region and the date of dislodgement into the ocean are known, to evaluate the potential for species introduction through transoceanic rafting. To do this, we used two complementary methods: (1) species distribution modelling to investigate the environmental suitability of the Pacific coast of the U.S. and Canada for Japanese species recorded on tsunami debris – many of which are not known to be previously introduced or established; and (2) an assessment of historical records of marine species introductions from Japan to the western U.S. and Canada, to place the recent rafting event within the context of historical anthropogenic biotic exchange between these regions. This analysis provides predictive evidence for the potential spatial distribution of species introduced through rafting, an approach which can inform management and monitoring efforts while providing data to assess a rarely quantified biogeographical process – long-distance dispersal.

2. Materials and Methods

2.1 Distribution modelling of species rafting on Japanese tsunami marine debris

In June 2012, confirmed items of Japanese tsunami marine debris (JTMD) began washing ashore along the Oregon coast (Carlton *et al.*, 2017). Shortly after, an extensive network of local, state, provincial and federal agencies, private citizens, and environmental groups from California to Alaska and Hawaii was established to recognize, record, and quantify tsunami debris items. To distinguish tsunami objects from other types of ocean debris, multiple lines of evidence were combined, including (a) formal identification through the Japanese Consulate using registration numbers or other identifying characteristics from floating objects; (b) the use of oceanographic models and tracking databases to predict debris fields and pulses; and (c) bioforensics using the known non-random diversity of coastal marine species from shores of the Tōhoku region to indicate location of origin (see Carlton *et al*., 2017). Recorded JTMD items included vessels, plastic totes, buoys, fishing gear, floating docks, post-and-beam wood, and many other human-made items associated with coastal communities. Overall, more than 630 pieces of confirmed JTMD objects that washed ashore on the Pacific Coast of the U.S. and Canada were sampled and found to carry over 289 species (Carlton *et al.*, 2017). The majority of the sampled debris was collected along the Oregon and Washington coasts, spanning from 42 to 48°N, but oceanographic models show that high amounts of tsunami generated debris likely landed within a much larger region spanning from Northern California to British Columbia and Alaska (Clarke Murray *et al.*, 2018).

We used MaxEnt (ver. 3.4.0) species distribution modelling (Phillips *et al.*, 2006) to locate areas along the Pacific Coast of the U.S. and Canada that are most suitable to the establishment of species identified from tsunami associated marine debris. We gathered geographically referenced global occurrence records from species native and non-native distributions using the Global Biodiversity Information System (GBIF.org 2016); the U.S. National Exotic Marine and Estuarine Species Information System (Fofonoff *et al.*, 2016); and detailed searches of literature from Japan, Russia, Korea, and China to contribute additional records from species' native ranges. Our aim was to collate data across resources to reduce the presence of sampling bias in occurrence records and produce the most accurate map of species current global distributions. For modeling, each species reported from tsunami debris (see species list in Carlton *et al.*, 2017) had to meet a series of criteria: (1) be identified to species level; (2) not be suspected to be part of a species complex; (3) be reported from at least one object that landed along the Pacific Coast of the U.S. or Canada (this excluded species reported only from debris landing in Hawaii); (4) have georeferenced occurrence records from Japan; and (5) have at least 20 global occurrence records at 5 arcminute (*c.* 9.2 km or 0.083°) grid cell resolution. We endeavored to only use occurrence records from established populations in our modelling, therefore species records from debris landings were not included in this analysis. Previous research shows that MaxEnt performs relatively well for species with low numbers of occurrence records (e.g. 20-30 spatially seperated points; Hernandez *et al.*, 2006; Pearson *et al.*, 2007), but simpler models are necessary for species with few occurrences to avoid over-fitting (Merow *et al.*, 2014). After applying these criteria, 48 species from 10 phyla of marine algae and invertebrates remained for modelling. A majority of species were sessile invertebrates (n=30), while 16 were mobile invertebrates and two were algae. Carlton et al. (2017) used body size as a way to infer ages of debris rafting species and excluded species which appeared to be newly settled and were therefore likely to be acquired as floating debris neared the North American coastline. Therefore, this subset of species can be linked directly to marine debris which transited across the Pacific from Japan to the Pacific Coast of North America.

Over 17,000 georeferenced occurrence points for the 48 species were collated and quality assessed using the software ModestR 2.0 (http://www.ipez.es/ModestR/) and "spThin" (Aiello-Lammens *et al.*, 2015) in R 3.4.2 (R Core Team, 2017). We conducted a systematic procedure to check the accuracy of species occurrences, which included: removing non-contemporary (i.e. fossil) records, removing duplicate points, removing coordinates with low spatial resolution (<2 decimal places), removing terrestrial records, reducing the number of points to match the resolution of the environmental data layers, and removing climatic outliers using jackknife resampling. This exhaustive data cleaning resulted in 3,215 occurrence records remaining, ranging from 20 to 211 georeferenced points per species (Table 1).

Sixteen candidate environmental data layers at 5-arcminute resolution were selected from Bio-ORACLE (Tyberghein *et al.*, 2012; Assis *et al.*, 2017) to represent the abiotic factors essential for marine invertebrate and algae distributions. Collinearity amongst environmental variables can decrease model performance and overall predictive accuracy (Dormann *et al.*, 2013); therefore we followed a variable selection protocol, using the R packages "sdmpredictors" (Bosch, 2017) and "usdm" (Naimi *et al.*, 2014), to remove correlated and multi-collinear variables. We used a pairwise Pearson-moment correlation matrix to identify highly correlated (r>0.70) variables and selected the most ecologically relevant data layers for modelling (Supporting Information TableS1 and S2). Variance inflation factors (VIFs) were also quantified, using a cut-off of 5, to determine how much variance of an estimated regression coefficient is increased because of multi-collinearity (Guisan *et al.*, 2017). In the end, seven suitable environmental predictor variables were chosen for marine invertebrate models: annual mean calcite concentration (mol/m^{-3}), annual mean chlorophyll A (mg/m^3), annual mean pH, mean primary productivity at minimum depth (g m^{-2} yr^{-1}), mean seawater salinity (psu), and annual maximum and range of sea surface temperature (°C). For algal species models, six variables were selected, including: mean cloud fraction (%), mean diffuse attenuation (m^{-1}), mean pH, mean seawater salinity (psu), and annual maximum and range of sea surface temperature (°C).

MaxEnt is a machine learning algorithm that uses presence only data, a random subset of 10,000 pseudo-absence background points, and a group of environmental data layers to determine the optimal probability distribution of a species in alternate space or time (Phillips *et al.*, 2006). There is increasing evidence that use of MaxEnt's default parameters does not always generate the best possible model output (Anderson & Gonzalez, 2011; Morales *et al.*, 2017). Therefore we used the R package "ENMeval" (Muscarella *et al.*, 2014) to reduce unnecessary model complexity and carry out model tuning for each species. ENMeval runs automated analyses to determine the most optimal feature class and regularization parameters using AICc scores, a version of the Akaike Information Criterion optimized for smaller sample sizes. Background points were generated by using the bathymetry layer from MARSPEC (Sbrocco & Barber, 2013) to create a global raster clipped to depths of 0-200m along the coastline. This 'depth raster' was randomly sampled for 10,000 points to be used as pseudo-absences in the model. This depth raster was also used as a mask in our raster stack of environmental layers to limit model predictions to nearshore (<200 m) water depth. Data partitioning for testing and training was carried out using jackknife cross-validation for species with >25 occurrence records, whereas block structured cross-validation was used for species with 25 or more records (Muscarella *et al.*, 2014). Block cross-validation is known to be most suitable for models including species transfers across space and time, such as native versus non-native regions (Wenger & Olden, 2012). The feature classes and regularization multiplier parameters selected to represent the simplest MaxEnt model with best fit for each of the 48 tsunami debris species are shown in Supporting Information Table S3. For MaxEnt runs using the R package 'dismo' (Hijmans *et al.*, 2017), parameters leading to the simplest model and best fit were set for each species individually, and global occurrence data were split into two parts – 70% of data were used for model training and 30% were used for model testing. Jackknife resampling was used to test the importance of each environmental variable, alone and relative to the other variables, to species distributions. Modeling output used complementary log-log (cloglog) (Phillips *et al.*, 2017) to produce an estimate of occurrence probability for each species for the Pacific Coast of the U.S. and Canada (Supporting Information Figures S1-48). The 48 suitability maps were transformed using MaxSST or the 'maximum test sensitivity plus specificity cloglog threshold' (Liu *et al.*, 2013) from the MaxEnt modelling output and combined into a single binary heat map reflecting the risk of invasion of 1-48 tsunami debris species. To determine which species landed attached to debris in areas of high predicted environmental suitability for survival and growth, we obtained the predicted cloglog probability score for each species within each 5 arcmin grid cell along the Pacific coast. MaxEnt modelling outputs are shown in Supporting Information Table S4 and debris landing locations for each species were garnered from the Supplementary Information in Carlton *et al*. (2017).

2.2 Prior anthropogenic biotic exchange from Japan to the Pacific coast of the U.S. and Canada

To understand earlier episodes of anthropogenic biotic exchange across the Pacific, we documented the number of marine invertebrates and algae (i.e. excluding vascular plants and vertebrates) that are native to Japan and have non-native populations on the Pacific Coast of the U.S. and Canada. This list was compiled using records from published literature, museum collections, and field-based surveys (Fofonoff *et al.*, 2016; G.M. Ruiz unpublished data). We restricted our analyses to species with established non-native populations, which we considered to exist if: (1) there were multiple occurrence records over multiple years for a given location; (2) local populations were reported to be numerous and successfully reproducing; or (3) the species was reported as established. Thus, we excluded some non-native species that were not known to be established or were considered to have diminished or failed populations. We measured latitudinal extent of species non-native ranges on the Pacific coast of North America by determining the most northerly and most southerly record of species established occurrence and assessed whether currently known non-native populations are centered in bays, harbors and estuaries, and/or open coastal locations.

3. Results

3.1 Distribution modelling of species rafting on Japanese tsunami marine debris

The hotspot of environmental suitability for the marine debris species modelled was centered on warm waters surrounding Baja California, Mexico, with an additional peak in San Francisco Bay (Figure 1). As most of the sampling for debris objects occurred in Oregon and Washington (Figure 1 inset), most species were recorded from debris that washed ashore in areas without suitable abiotic conditions for survival and growth. Still, of the 48 species, 13 have high (>0.50) occurrence probability rates in locations where tsunami debris was actively retrieved and sampled (Figure 2), indicating that these species may be able to establish new populations or introduce greater genetic diversity to already established non-native populations. Two of these species are not currently introduced or established on the Pacific Coast of the U.S. or Canada – the bryozoan *Exochella tricuspis,* and the worm *Hydroides* *ezoensis*; two species are already established in areas along this coast, but are not currently introduced in Oregon or Washington where marine debris was sampled – the gastropod *Crepidula onyx* (which is native to California) and the algae *Undaria pinnatifida* (which is introduced in California); and the other nine species are introduced and established near debris landing locations already – the amphipods *Ampithoe valida* and *Caprella mutica*, the oyster *Crassostrea gigas*, the bryozoan *Cryptosula pallasiana*, the sea anemone *Diadumene lineata*, the sea-squirt *Didemnum vexillum*, the isopod *Ianiropsis serricaudis*, the mussel *Mytilus galloprovincialis*, and the bryozoan *Schizoporella japonica*. Interestingly, an additional 22 species have high occurrence probability (>0.50) for some areas of British Columbia and Alaska (Figure 2 and Supporting Information Figures S1-48) where tsunami debris likely arrived (Clarke Murray *et al.*, 2018), but was not able to be retrieved and sampled. Nineteen of these species are not currently known to be introduced and established anywhere on the Pacific Coast of the U.S. or Canada – including the barnacles *Chthamalus challengeri, Megabalanus rosa* and *Tetraclita japonica*; the bivalve mollusks *Arca boucardi*, *Bankia carinata*, *Hiatella orientalis*, *Mizuhopecten yessoensis*, *Modiolus nipponicus*, *Mytilisepta virgata*, and *Mytilus coruscus*; the crab *Hemigrapsus sanguineus*; the gastropods *Lottia dorsuosa*, *Lottia kogamogai*, *Reishia bronni*, *Siphonaria japonica*, and *Siphonaria sirius*; the parasitic hydroid *Eutima japonica*, and the sea stars *Aphelasterias japonica* and *Patiria pectinifera*.

3.2 Prior anthropogenic biotic exchange from Japan to the Pacific coast of the U.S. and Canada

There are 319 known marine and estuarine invertebrate and algal species introduced and established on the Pacific Coast of the U.S. and Canada, and 99 (or 31%) of these are native to Japan. This represents 19 algae and 80 marine invertebrates, spanning 13 marine phyla (Supporting Information Table S5). Although this number is a comprehensive assessment based on current knowledge, it is also likely a conservative estimate, as the taxonomic and biogeographic history of many marine species is still unknown or developing. The hotspot of invasion for non-native species originally from Japan (Figure 3) is centered on San Francisco Bay and central California, extending from 36 to 38°N. Many of these species have introduced ranges which extend further south into southern California, while far fewer species of Japanese origin have ranges known to extend north into Oregon, Washington, British Columbia and Alaska. A majority of these species have non-native populations in bays, harbors and estuaries (n=96), while fewer (n=24) have known non-native populations on more open and exposed coastlines (Supporting Information Table S5).

4. Discussion

The role of long-distance dispersal in population expansion is historically difficult to enumerate, but evidence from the Japanese tsunami of 2011 shows that a wide variety of marine organisms are able to survive for years adrift on debris across more than 7,000 km of ocean (Carlton *et al.*, 2017). As the amount of oceanic debris continues to increase (Eriksen *et al.*, 2014; Lebreton *et al.*, 2018), this dispersal mechanism is likely to grow in prevalence and may lead to increased likelihood of species invasions. Dispersal is a critical first step to population establishment, but on arrival, individuals surviving oceanic transport on debris face several barriers to population growth (Carlquist, 1966; Blackburn *et al.*, 2011). The first such barrier is suitable abiotic conditions for survival and reproduction. Our species distribution models show that 13 of the 48 marine debris species have abiotic tolerances which match the environmental conditions in areas where they were sampled from tsunami debris, and a further 22 have some environmental match to conditions in portions of British Columbia and Alaska where large amounts of tsunami debris may have landed, but was not sampled. Twenty one of the species we modelled are known to be introduced to other locations around the globe (Table 1). Past invasion history is often considered a predictor of future invasion success (Kolar & Lodge, 2001) indicating that a species is capable of establishing populations under novel environmental conditions in other non-native ecosystems. New research, however, has highlighted the increasing proportion of non-native species that have no prior invasion history and this is driven by links between new regions and species pools (Seebens *et al.*, 2018), for which, the emergence of anthropogenic floating debris as a vector for species dispersal is a good example. These novel and emerging species and vectors pose a particular challenge for introduced species management, but species distribution models (when possible) can provide early predictions to aid targeted monitoring and quick responses to new invaders.

The 48 species modelled here are a small subset of the total species pool rafting on ocean debris. For Japanese tsunami debris alone, at least 289 species (Carlton *et al.*, 2017) have been recorded and rarefaction curves show that this number is only a portion of the total taxa that arrived (Carlton *et al.*, 2017). Furthermore, a large amount of debris likely washed up along the coastline without detection or without identifying characteristics to connect it to the 2011 Japanese tsunami event and this debris may have carried varied species richness. Ongoing field surveys show that tsunami debris from this event is still washing ashore, although the frequency has decreased steadily since summer 2015 (Carlton *et al.*, 2018). A greater number of species likely pose invasion risks for the Pacific coast of North America, but without more knowledge of their arrival, along with the limited availability of global georeferenced distribution records for most species, our ability to provide an assessment of the invasion risks posed by species rafting on marine debris is hindered. Our data show, however, that 27% of species modeled here have high environmental match with known debris landing locations. Further, most (n=45) of the 48 species have a planktonic life phase ranging from 130 days in the case of the sea star *Asterias amurensis* to the minutes to hours of most of the ascidian and bryozoan species, highlighting that natural dispersal across the Pacific Ocean is not possible (Table 1).

Nine of the marine debris species with high environmental suitability in the region of tsunami debris landings are already established with large introduced ranges (from California to Alaska) on the Pacific Coast of the U.S. and Canada. These species are clearly capable of survival, growth and reproduction in this introduced range and the arrival of new propagules may increase genetic diversity of currently established populations (Hanyuda *et al.*, 2018). The Japanese tsunami debris dataset highlights the ability of these species to raft across large swaths of ocean, and although these long-distance dispersal events are historically rare, they may play a crucial role in the maintenance of genetic connectivity within meta-populations (Trakhtenbrot *et al.*, 2005). Increased levels of genetic diversity and mixing can enhance spread and persistence of non-native populations by increasing the likelihood of local adaptation, increasing fitness levels through greater mixing of genotypes, and producing novel hybrids that are able to exploit new environments and habitats (Roman & Darling, 2007). In time, genetic tools, used in combination with data from species sampling campaigns, could be used to determine genetic differentiation between populations and estimate historical genetic admixture and linkages, providing evidence for the role of long-distance dispersal in population connectivity.

A total of 99 invertebrates and algae from Japan have previously established populations on the Pacific Coast of the U.S. and Canada, further supporting the environmental suitability between these regions. The area of highest prevalence is centered on San Francisco Bay and the north-central part of California. This region has historically been connected to Japan through varied human-mediated vectors, including commercial shipping and Japanese oyster aquaculture (Carlton, 1979; Andrews, 1980). Most debris from the Japanese tsunami is thought to have landed further north along the coastline, from Northern California through Alaska (Clarke Murray *et al.*, 2018). Marine debris represents a novel vector for non-native species spread, in that it differs from other contemporary transport mechanisms, like commercial shipping and aquaculture shipments, by connecting locations that are not typically linked (i.e. outside ports and harbors). Furthermore, the origin and endpoint locations of marine debris are difficult to predict and generally spatially haphazard. Debris, therefore, may act as a species transport mechanism to areas rarely associated with traditional vector hubs (shipping terminals, marinas, and aquaculture facilities) such as outer coastlines, which contemporary data show are currently less impacted by introduced species (Zabin *et al.*, 2018). Also, human-made debris dislodged during extreme events often originates from populated and modified coastal ecosystems, with high amounts of coastal infrastructure, which are hubs for non-native species (Ruiz *et al.*, 2009). Landing locations, on the other hand, are wide-ranging and random, and can include pristine, protected and remote areas of low human density – which are typically less impacted by non-native species (Ardura *et al.*, 2016; Gallardo *et al.*, 2017). Of the 99 species previously introduced, only 24 are known to have established non-native populations in locations beyond bays and harbors; although this pattern could also be driven by sampling bias as a majority of surveys for non-native species are conducted in bays and harbors, whereas the distribution of non-native species in open coastal sites is far less known (Ruiz *et al.* 2009).

The survival of species attached to debris washing ashore on the U.S. and Canadian Pacific coasts shows that some coastal species can withstand oceanic conditions for years. These data challenge the idea that coastal organisms experience low survival in open ocean conditions because of decreased food availability in oligotrophic conditions (Polovina *et al.*, 2008) and long-term exposure to harmful UV-B (Smith & Baker, 1979). Not only did these species survive the long-distance ocean transit, but some are known to have either undergone gametogenesis during the crossing, such as the mussel *Mytilus galloprovincialis* (Miller *et al.*, 2018a), or produced multiple filial populations, such as amphipods, isopods, and marine insects. The reported debris species therefore represent a unique subset of organisms which are hardy enough to withstand varying environmental conditions during transit. Previous analyses indicate that some traits, like smaller adult size, a sessile lifestyle, and the ability to reproduce both sexually and asexually may enhance survival of rafting species (Thiel & Gutow, 2005b). An investigation of the traits associated with tsunami debris species more specifically, indicates that having a greater occurrence on artificial substrates amongst biofouling communities and greater salinity tolerance are consistent across species which have prior global invasion histories and are therefore considered the most likely to establish in the U.S. and Canada (Miller *et al.*, 2018b).

There are limitations to how accurate species distribution models can be for detecting newly established species. For instance, despite having suitable environmental conditions at debris landing sites, species must overcome a number of additional barriers for successful population growth and establishment. These barriers include Allee effects, or the tendency for small populations to experience limited growth due to low genetic diversity, inbreeding, and difficulty finding mates; the potentially limited availability of suitable habitat in the receiving environment; and biotic interactions such as predation and competition that can limit establishment success. The lack of consideration for these additional factors is a more general criticism of species distribution models, and efforts are being made to incorporate habitat mosaics, dispersal, and biotic information into mechanistic models to increase predictive accuracy (e.g. Mellin *et al.*, 2016). Habitat filtering, specifically, is likely to limit colonization and establishment for debris species. For instance, species that need hard substrates for attachment and growth are not likely to survive for long durations on sandy beaches, where a majority of the tsunami debris was detected (Carlton *et al.* 2017). This detection could be an artifact of search effort, however, as rocky shores, especially along high energy open coastlines such as the those in the northeastern Pacific, are less likely to be visited by coastal resource rangers, beach walkers, and beachcombers. Similarly, tsunami debris items washing into bays and estuaries were rarely detected (per Carlton *et al.* 2017), but these areas have mostly inaccessible shorelines and are closer to urbanized areas increasing the incidence of floating debris overall, making detection of tsunami related items more challenging.

Furthermore, choices made during the modelling process itself, specifically in addressing sampling biases in presence and pseudo-absence background points can have large effects on predicted species distributions (Merow et al., 2013; Yuckulic et al., 2013). We attempted to reduce spatial bias in our models by carrying out a randomized selection process for coastal pseudo-absence points, incorporating data from a range of sources (e.g. online global repositories and detailed searches of the research literature) for presence points, and running detailed quality analysis of known occurrence records (described in the methods). We considered using a target list (as suggested by Phillips et al. 2009 and Yuckulic et al., 2013), but this could introduce spatial bias in another way by assuming that researchers investigating nearshore marine invertebrates have broad search images and data collection protocols for the full suite of species modelled here, which is unlikely. This issue of spatial bias is an important one, and greater knowledge of a species true presence and absence in a given location would certainly improve predictive accuracy. Lastly, the occurrence probability estimates shown for each species are not representative of predicted species density or habitat suitability in any way (Elith *et al.* 2011). The density of an organism is likely to vary greatly, and this is especially true for newly establishing species which are often at low-densities and therefore challenging to detect (Crooks, 2005).

Humans are notoriously successful dispersal agents and have been transporting species around the globe, intentionally and unintentionally, for centuries. In modern times, these transits are often recorded and can be enumerated over large scales (e.g. Verling *et al.*, 2005; Seebens *et al.*, 2013). The global increase in floating human-made debris, however, changes this association, as these dispersal events often go unnoticed or unaccounted for. The Japanese tsunami provided a unique case in which to understand long-distance dispersal through rafting in the modern era (Carlton *et al.*, 2017; Chown, 2017). It is clear that large numbers of coastal marine organisms can withstand varying durations of open ocean transport attached to marine debris, although species-specific variability in growth, reproduction, and survival while attached to oceanic debris is still unknown. The predictive maps and models developed here can be used to set priorities for monitoring for establishment of tsunami debris species, increasing the likelihood of early detection and successful eradication, and providing testable hypotheses for investigating the frequency of successful long-distance dispersal across the world’s oceans.

References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B. & Anderson, R.P. (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, **38**, 541-545.

Anderson, R.P. & Gonzalez, I. (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecological Modelling*, **222**, 2796-2811.

Andrews, J.D. (1980) A review of introductions of exotic oysters and biological planning for new importations. *Marine Fisheries Review*, **42**, 1-11.

Ardura, A., Juanes, F., Planes, S. & Garcia-Vazquez, E. (2016) Rate of biological invasions is lower in coastal marine protected areas. *Scientific Reports*, **6**, 33013.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A. & De Clerck, O. (2017) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, **27**, 277-284.

Barnes, D.K.A. (2002) Invasions by marine life on plastic debris. *Nature*, **416**, 808-809.

Blackburn, T.M., Pysek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarosik, V., Wilson, J.R. & Richardson, D.M. (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, **26**, 333-9.

Bosch, S. (2017) *sdmpredictors: species distribution modelling predictor datasets*. R package version 0.2.6.

Carlquist, S. (1966) The biota of long-distance dispersal, I: Principles of dispersal and evolution. *The Quarterly Review of Biology*, **41**, 247-270.

Carlquist, S. (1981) Chance dispersal: long-distance dispersal of organisms, widely accepted as a major cause of distribution patterns, poses challenging problems of analysis. *American Scientist*, **69**, 509-516.

Carlton, J., Chapman, J., Geller, J., Miller, J., Ruiz, G., Carlton, D., McCuller, M., Treneman, N., Steves, B., Breitenstein, R., Lewis, R., Bilderback, D., Bilderback, D., Haga, T. & Harris, L. (2018) Ecological and biological studies of ocean rafting: Japanese tsunami marine debris in North America and the Hawaiian Islands. *Aquatic Invasions*, **13**, 1-9.

Carlton , J.T. (1979) *Introduced invertebrates of San Francisco Bay*. Pacific Division of the American Association for the Advancement of Science, San Francisco.

Carlton, J.T., Chapman, J.W., Geller, J.B., Miller, J.A., Carlton, D.A., McCuller, M.I., Treneman, N.C., Steves, B.P. & Ruiz, G.M. (2017) Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. *Science*, **357**, 1402-1406.

Censky, E.L., Hodge, K., Dudley, J. (1998) Over-water dispersal of lizards due to hurricans. *Nature* **395** (6702): 556.

Chown, S.L. (2017) Tsunami debris spells trouble. *Science*, **357**, 1356.

Clarke Murray, C.C., Maximenko, N. & Lippiatt, S. (2018) The influx of marine debris from the Great Japan Tsunami of 2011 to North American shorelines. *Marine Pollution Bulletin*, **132**: 26-32.

Cohen, A.N., Weinstein, A., Emmett, M.A., Lau, W. & Carlton , J.T. (2001) Investigations into the introduction of non-indigenous marine organisms via the cross-continental trade in marine baitworms. In: *A report for the U.S. Fish and Wildlife Service*, p. 28, Sacramento, CA.

Cozar, A., Echevarria, F., Gonzalez-Gordillo, J.I., Irigoien, X., Ubeda, B., Hernandez-Leon, S., Palma, A.T., Navarro, S., Garcia-de-Lomas, J., Ruiz, A., Fernandez-de-Puelles, M.L. & Duarte, C.M. (2014) Plastic debris in the open ocean. *Proceedings of the National Academy of Sciences of the U.S.A.*, **111**, 10239-44.

Crooks, J.A. (2005) Lag-times and exotic species: The ecology and management of biological invasions in slow motion. *Ecoscience*, **12**, 316-329.

Darwin, C. (1859) *On the orgin of species by means of natural selection*. John Murray, London.

Davidson, I.C., Scianni, C., Minton, M.S., Ruiz, G.M. & Vamosi, S. (2018) A history of ship specialization and consequences for marine invasions, management and policy. *Journal of Applied Ecology*, **55**, 1799-1811.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27-46.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43-57.

Eriksen, M., Lebreton, L.C., Carson, H.S., Thiel, M., Moore, C.J., Borerro, J.C., Galgani, F., Ryan, P.G. & Reisser, J. (2014) Plastic Pollution in the World's Oceans: More than 5 Trillion Plastic Pieces Weighing over 250,000 Tons Afloat at Sea. *PLoS One*, **9**, e111913.

Floerl, O., Inglis, G.J. & Hayden, B.J. (2005) A risk-based predictive tool to prevent accidental introductions of nonindigenous marine species. *Environmental Management*, **35**, 765-78.

Fofonoff, P., Ruiz, G., Steves, B., Simkanin, C. & Carlton, J. (2016) *National Exotic Marine and Estuarine Species Information System*. Available at: http://invasions.si.edu/nemesis/ (accessed November 1 2016)

Gallardo, B., Aldridge, D.C., Gonzalez-Moreno, P., Pergl, J., Pizarro, M., Pysek, P., Thuiller, W., Yesson, C. & Vila, M. (2017) Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology*, **23**, 5331-5343.

GBIF.org (2016), GBIF Home Page. Available from: http://www.gbif.org (accessed 13 September 2016).

Gil, M.A. & Pfaller, J.B. (2016) Oceanic barnacles act as foundation species on plastic debris: implications for marine dispersal. *Scientific Reports*, **6**, 19987.

Gillespie, R.G., Baldwin, B.G., Waters, J.M., Fraser, C.I., Nikula, R. & Roderick, G.K. (2012) Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology & Evolution*, **27**, 47-56.

Goldstein, M.C., Carson, H.S. & Eriksen, M. (2014) Relationship of diversity and habitat area in North Pacific plastic-associated rafting communities. *Marine Biology*, **161**, 1441–1453.

Goto, T. & Shibata, H. (2015) Changes in abundance and composition of anthropogenic marine debris on the continental slope off the Pacific coast of northern Japan, after the March 2011 Tohoku earthquake. *Marine Polution Bulletin*, **95**, 234-41.

Guisan, A., Thuiller, W. & Zimmermann, N.E. (2017) *Habitat Suitability and Distribution Models: with applications in R*. Cambridge University Press, Cambridge, UK.

Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C. & Kueffer, C. (2014) Unifying niche shift studies: insights from biological invasions. *Trends in Ecology and Evolution*, **29**, 260-9.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P. & Buckley, Y.M. (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, **16**, 1424-35.

Hanyuda, T., Hansen, G.I. & Kawai, H. (2018) Genetic identification of macroalgal species on Japanese tsunami marine debris and genetic comparisons with their wild populations. *Marine Pollution Bulletin*, **132**, 74-81.

Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribtion modelling methods. *Ecography*, **29**, 773-785.

Hewitt, C. & Campbell, M. (2010) The relative contribution of vectors to the introduction and translocation of marine invasive species. In, p. 56. Department of Agriculture, Fisheries and Forestry, Australia, Canberra, Australia.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2017) *dismo: Species Distribution Modeling*. R package version 1.1-4.

Jambeck, J.R., Geyer, R., Wilcox, C., Sieger, T.R., Perryman, M., Andrady, A., Narayan, R. & Law, K.L. (2015) Plastic waste imputs from land into the ocean. *Science*, **347**, 768-771.

Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199-204.

Lavers, J.L. & Bond, A.L. (2017) Exceptional and rapid accumulation of anthropogenic debris on one of the world's most remote and pristine islands. *Proceedings of the National Academy of Sciences of the U.S.A.*, **114**, 6052-6055.

Law, K.L. (2017) Plastics in the Marine Environment. *Annual Review of Marine Science*, **9**, 205-229.

Lebreton, L., Slat, B., Ferrari, F., Sainte-Rose, B., Aitken, J., Marthouse, R., Hajbane, S., Cunsolo, S., Schwarz, A., Levivier, A., Noble, K., Debeljak, P., Maral, H., Schoeneich-Argent, R., Brambini, R. & Reisser, J. (2018) Evidence that the Great Pacific Garbage Patch is rapidly accumulating plastic. *Scientific Reports*, **8**, 4666.

Liu, C., White, M., Newell, G. & Pearson, R. (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, **40**, 778-789.

Mellin, C., Lurgi, M., Matthews, S., MacNeil, M.A., Caley, M.J., Bax, N., Przeslawski, R. & Fordham, D.A. (2016) Forecasting marine invasions under climate change: Biotic interactions and demographic processes matter. *Biological Conservation*, **204**, 459-467.

Merow, C., Smith, M.J., Silander J.A. (2013) A pracitcal guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, **36**, 1058-1069.

Merow, C., Smith, M.J., Edwards, T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, W., Wüest, R.O., Zimmermann, N.E. & Elith, J. (2014) What do we gain from simplicity versus complexity in species distribution models? *Ecography*, **37**, 1267-1281.

Miller, J.A., Carlton, J.T., Chapman, J.W., Geller, J.B. & Ruiz, G.M. (2018a) Transoceanic dispersal of the mussel *Mytilus galloprovincialis* on Japanese tsunami marine debris: An approach for evaluating rafting of a coastal species at sea. *Marine Pollution Bulletin*, **132**, 60-69.

Miller, J.A., Gillman, R., Carlton, J.T., Murray, C.C., Nelson, J.C., Otani, M. & Ruiz, G.M. (2018b) Trait-based characterization of species transported on Japanese tsunami marine debris: Effect of prior invasion history on trait distribution. *Marine Pollution Bulletin*, **132**, 90-101.

Morales, N.S., Fernandez, I.C. & Baca-Gonzalez, V. (2017) MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ*, **5**, e3093.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P. & McPherson, J. (2014) ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity forMaxentecological niche models. *Methods in Ecology and Evolution*, **5**, 1198-1205.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014) Where is positional uncertainty a problem for species distribution modelling? *Ecography*, **37**, 191-203.

Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786-788.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Townsend Peterson, A. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102-117.

Peterson, T.A. & Vieglais, D.A. (2001) Predicting Species Invasions Using Ecological Niche Modeling: New Approaches from Bioinformatics Attack. *BioScience*, **51**, 363-371.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231-259.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017) Opening the black box: an open-source release of Maxent. *Ecography*, **40**, 887-893.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181-197.

Polovina, J.J., Howell, E.A. & Abecassis, M. (2008) Ocean's least productive waters are expanding. *Geophysical Research Letters*, **35**, 1-5.

R Core Team (2017) *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. Available at: https://www.R-project.org/ (accessed 2018).

Rech, S., Borrell, Y. & Garcia-Vazquez, E. (2016) Marine litter as a vector for non-native species: What we need to know. *Marine Pollution Bulletin*, **113**, 40-43.

Roman, J. & Darling, J.A. (2007) Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology & Evolution*, **22**, 455-464.

Ruiz, G.M., Freestone, A.L., Fofonoff, P.W. & Simkanin, C. (2009) Habitat distribution and heterogeneity in marine Invasion dynamics: the importance of hard substrate and artificial structure. *Marine Hard Bottom Communities,* (ed. by M. Wahl), pp. 321-332. Springer-Verlag, Berlin Heidelberg.

Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J. & Hines, A.H. (2000) Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics*, **31**, 481-531.

Ryan, P.G. (2015) *A Brief History of Marine Litter Research*. Springer, Cham.

Sbrooco, E.J. & Barber, P.H. (2013) MARSPEC: ocean climate layers for marine spatial ecology. *Ecology*, **94**, 979.

Seebens, H., Gastner, M.T. & Blasius, B. (2013) The risk of marine bioinvasion caused by global shipping. *Ecology Letters*, **16**, 782-790.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pysek, P., van Kleunen, M., Winter, M., Ansong, M., Arianoutsou, M., Bacher, S., Blasius, B., Brockerhoff, E.G., Brundu, G., Capinha, C., Causton, C.E., Celesti-Grapow, L., Dawson, W., Dullinger, S., Economo, E.P., Fuentes, N., Guenard, B., Jager, H., Kartesz, J., Kenis, M., Kuhn, I., Lenzner, B., Liebhold, A.M., Mosena, A., Moser, D., Nentwig, W., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H.E., Scalera, R., Schindler, S., Stajerova, K., Tokarska-Guzik, B., Walker, K., Ward, D.F., Yamanaka, T. & Essl, F. (2018) Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences of the U.S.A.*, **115**, E2264-E2273.

Smith, R.C. & Baker, K.S. (1979) Penetration of UV-B and biologically effective does-rates in natural waters. *Photochemistry and Photobiology*, **29**, 311-322.

Thiel, M. & Gutow, L. (2005a) The ecology of rafting in the marine environment. I. The floating substrata. *Oceanography and Marine Biology: An Annual Review*, **42**, 181-263.

Thiel, M. & Gutow, L. (2005b) The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanography and Marine Biology: An Annual Review*, **43**, 279-418.

Thompson, R.C., Olsen, Y.S., Mitchell, R.P., Davis, A., Rowland, S.J., John, A.W.G., McGonigle, D. & Russel, A.E. (2004) Lost at sea: where is all the plastic? *Science*, **304**, 838.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173-181.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F. & De Clerck, O. (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, **21**, 272–281.

Verling, E., Ruiz, G.M., Smith, D., Galil, B., Miller, A.W. & Murphy, K.R. (2005) Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proceedings of the Royal Society of London Series B*, **272**, 1249-1257.

Wenger, S.J. & Olden, J.D. (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution*, **3**, 260-267.

Winston, J.E., Gregory, M.R. & Stevens, L.M. (1997) *Encrusters, epibionts, and other biota associated with pelagic plastics: a review of biogeographical, environmental, and conservation issues*. Springer, New York, NY.

Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H., Veran, S. (2013) Presence-only modelling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution*, **4**, 236-243.

Zabin, C.J., Marraffini, M., Lonhart, S.I., McCann, L., Ceballos, L., King, C., Watanabe, J., Pearse, J.S. & Ruiz, G.M. (2018) Non-native species colonization of highly diverse, wave swept outer coast habitats in Central California. *Marine Biology*, **165**, 1-18.

Data Accessibility Statement

The species distribution data used in this study are available through the Dryad Digital Repository: http://doi.org/10.5061/dryad.b6np614. These occurrence data were collected from GBIF.org (2016), Fofonoff et al. (2016), and published articles or reports garnered from the scientific literature, and were quality assessed and cleaned for accuracy prior to use.

Table 1: List of the 48 Japanese tsunami debris species used in species distribution models. Table includes information on the species population status in Japan (i.e. native, introduced or cryptogenic – meaning origin unknown), whether the species is currently known to be established on the Pacific coast of North America, the total number of global occurrence records used in modelling, the total number of debris items the species was record on, and the predominate planktonic phase of the species. *Species in bold have a known invasion history somewhere in the world.

Taxa	Species	Status in Japan	Currently established US/Canada West Coast?	Global occurrence records	Number of tsunami debris items	Planktonic phase
Amphipod	***Ampithoe valida***	**Cryptogenic**	**Yes**	**82**	**2**	**direct developer**
Sea Star	*Aphelasterias japonica*	Native	No	20	1	planktotrophic
Bivalve	*Arca boucardi*	Native	No	29	6	planktotrophic
Sea Star	***Asterias amurensis***	**Native**	**No**	**191**	**1**	**planktotrophic**
Bivalve	***Bankia carinata***	**Native**	**No**	**38**	**33**	**planktotrophic**
Bivalve	*Barbatia virescens*	Native	No	40	2	planktotrophic
Amphipod	***Caprella mutica***	**Native**	**Yes**	**144**	**7**	**direct developer**
Bivalve	*Chama dunkeri*	Native	No	22	1	planktotrophic
Bivalve	*Chama japonica*	Native	No	20	2	planktotrophic
Barnacle	***Chthamalus challengeri***	**Native**	**No**	**26**	**7**	**planktotrophic**
Bivalve	***Crassostrea gigas***	**Native**	**Yes**	**211**	**54**	**planktotrophic**
Gastropod	***Crepidula onyx***	**Introduced**	**Yes**	**90**	**1**	**planktotrophic**
Bryozoan	***Cryptosula pallasiana***	**Cryptogenic**	**Yes**	**117**	**10**	**lecithotrophic**
Bivalve	***Dendostrea folium***	**Native**	**No**	**91**	**2**	**planktotrophic**
Anemone	***Diadumene lineata***	**Native**	**Yes**	**102**	**3**	**lecithotrophic**
Ascidian	***Didemnum vexillum***	**Native**	**Yes**	**88**	**3**	**lecithotrophic**
Hydrozoan	*Eutima japonica*	Native	No	20	6	lecithotrophic
Bryozoan	*Exochella tricuspis*	Native	No	21	5	lecithotrophic
Bivalve	*Glorichlamys quadrilirata*	Native	No	41	1	planktotrophic
Algae	***Grateloupia turuturu***	**Native**	**Yes**	**75**	**3**	**non-flagellated spores**
Crab	***Hemigrapsus sanguineus***	**Native**	**No**	**139**	**1**	**planktotrophic**
Bivalve	*Hiatella orientalis*	Native	No	25	38	planktotrophic
Serpulid	***Hydroides ezoensis***	**Native**	**No**	**38**	**48**	**planktotrophic**
Isopod	***Ianiropsis serricaudis***	**Native**	**Yes**	**24**	**36**	**direct developer**
Bivalve	*Isognomon legumen*	Native	No	44	3	planktotrophic
Bivalve	*Laevichlamys cuneata*	Native	No	129	3	planktotrophic
Bivalve	*Laevichlamys squamosa*	Native	No	121	2	planktotrophic
Gastropod	*Lottia dorsuosa*	Native	No	20	5	lecithotrophic
Gastropod	*Lottia kogamogai*	Native	No	34	2	lecithotrophic
Barnacle	***Megabalanus rosa***	**Native**	**No**	**44**	**96**	**planktotrophic**
Bivalve	*Mizuhopecten yessoensis*	Native	No	34	1	planktotrophic
Bivalve	*Modiolus nipponicus*	Native	No	24	7	planktotrophic
Bivalve	*Mytilisepta virgata*	Native	No	26	6	planktotrophic

Bivalve	*Mytilus coruscus*	Native	No	17	2	planktotrophic
Bivalve	***Mytilus galloprovincialis***	**Introduced**	**Yes**	**199**	**224**	**planktotrophic**
Bivalve	*Pascahinnites coruscans*	Native	No	77	1	planktotrophic
Sea Star	*Patiria pectinifera*	Native	No	39	2	planktotrophic
Sipunculid	***Phascolosoma scolops***	**Native**	**No**	**44**	**1**	**planktotrophic**
Coral	*Pocillopora damicornis*	Native	No	150	18	lecithotrophic
Gastropod	*Reishia bronni*	Native	No	34	1	planktotrophic
Bryozoan	***Schizoporella japonica***	**Native**	**Yes**	**44**	**2**	**lecithotrophic**
Bivalve	***Septifer bilocularis***	**Native**	**No**	**179**	**2**	**planktotrophic**
Gastropod	*Siphonaria japonica*	Native	No	23	1	planktotrophic
Gastropod	*Siphonaria sirius*	Native	No	20	2	planktotrophic
Crab	*Sphaerozius nitidus*	Native	No	20	1	planktotrophic
Bivalve	*Spondylus squamosus*	Native	No	83	1	planktotrophic
Barnacle	*Tetraclita japonica*	Native	No	20	1	planktotrophic
Algae	***Undaria pinnatifida***	**Native**	**Yes**	**96**	**1**	**flagellated spores**

Figure Legends

Figure 1: Heat map showing the cumulative predicted presence of the 48 species recorded on marine debris associated with the 2011 Japanese tsunami. Separate maps for each species can be found in the Supporting Information Figures S1-S48. Inset shows the cumulative number of Japanese tsunami debris items found and sampled along the US and Canadian Pacific coast.

Figure 2: The MaxEnt complementary log-log probability scores garnered from each 5-arcmin pixel along the Pacific coastline of North America (represented as grey dots) for each of the 48 tsunami marine debris species. Landing locations are shown as black dots. Larger versions of these graphs can be found in the Supporting Information Figures S1-S48. NB: Images are meant to represent broad species groups and are not diagnostic of the species themselves.

Figure 3: Heat-map showing the cumulative distributions of the 99 marine invertebrate and algal species which are native to Japan and introduced and established along the Pacific Coast of North America.

Figure 1: Heat map showing the cumulative predicted presence of the 48 species recorded on marine debris associated with the 2011 Japanese tsunami. Separate maps for each species can be found in the Supporting Information Figures S1-S48. Inset shows the cumulative number of Japanese tsunami debris items found and sampled along the US and Canadian Pacific coast.

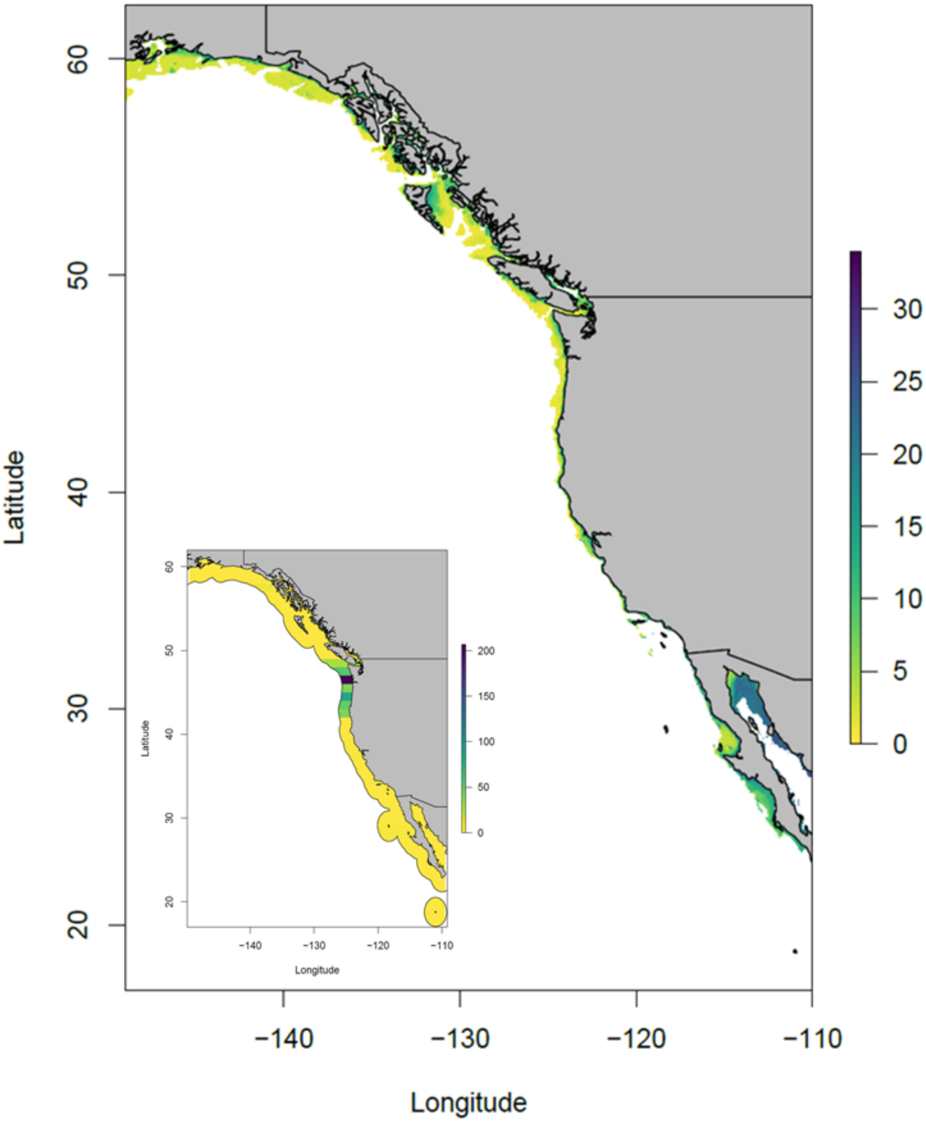


Figure 2: The MaxEnt complementary log-log probability scores garnered from each 5-arcmin pixel along the Pacific coastline of North America (represented as grey dots) for each of the 48 tsunami marine debris species. Landing locations are shown as black dots. Larger versions of these graphs can be found in the Supporting Information Figures S1-S48. NB: Images are meant to represent broad species groups and are not diagnostic of the species themselves.

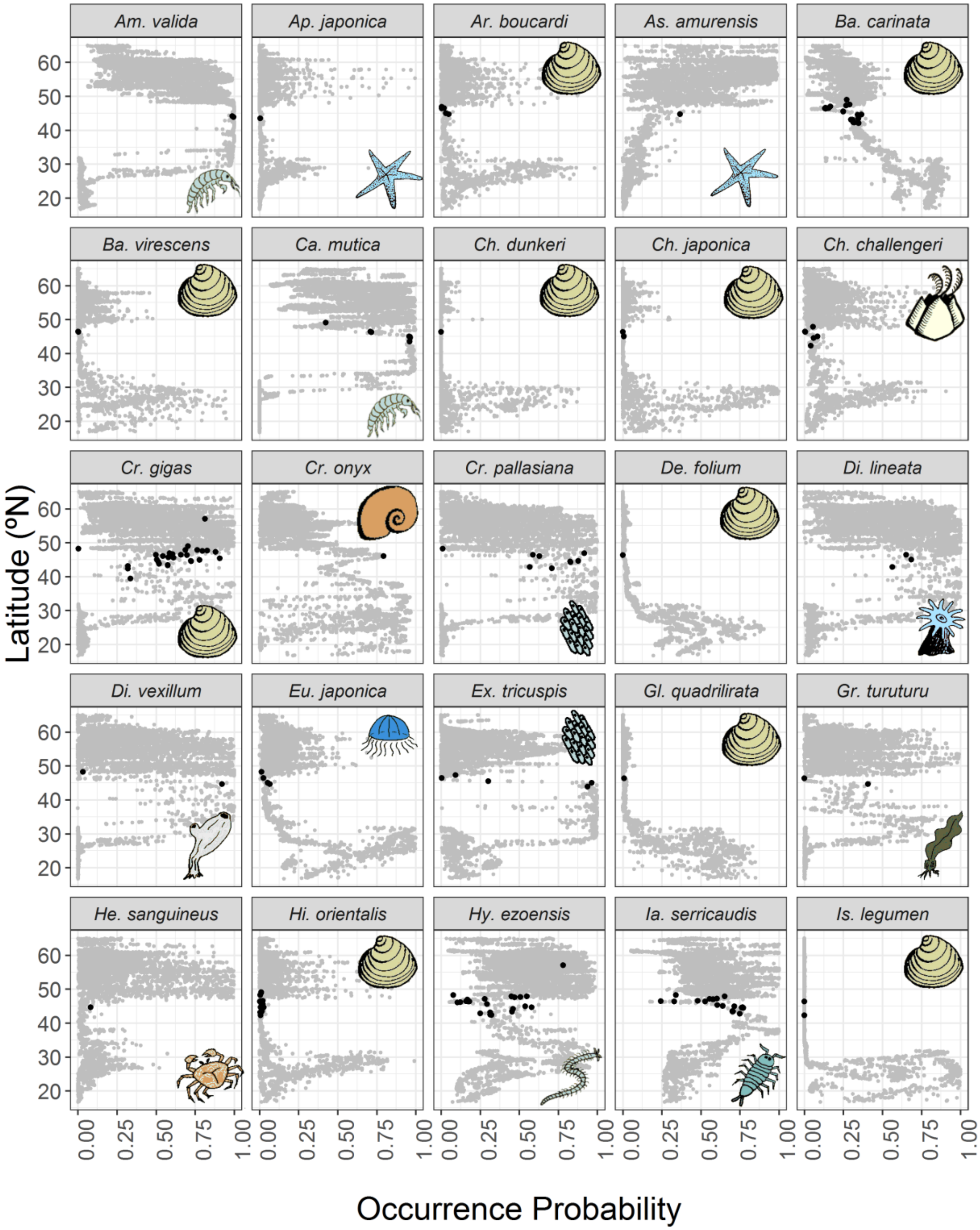


Figure 2 cont.

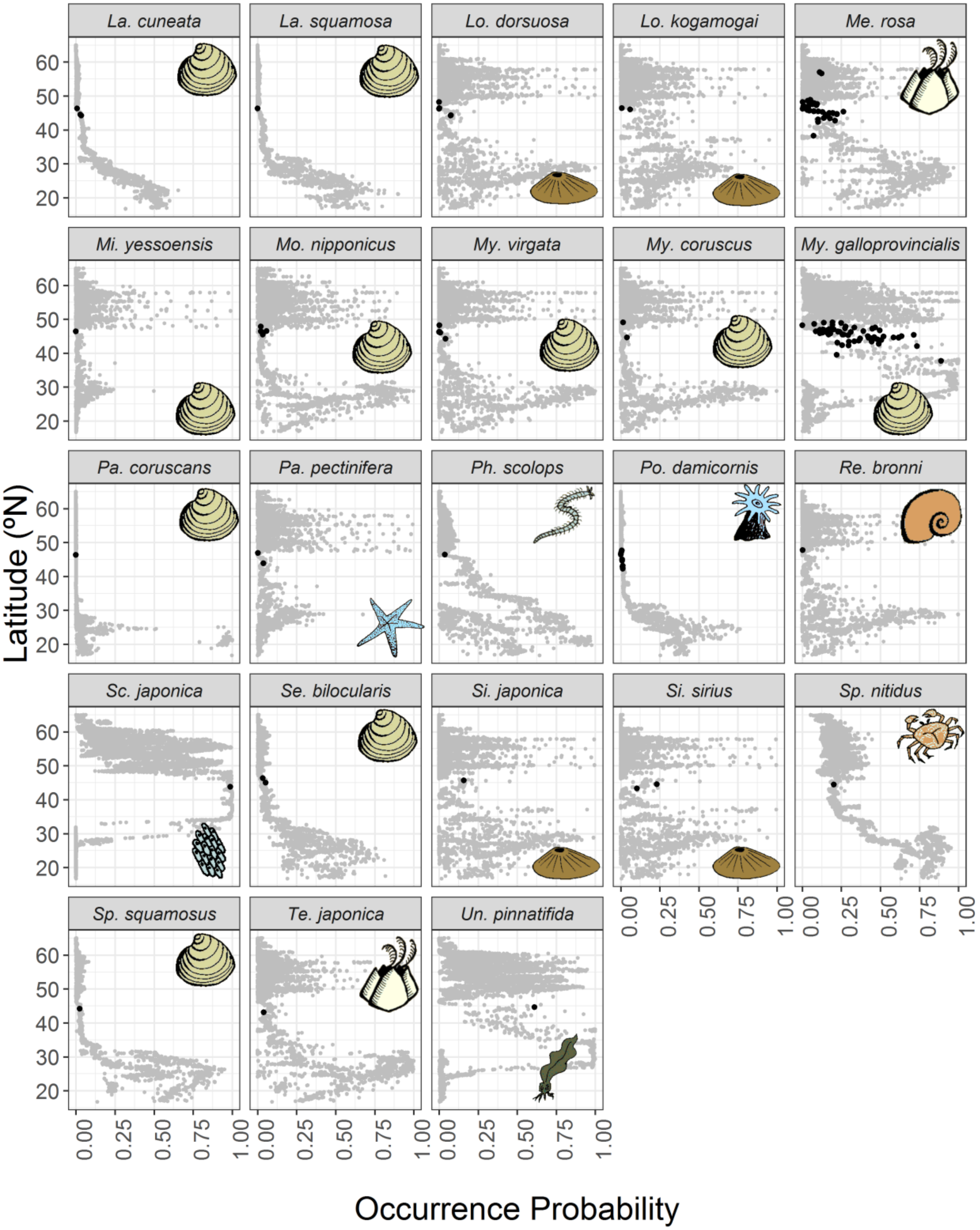
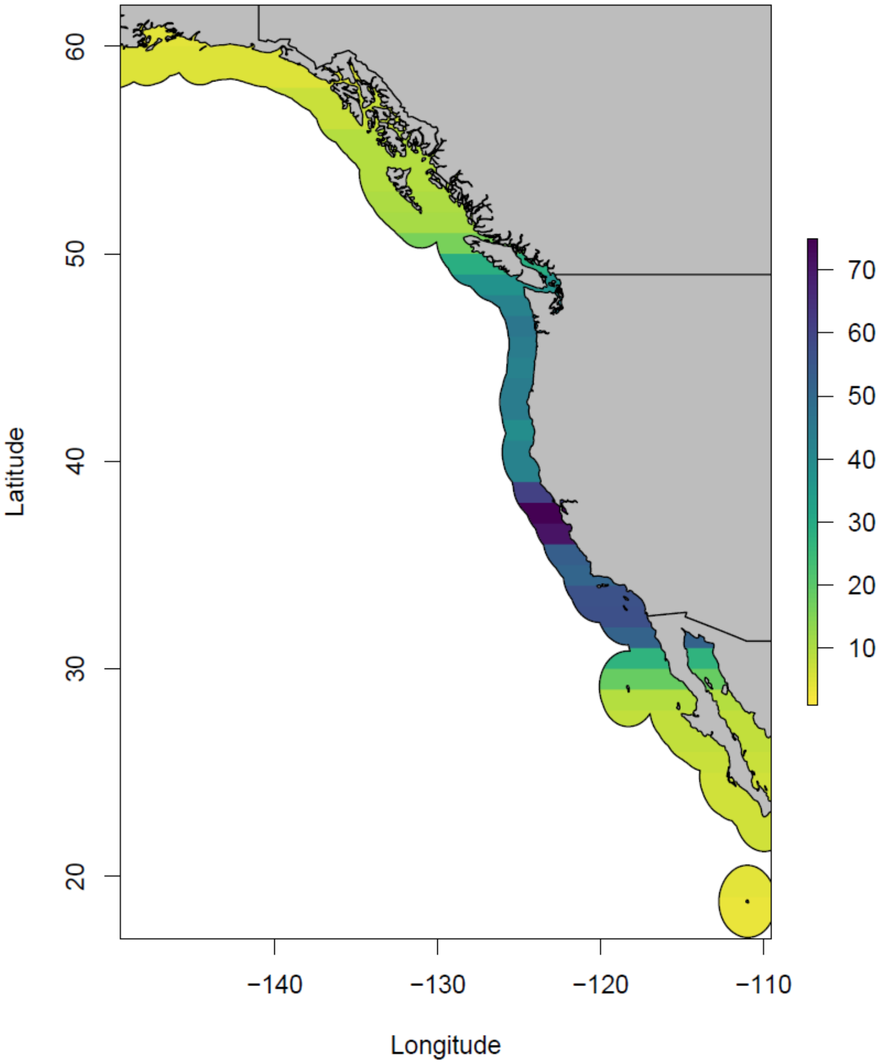


Figure 3: Heat map showing the cumulative distributions of the 99 marine invertebrate and algal species which are native to Japan and introduced and established along the Pacific Coast of North America.



The supporting files include:

Table S1: Correlation matrix of candidate Bio-ORACLE marine environmental layers for modelling marine invertebrate species.

Table S2: Correlation matrix of candidate Bio-ORACLE marine environmental layers for modelling algal species.

Table S3: The feature classes and regularization multiplier parameters selected to represent the simplest MaxEnt model for each species.

Table S4: Statistics from MaxEnt species distribution models.

Table S5: Marine invertebrates and algae of Japanese origin that are currently introduced and established on the Pacific coast of the United States and Canada.

Figures S1 to S48: Individual species maps showing occurrence probability along the Pacific coast of North America.