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Modelling present and future global distributions of razor clams (Bivalvia: Solenidae)

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Abstract

Razor clams (Pharidae and Solenidae) are deep-burrowing bivalves that inhabit shallow waters of the tropical, subtropical, and temperate seas. Using 'maximum entropy', a species distribution modelling software, we predicted the most suitable environments for the entire family and 14 *Solen* species to indicate their present and future geographic distributions. Distance to land, depth, and sea surface temperature (SST) were the most important environmental variables in training and creating the present and future distribution models both at the family and species level. In the present distribution models at the family level, the most suitable environment was where distance to land was between 0 and 100 km, a depth of 0–150 m, wave height of 5–7 m, a mean chlorophyll-*a* concentration about 0.7 mg m^{-3}, and mean SST between 12 and 28 °C. Comparison with the future distribution models at the species level, found that most species were predicted to shift their distribution ranges poleward under the future environmental scenarios; i.e. species in the northern hemisphere would shift northward and southern species southward. Models also predicted that half of the species would expand their distribution ranges, 29% of species would not change their distribution, and 21% of species would shrink their distribution ranges under future climate change. Expanding geographic ranges would result in overlap in species ranges and thus greater species richness at regional scales. Model results predict that the mid-latitude peaks of species richness will move further apart, increasing the dip in richness near the equator, due to global climate change.

Keywords: Species distribution modelling, MaxEnt, Climate change, Range shifts, Mollusca, Ocean Biogeographic Information System, Global Biodiversity Information Facility

Background

Global climate change will influence the future distributions of marine species [1, 2]. Distribution maps indicating future suitable environments can predict the possible range shift of benthic species as a response to increasing temperatures [1, 3, 4]. Species are likely to respond to climate warming by shifting their distributions poleward [2, 5]. Predictive suitable environmental modelling is widely used to identify the environmental factors that control organisms' distribution and predict their geographic range from reported locations [3, 6–10].

One of the most ecologically and economically important superfamilies of marine Bivalvia is Solenoidea which has two families, Pharidae and Solenidae, referred to as razor clams [11–13]. In an ecological context, razor clams' contributions to trophic food webs include serving as prey to crabs, gastropods, sea birds, and demersal fish [14, 15]. In some countries such as Iran, some species of razor clams (e.g., *Solen dactylus*) are being harvested by the local fishermen as bait for fishing and/or shrimp aquaculture [12, 16].

The family Solenidae has two genera, *Solen* Linnaeus, 1758 (65 accepted species) and *Solena* Mörch, 1853 (2 accepted species) with long narrow shells. Solenidae are deep-burrowing bivalves which dig to about 30 cm depth in low intertidal and subtidal sediments [11, 13, 16]. They have free-swimming larvae and may grow 20–30 mm per year [12]. Solenidae are mostly distributed in subtidal zones down to about 100 m in the tropical and temperate seas along the Indo-Pacific and Indian Ocean, east and north-west Pacific, European Atlantic coasts, western

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south Atlantic Ocean, and north and south American coasts. They are absent from the polar regions in both the southern and northern hemispheres. The tropical Indo-Pacific area contains the highest number of species (about 75–80% of all known species) [11, 17].

Despite their wide distribution and ecological importance, limited sampling and ease of mis-identification (due to subtle morphological differences between species) contribute to gaps in knowledge of Solenidae global distribution patterns [15, 18, 19]. Environmental modelling may provide a better indication of the actual geographic distribution than reported locations alone, and can enable predictions of the effects of climate change.

Saeedi et al. (in press) found that the latitudinal gradient of species richness in razor clams was asymmetric and bimodal, with more species in the northern hemisphere and a dip between 0° and −15° latitude. Chaudhary et al. (2016) found this was typical for marine taxa, so razor clams may be a good model taxon for other marine species' biogeography [20]. Indeed, the biogeography of razor clams species' endemicity matched well that of marine species overall [21]. This study predicts the global distribution of the Solenidae family and 14 species based on environmental variables. We then test the hypothesis that species distributions would shift polewards from their present distributions under future climate change. Thus, our findings may be applicable to a wide range of marine taxa.

Methods

Geographic distribution

Data on species geographic distributions were gathered from the Global Biodiversity Information Facility (GBIF), Ocean Biogeographic Information System (OBIS), published literature, museum collections, and personal contacts. We cross-referenced OBIS and GBIF data to avoid duplication of records. We excluded all records that were classified as fossils, were mapped on land, had location coordinates that either had no precision estimates, or if location precision was more than 100 km. All species' names were verified in World Register of Marine Species (WoRMS), and their synonyms and misspellings were reconciled. We also re-examined razor clams in the collections of the Natural History Museum of Paris, Auckland Museum in New Zealand, the National Museum of Natural History (Smithsonian) in Washington, D.C., and the Natural History Museum of London. The specimens' identify was corrected if misidentified and geographic locations recorded. The museums were selected because of convenience of access (Auckland) and likelihood of holding large *Solen* collections. We found reliable coordinates for all 67 accepted *Solen* and *Solena* species that were listed in WoRMS. For the family level distribution modelling, we also included *Solen gordonis* which is described as taxon inquirendum (a questionable species that requires revision and may or may not prove to be a valid species) in WoRMS. We further found an extra nine potential species described as aff. and cf. In total, 77 Solenidae taxa were used in this study [17].

Environmental data

Developing a species distribution model needs environmental variables which are likely to influence the species' distribution [22]. Environmental variables were selected regarding their relevance to Solenidae distribution and their biological importance in affecting *Solen* species populations and diversity [23]. As razor clams are distributed in coastal waters, distance to land, depth, salinity, pH, tidal height, and wave height could be important factors in limiting their distributions [14, 17, 24, 25]. While regionally depth and distance to land may be correlated, they are not globally ($r = -0.46$, $p \geq 0.05$, Additional file 1: Table S1) because of the variation in sizes of continental shelves and occurrence of mid-ocean islands. Sea surface temperature (SST), dissolved and saturated oxygen, and surface current may also affect the distribution, growth, reproduction, juvenile survival and mortality of *Solen* species [14, 17, 26–29]. Razor clams are filter feeders and consume phytoplankton as a food source. Thus, inorganic nutrients (such as silicate, nitrate, and phosphate), photosynthetically active radiation, diffuse attenuation coefficient (an indicator which shows how deeply visible light penetrates into the water column), chlorophyll-*a* concentrations, and primary productivity could indirectly or directly affect the distribution of Solenidae [14, 25, 30, 31]. Calcite was included because razor clams need calcium carbonate ($CaCO_3$) for shell growth [32].

Most environmental data layers were extracted from Global Marine Environment Datasets (GMED) [33] at a spatial resolution of 5 arcmin (0.083° grid cell pixel size, ca. 9 km at equator) (Table 1). Ocean area (km^2) and coastline length including islands (km) were extracted from Biogeoinformatics of Hexacorals (http://www.kgs.ku.edu/Hexacoral/) [34]. Layers were cropped to 70°N–70°S based on the maximum geographic distributions recorded for Solenidae species at latitudes 60°N and 50°S. Merow et al. (2013) found that, with the exception of SST range, using multiple derivatives of SST did not improve the performance of their model compared to using only a single derivation of SST [35]. For this reason, we calculated correlation coefficients of all selected GMED variables in ArcGIS using multivariate analysis (Band Collection Statistics) (Table S1), and select only one derivation of each metric, that is the mean, minimum, or maximum of temperature and chlorophyll-*a* concentration following Basher et al. (2014) [36]. Thus,

Table 1 List of environmental variables used in this study (from Basher et al. 2014) which were cropped to an extension of 70°N–70°S

Layer	Unit	Type	Temporal range	Minimum	Maximum	Mean	Std. Dev.
Land distance	km × 100	–	–	0.00	24.92	6.80	5.22
Sea surface temperature (annual mean)	°C	Monthly climatology	2002–2009	−1.00	31.54	15.89	10.44
Sea surface temperature (range)	°C	Monthly climatology	2002–2009	0.00	27.81	4.26	3.08
Depth	m	–	–	−10,293.65	0	−3671.68	1602.58
Wave height	m	–	–	0.00	7.00	0.29	1.02
Photosynthetically active radiation (annual mean)	Einstein m^{-2} day^{-1}	Monthly climatology	1997–2009	0.00	64.82	35.22	8.55
Chlorophyll-*a* concentration (annual mean)	mg m^{-3}	Monthly climatology	2002–2009	0.02	0.90	0.05	0.04
Diffuse attenuation coefficient* (at 490 nm)	m^{-1}	Monthly climatology	2002–2009	0.02	0.90	0.05	0.04
Primary Productivity	mg C m^{-2} day^{-1} cell^{-1}	Annual climatology	–	0.00	4875.00	385.08	285.55
Tide average (average of maximum tidal height)	m	Annual climatology	–	0.00	6.38	0.51	0.44
Surface current	m s^{-1}	Monthly climatology	2009–2010	−0.93	1.00	0.00	0.08
Salinity	PSS	In situ measure: 2009	1961–2009	0.00	41.00	33.96	2.09
pH	–	In situ measure: 2009	1910–2007	6.73	8.62	8.19	0.06
Dissolved oxygen	ml l^{-1}	In situ measure: 2009	1898–2009	2.00	9.86	5.29	1.27
Saturated oxygen	ml l^{-1}	In situ measure: 2009	1874–2000	76.05	113.11	100.10	3.23
Calcite concentration	mol m^{-3}	Seasonal climatology	2002–2009	0.00	9.00	2.87	3.18
Silicate	μmol l^{-1}	In situ measure: 2009	1930–1986	0.00	69.00	9.85	13.86
Nitrate	μmol l^{-1}	In situ measure: 2009	1922–1986	0.00	45.96	5.52	6.13
Phosphate	μmol l^{-1}	In situ measure: 2009	1874–2000	0.00	2.00	0.26	0.44
Sea surface temperature at 2100	°C	Monthly climatology	2087 – 2096	0.00	35.05	18.04	10.91
Salinity at 2100	PSS	Monthly climatology	2087–2096	0.00	40.05	34.37	1.99
Primary productivity at 2100	mg C m^{-2} day^{-1} cell^{-1}	Annual climatology	2090–2099	0.00	5004.00	354.76	277.07

Future environmental variables are in italics. Note that there were 19 variables for the Present, and 5 (including present land distance and depth as constant variables, and three future environmental variables in italics) for the Future model. Annual means were used and for sea surface temperature the annual range was also used as it was significantly different from the sea surface temperature annual mean. * An indicator of water clarity which expresses how deeply visible light in the blue to the green region of the spectrum penetrates into the water column. Distance to land was the distance to the nearest land using the Euclidean distance formula in ArcGIS

we only used annual mean SST and mean chlorophyll-*a* concentration.

In total, 19 environmental data layers were used to create the present day distribution models at both a family level and a species level (Table 1). However, for the future climate change scenarios there were only three environmental variables available, namely salinity, primary productivity, and SST mean. We assumed distance to land and depth would be similar until 2100, and thus predicted future geographic distributions by comparing the five variables including distance to land, depth, salinity, primary productivity, and SST mean for the present (reduced present day model) and future scenarios (Table 1). The differences between the mean values for the present and future environmental variables were 2 °C greater for sea surface temperature, 0.4 PSS less for salinity, and 30 mg C m^{-2} day^{-1} cell^{-1} less for primary productivity (but 129 mg C m^{-2} day^{-1} cell^{-1} greater maximum) (Table 1).

Modelling of species distributions

MaxEnt was selected in this study due to its success in developing species distribution models for marine species [37–40]. It has been widely used in conservation planning, ecology, evolution, epidemiology, invasive-species management and other fields [3, 6, 37]. MaxEnt minimizes the relative entropy, or dispersion, between two probability densities, one estimated from presence data, and one from the landscape in the context of covariate space. MaxEnt is optimized for predicting the realised or actual (rather than the fundamental) species distributions. Predictions of presence will thus still be dependent on the sample locations of the available data [7, 37]. Thus, any deficiency in sampling coverage might still bias the results [7, 41, 42].

MaxEnt version 3.3.3e was used to predict present and future (at year 2100) suitable environments for Solenidae on a global scale at both the family and species level. At the family level, a total of 526 distribution records of

77 Solenidae species were used for training the model [17] (see also Additional file 1: Table S2). Modelling at the family level allowed coverage of all species globally. Because of the greater number of distribution records the family level mapping would encompass each species level prediction. This if a species level model predicted a distribution outside the family level it would suggest poor model accuracy due to insufficient primary data.

MaxEnt was used to predict the suitable present and future environments for 14 *Solen* species which had more than 10 presence records separately (Table S2). We used one observation point per 0.083° pixel, to eliminate any duplicate points and reduce clumping. Models were created with 10 bootstrap replicates using default parameters for a random seed: randomly select 75% of the species presence records for training and 25% for testing the model in each replication stage [37, 43]. Then the average predictions across the all replicates were used for further analysis. The regularization multiplier was set to 1, and the maximum number of background points was increased to 100,000 instead of the default because of our large-scale mapping objective. There were 900 maximum iterations, and a convergence threshold of 0.00001 for the present day modelling [7, 23, 44]. We kept the default regularization values following Dudik et al. (2006) [45] as they result in better performance of evaluation data for presence only datasets. For the future projections, 10 cross-validated replicate models were generated. Default parameters including hinge features, random test percentage of zero [37, 43], and the other settings were the same as in the present day modelling.

To test the performance of MaxEnt models we used the Receiver Operating Characteristic (ROC) analysis. ROC analysis characterises the performance of a model at all possible thresholds using the Area Under the Curve (AUC) [6, 23, 44]. The highest numbers of AUC show more sensitive and specific model sets, ranging from 0.5 (random accuracy) to 1.0 (perfect discrimination) [7, 44]. We used the cumulative threshold value from the MaxEnt output which is a balance among training omission, predicted area, and threshold value. Values observed below the thresholds were considered to be unsuitable for the species. To determine the most important factors in training the distribution models and creating the final distribution models, we used the model outputs of the jacknife test as well as contribution rate (represents the importance of a given variable in model training), and permutation importance [46]. Permutation importance depends only on the final Maxent model (not for the replicates). The contribution for each factor is determined by randomly permuting the values of that factor among the points used for training the model and measuring the variation of AUC (training) value. A large decrease indicates that the model depends heavily on that factor. Final values are normalized to a percentage for easier interpretation [46].

A map of environment suitability for Solenidae was generated to reflect the predicted probability of species occurrence using ArcGIS v10 [36, 43]. The model often predicted suitable environment in areas that were not contiguous with species' present distributions. For example, an Australian species in Japan, an Atlantic species on both coasts of north America, and Indian Ocean species in the Mediterranean. Such distributions are only likely if species are introduced by human activities. No marine species' are known to have larvae that disperse more than 1000 km [47, 48]. Thus, when determining both present and future predicted distribution ranges, only continuous distribution ranges within a maximum of 30° latitude (equivalent to 3300 km) and 30° longitude, and with more than a 75% prediction rate beyond the reported distribution were considered.

Results

Present model with 19 variables at family level

Distance to land and depth had the highest contribution rates and importance in creating the present distribution models at the family level (about 75%) (Additional file 1: Fig S1). After distance to land and depth, mean SST had the highest contribution rate (9.3%) in training the models, and wave height had the most importance rate in creating the final distribution models (Fig S1). The probability of Solenidae family occurrence in the present distribution models was close to 1 (the highest probability rate) where: distance to land was between 0 and 100 km; depth was 0–150 m; mean SST between 12 and 28 °C; wave height 5–7 m; and mean chlorophyll-*a* concentration 0.7 mg m^{-3} (Additional file 1: Fig S2).

Present model with 19 variables for 14 species

Species occurrences were strongly associated with wave height and distance to land which had the highest contribution rates in training the present distribution models of 10 species (about 70%) (Table 2). In the remaining four species, SST mean, SST range, dissolved oxygen, and depth had the highest contribution rates in training the present distribution models. Depth, distance to land, and calcite had the highest permutation importance in creating the final present distribution models (Table 2). The probability of *Solen* species occurrence in the present distribution models was close to 1 where: distance to land was approximately less than 200 km; depth less than 150 m; mean SST between 12 and 32 °C; primary productivity between 500 and 2500 mg C m^{-2} day^{-1} $cell^{-1}$, and salinity between 23 and 41 PSS (Table 3). In a total of 14 species, four cold temperate species including *Solen*

Table 2 The output of highest contribution and importance values of environmental variables in creating the present MaxEnt distribution models for 14 species using 19 variables

Solen species	Training records	Contribution		Permutation importance	
		Highest	Rate (%)	Highest	Rate (%)
aureomaculatus	15	Wave height	22.8	Depth	32.2
canaliculatus	12	SST mean	19.0	Land distance	39.2
fonesii	50	Wave height	22.2	Calcite	28.7
grandis	24	SST range	53.2	Land distance	56.7
kajiyamai	12	Dissolved oxygen	29.6	Depth	56.1
marginatus	126	Land distance	42.8	Calcite	34.5
roseomaculatus	35	Wave height	33.6	Land distance	84.7
sicarius	30	Land distance	60.9	Depth	67.4
sloanii	15	Land distance	60.9	Depth	67.4
strictus	17	Land distance	28.0	Depth	46.4
thuelchus	12	Wave height	25.1	Land distance	52.0
vagina	10	Land distance	28.4	Calcite	21.6
vaginoides	85	Depth	24.4	Calcite	38.5
viridis	33	Wave height	29.3	Land distance	33.2

Values are normalized to give percentages. The average AUC of training data was from 0.97 to 1 from the ten model runs, with little variation between runs indicating a good model fit

grandis, S. marginatus, S. thuelchus, and *S. viridis* preferred the lowest temperature ranges from 12 to 16 °C, two warm temperate species including *Solen sicarius* and *S. strictus* had a temperature preferences from 16 to 19 °C, and the rest were tropical species with high temperature preferences from 25 to 32 °C. Four species of 14 species including *Solen canaliculatus*, *S. roseomaculatus*, *S. sloani*, and *S. vagina* favoured high salinities from 40 to 41 PSS, *S. sicarius* preferred the low salinity from 23 to 25 PSS, and the rest of species mostly predicted in salinities from 29 to 39 PSS (Table 3).

Reduced present models with 5 variables for 14 species

Depth and distance to land had the highest contribution rates in training and creating the reduced present distribution models for almost all *Solen* species, except for *Solen marginatus* where mean SST had the highest importance permutation rate in creating the final distribution models (Table 4).

Future models with 5 variables at family level

Distance to land and depth had the highest contribution rates and importance in creating the future distribution models at the family level (about 85%) (Fig S1). Mean SST had the highest contribution rate (11.7%) in training the future projections after distance to land and depth. However, primary productivity was the third important factor in creating the future distribution models after distance to land and depth (Fig S1). The probability of Solenidae family occurrence in the future distribution models was close to 1 where: distance to land was between 0 and 100 km; depth 0–150 m; mean SST 12–28 °C; primary productivity between 500 and 2000 mg C m^{-2} day^{-1} $cell^{-1}$; and salinity between 30 and 38 PSS (Additional file 1: Fig S3).

Future models with 5 variables for 14 species

In all 14 species excluding *S. aureomaculatus*, distance to land had the highest contribution rate in training the future distribution models (Table 4). However, mean SST was the most important factor in creating the final future distribution models in half of the 14 *Solen* species (50%). After mean SST, depth in five species (36%), and distance to land in two species (14%) were the most important factors in creating the final future distribution models. The probability of *Solen* species future distributions was close to 1 where distance to land was less than 200 km; depth less than 150 m; mean SST 11–29 °C; primary productivity between 500 and 2300 mg C m^{-2} day^{-1} $cell^{-1}$; and salinity between 32 and 42 PSS (Table 3).

The maximum averages of predicted suitable primary productivity for *Solen canaliculatus*, *S. kajiyamai*, *S. marginatus*, and *S. roseomaculatus* were lower in the future distribution models compared to the present distribution models (Table 3). Predicted suitable salinities in the future distribution models were higher compared to the present distribution models in all species, except for *S. canaliculatus*. The maximum predicted suitable SST mean in half of the species was lower in the future distribution models compared to the present distribution

Table 3 The variables that had the highest predicted probability of *Solen* species occurrence for the present and future distribution models

***Solen* Species**	**Depth (m)**	**Present**			**Depth (m)**	**Future**		
		Primary productivity (mg C m^{-2} day^{-1} cell^{-1})	**Salinity (PSS)**	**Mean sea surface temperature (°C)**		**Primary productivity (mg C m^{-2} day^{-1} cell^{-1})**	**Salinity (PSS)**	**Mean sea surface temperature (°C)**
aureomaculatus	0–150	500–750	35–36	26–28	0–150	500–1000	40–42	25–28
canaliculatus	0–150	2000–2500	40–41	29–31	0–150	750–1000	32–34	25–28
fonesii	0–150	800–1100	34–35	27–30	0–150	800–1100	35–36	25–29
grandis	0–150	1900–2000	30–32	13–14	0–150	1800–2000	30–33	13–14
kajiyamai	0–150	1800–2000	39–40	30–31	0–150	1500–1700	40–41	22–25
marginatus	0–100	1500–1900	39–40	12–13	0–100	1400–1600	40–41	11–13
roseomaculatus	0–150	1400–1600	40–41	31–32	0–150	1000–1200	41–42	23–26
sicarius	0–150	2200–2300	23–25	16–17	0–150	2200–2300	32–33	15–17
sloanii	0–100	750–850	40–41	25–26	0–100	750–1000	41–42	23–25
strictus	0–100	1800–2000	29–31	17–19	0–100	1500–1700	32–33	18–19
thuelchus	0–100	2200–2100	39–41	13–16	0–100	2200–2000	40–41	15–16
vagina	0–150	1600–1900	40–41	25–28	0–150	1600–2100	41–42	26–28
vaginoides	0–100	800–1100	38–40	26–28	0–100	800–1100	39–41	26–27
viridis	0–100	2000–2100	38–39	12–14	0–100	2000–2200	38–40	12–13

Distance to land was approximately less than 200 km for all species in both present and future distribution models

models, and it did not change for the remainder. Temperate species such as *Solen grandis, S. marginatus, S. strictus*, *S. sicarius*, *S. thuelchus*, and *S. viridis* had the lowest predicted suitable SST ranges from 12 to 19 °C in both present and future distribution models (Table 3).

Present distributions

More than 50% of species showed similar present predicted distribution ranges compared to their actual distribution ranges (Fig. 1). MaxEnt distribution model outputs at the family level indicated that the most suitable environments for Solenidae at present are in the shallow waters of the northern east Pacific (California, USA), tropical west Atlantic (north Carolina, USA), European Atlantic, Gulf of Thailand, and eastern (Brisbane and Melbourne) and western coast of Australia (Additional file 1: Fig S4).

Future distributions

Solen sloanii and *S. roseomaculatus* were distributed in both hemispheres and had the widest latitudinal distribution ranges of all the species (Figs. 1, 2). They were predicted to shift northward in the northern, and southward in the southern hemisphere under the future climate change scenarios (Table S2, Figs. 1, 2, 3). *Solen vagina* seems to be an endemic species to the Gulf of Thailand and was predicted to shift southward to Malaysia, Singapore, and Indonesia. *Solen strictus* and *S. grandis* showed similar future distribution ranges compared to their current distributions. *Solen canaliculatus* was predicted to shift northward from its present distributions and disappear from Taiwan in the future distribution model. High latitude species such as *Solen marginatus*, *S. sicarius*, and *S. viridis* were predicted to shift northward in the northern, and *S. thuelchus* southward in the southern hemisphere. However, the extent of their predicted distribution ranges in the present and future distribution models were similar. All Australian species including *Solen fonesii*, *S. kajiyamai*, *S. aureomaculatus*, and *S. vaginoides* were predicted to shift southward along the eastern and southern Australia coasts in the future models such that the species' would split into east and west coast populations. All Australian species disappeared from the northern part of Australia under future climate change (Table S2, Figs. 1, 2).

At the family level, more geographic areas were predicted to be suitable for razor clams in the future compared to the present distribution models (Additional file 1: Fig S5). This is supported by the results of individual species models. Considering predicted present and future distribution models at the species level, half of the 14 species had a wider distribution range in the future compared to predicted present distribution models (Fig. 3). In contrast, three species (21%), namely *Solen vaginoides*, *S. strictus*, and *S. viridis* were predicted to have narrower latitudinal distribution ranges in the

Table 4 Output contribution and importance values of five environmental variables used to create the reduced present day and future MaxEnt distribution models for 14 *Solen* species

Solen species	Training records	Present					Training records	Future				
		Environmental variables Contribution rate/permutation importance (%)						Environmental variables Contribution rate/permutation importance (%)				
		Depth (m)	Land distance (km × 100)	Primary productivity (mg C m^{-2} day^{-1} $cell^{-1}$)	Salinity (PSS)	Mean sea surface temperature (°C)		Depth (m)	Land distance (km × 100)	Primary productivity (mg C m^{-2} day^{-1} $cell^{-1}$)	Salinity (PSS)	Mean sea surface temperature (°C)
aureomaculatus	13	53/16	21/78	8/2	0.2/0.0	18/5	17	35/68	35/3	7/3	2/0.3	22/25
canaliculatus	10	23/86	52/1	4/0.1	4/0.9	17/12	13	13/1	56/28	4/2	5/7	21/62
fonesii	41	54/11	33/86	0.0/0.0	0.0/0.0	12/3	55	30/56	46/7	4/1	3/3	16/32
grandis	20	22/8	37/83	0.6/0.1	16/2	25/6	36	27/47	39/13	12/7	7/5	15/29
kajiyamai	10	64/58	18/39	3/0.2	0.4/0.0	14/2	13	25/47	53/12	4/2	0.8/0.4	17/39
marginatus	105	21/4	44/8	14/1	7/3	14/84	142	2/2	62/29	12/2	5/3	19/65
roseomaculatus	11	52/8	33/90	0.0/0.0	0.7/0.0	14/2	15	18/10	62/41	0.2/0.4	0.2/0.2	19/49
sicarius	24	4/0.1	56/89	23/2	2/1	14/8	32	3/1	58/57	23/11	3/6	14/25
sloanii	12	42/3	46/95	0.7/0.0	0.6/0.0	11/2	17	7/0.6	67/59	2/0.5	1/0.2	24/40
strictus	12	58/21	36/78	0.1/0.0	0.4/0.1	5/1	17	11/12	59/37	2/0.4	9/8	18/42
thuelchus	10	56/17	38/83	0.1/0.0	1/0.2	4/0.2	13	6/5	65/38	7/3	0.0/0.1	21/54
vagina	6	49/15	25/80	0.0/0.0	2/0.2	24/5	9	11/3	63/37	0.4/0.0	4/2	22/58
vaginoides	69	16/90	54/2	7/1	6/2	16/5	93	21/69	49/8	8/3	5/5	17/15
viridis	28	10/84	53/8	11/0.2	6/0.6	20/8	37	18/5	47/30	9/0.8	5/4	20/60

Values are normalized to give percentages. Environmental variables with highest contribution and permutation importance rates represent the most important variables in training and creating the final distribution models. The average AUC of training data in both present and future distribution models was from 0.97 to 1 from the ten model runs, with little variation between runs indicating a good model fit

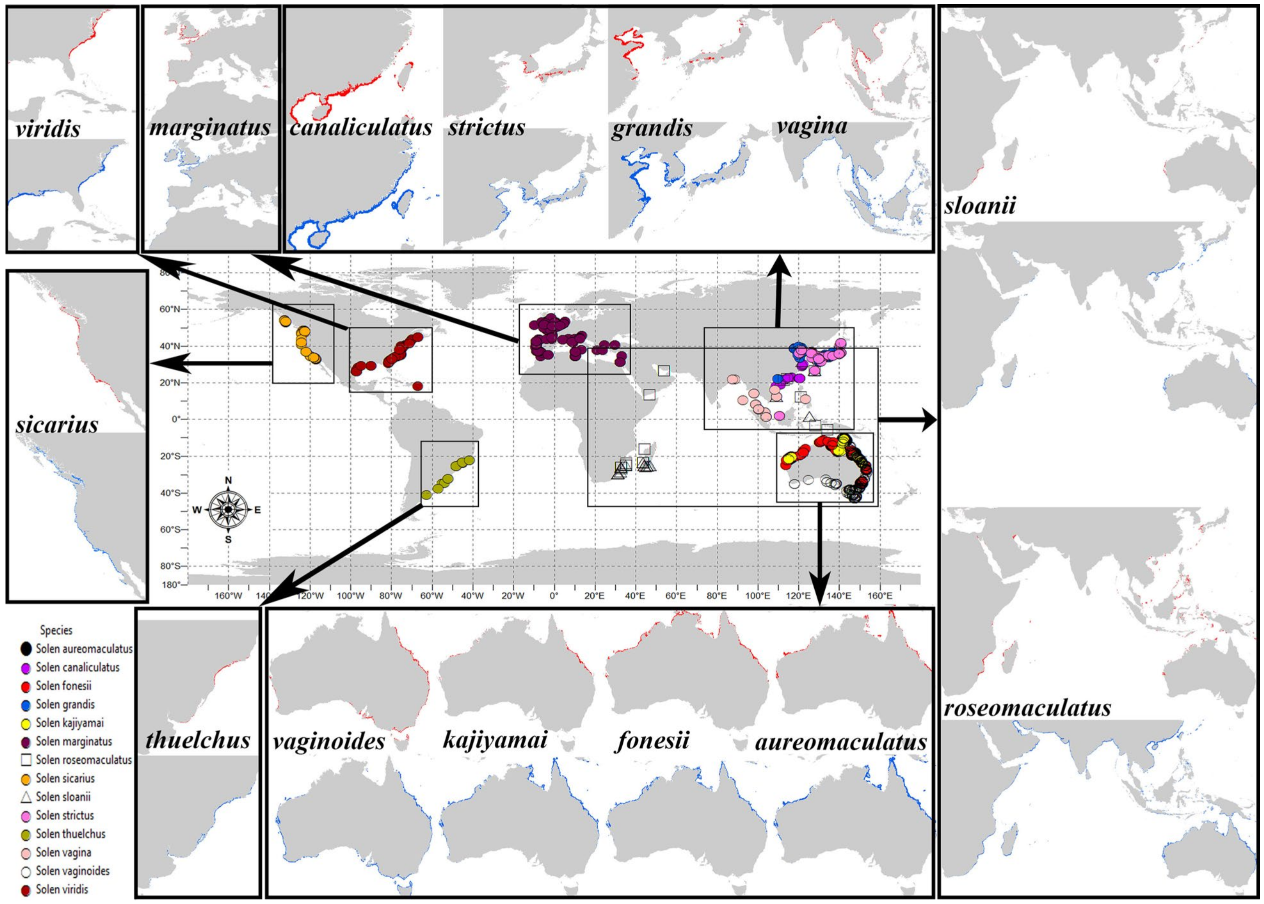

Fig. 1 The reported species distribution map of 14 *Solen* species is presented in the *central panel*. The *symbols* show the actual distributions of each species. Predicted present (top models in *red*) and future (2100) (bottom models in *blue*) distribution models of environment suitability for 14 *Solen* species with a probability of occurrence >0.5

future. Four species (29%) had similar present and future distribution ranges indicating that their distribution would not change due to future climate change. A species range may change but the mean latitude of its ranges may or may not change. The mean latitudes of the northern hemisphere species were predicted to change showing a negligible change in the future (Fig. 4). However, the mean latitude of southern species would shift southward.

Discussion

Present distributions

The majority of the predicted suitable environments were in the shallow waters of the temperate and tropical north America, Indo-West Pacific, and the European Atlantic Ocean where Solenidae have been reported. Some of these areas may not be inhabited by *Solen* at present due to dispersal constraints. For example, there were no distribution records of Solenidae in New Zealand; although the model predicted this area had a suitable environment now and in the future. This would suggest that this family had not occurred on Gondwanaland or evolved prior to the separation of New Zealand from Australia (around 80 million years ago). During glaciations, SST in northern New Zealand were above 10 °C [49] which is within the temperature tolerance of Solenidae. Evidently, the duration and/or behaviour of Solenidae planktonic larvae might have been insufficient for species to colonise New Zealand from Australia.

The environment suitability model developed in this study indicated that Solenidae species' distributions were highly correlated with distance to land, depth, SST, and wave height. Distance to land and depth contributed to over 70% of the variation in the models. Mean SST had the next most contribution rate (about 9%) to the global models after distance to land and depth. SST is a major factor in the reproduction, larval development, recruitment, and mortality of Solenidae [14, 31].

The models predicted Solenidae to occur in coastal areas (≤200 km from the land) with depths of less than

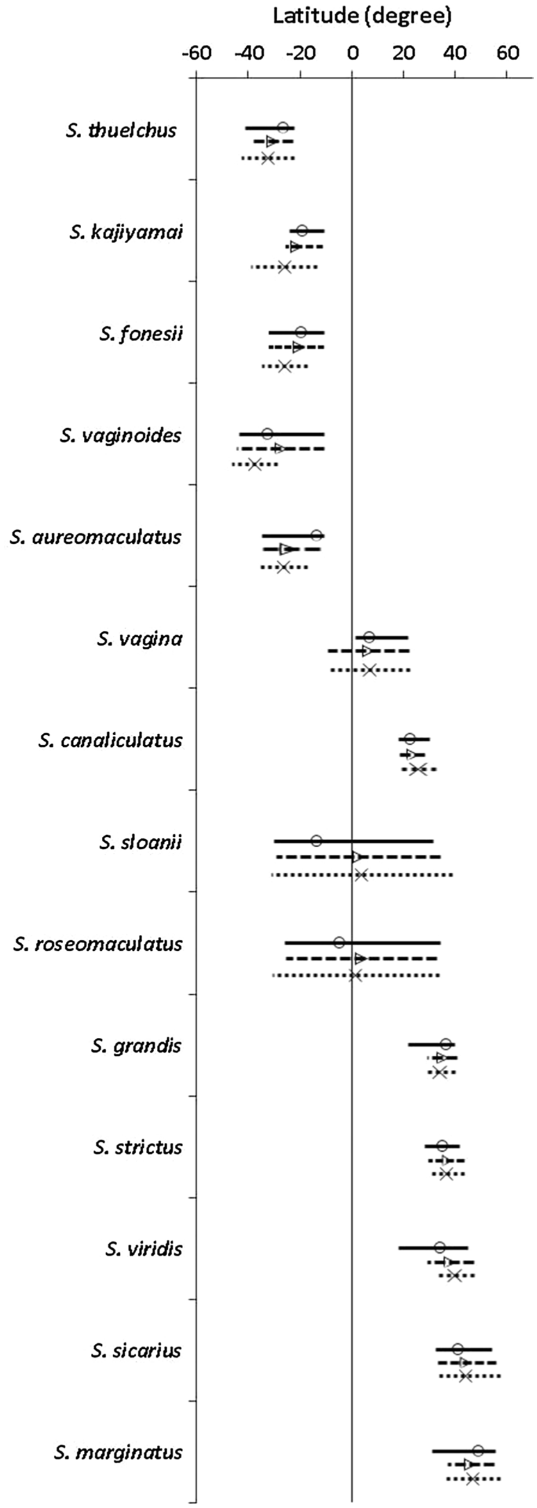

Fig. 2 The latitudinal distribution ranges of *Solen* species according to field data (*continuous lines*), the predicted present (*dashed lines*) and future distribution (*dotted lines*) range with more than 75% prediction rates. The central line shows the Equator. The distribution median (*open circle*) and mean (*triangle* and *cross*) are indicated

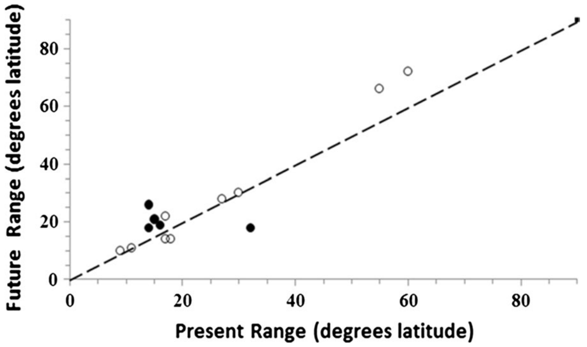

Fig. 3 The predicted present and future latitudinal ranges of 14 *Solen* species. Symbols *above the line* indicate a wider latitudinal range, and symbols below the *line* indicate a predicted decrease in the species latitudinal range. *Black circles*: southern latitudes (5 species); *open circles*: northern latitudes (9 species)

150 m, wave height of 5–7 m, mean SST of 12–28 °C, and primary productivity of 400–700 mg C m^{-2} day^{-1} $cell^{-1}$). The suitable environments for Solenidae species were similar to the temperate razor clam *Ensis directus* (Pharidae) [50]. They also found high probabilities of occurrence for *E. directus* at depths between 0 and 67 m, minimum annual SSTs between 3 and 18 °C and maximum annual SSTs between 20 and 26.5 °C [50].

Wave height had the highest contribution rate in training the present distribution models of most high latitude species including *Solen aureomaculatus*, *S. fonesii*, *S. thuelchus*, and *S. viridis*. The greater occurrence of Solenidae in areas with 5–7 m wave height, which is at the upper end of the range of potential wave height, may be an indicator of the occurrence of sandier sediments. Nickerson (1975) reported that densities of razor clams were highest on sandy beaches with least silt, and that silt-laden sediments might be responsible for suffocation of razor clams in early life stages [51].

Future distributions

Mean SST was the most important environmental variable in half of the species in creating the final future distribution models. The future species distribution models showed that northern and southern hemisphere species would shift northward and southward respectively under future climate warming. Half of the species were predicted to expand their distribution ranges 21% of species to shrink, and 29% of species did not change their distribution under future climate change. The potential poleward range shifts due to global warming have been also reported for sandy-beach invertebrates [5] and tropical molluscs [2]. Indo-West Pacific areas (especially China Sea, Sea of Japan, Bay of Bengal, Gulf of Thailand, Andaman Sea, Philippines, Indonesia, and Papua New Guinea)

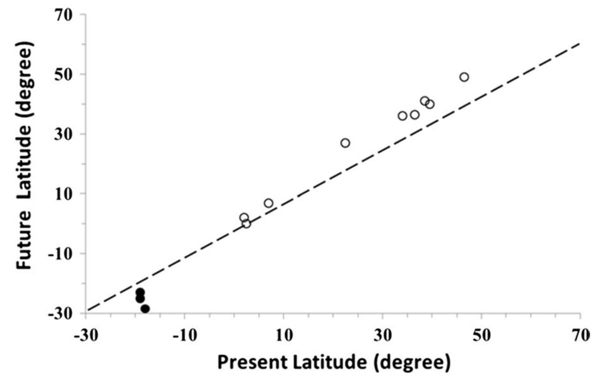

Fig. 4 The predicted present and future mean latitude of distribution in 14 *Solen* species. Symbols above the *dashed line* indicate a northward, and below a southward, shift in mean latitude under the predicted future climate change. *Black circles*: southern latitudes (5 species); *open circles*: northern latitudes (9 species). All northern latitude species shift northward and all southern latitude species shift southward

would be occupied by more *Solen* species due to the warming average temperatures, as predicted for other tropical molluscs [2]. Distributions of tropical *S. canaliculatus, S. vagina*, *S. strictus*, and *S. grandis* could also expand northward and southward along the coastal areas of the China Sea, Sea of Japan, Bay of Bengal, and Gulf of Thailand under future climate change. However, physical geographical barriers would limit future distribution changes into these areas [11, 18].

Almost all Australian species were predicted to shift their distribution southwards and disappear from its northern territory. The sea surface temperature in northern Australia is predicted to become 2–3 °C warmer (33 °C) in the future [52] which would be out of these species temperature tolerance [17]. In contrast, the predicted future distribution models of some high latitude species, such as *S. marginatus* and *S. sicarius,* would not expand outside their current distribution ranges.

The present and future distribution models in *Solen roseomaculatus* and *S. sloanii* showed exceptionally wide disjunct distributions. These merit confirmation because they may reflect misidentifications as a consequence of their subtle differences in shell morphology and lack of molecular taxonomy studies. Thus they could be more than one species [17, 53].

Conclusions

Saeedi et al. (in press) found that the latitudinal distribution of Solenidae was bimodal, with most species at the edges of the tropics. They suggested this may be typical for marine species in general, because such bimodality has also been found for taxa as varied as planktonic foraminifera and marine mammals [20]. The results of the present study show that this bimodality is likely to increase due to climate warming, and will result in increased species richness at regional scales because most species will increase their geographic range. Thus climate warming can be considered as an unintended global experiment that confirms the role of temperature in defining the latitudinal distribution of marine species.

Additional file

Additional file 1. Input environmental variables and geographic distribution data, and output results of the present and future distribution modelling. This file includes the additional data on correlations between the environmental variables, input geographic distribution points of Solenidae species used in the present and future modelling, and the models' output which could not be fitted inside the paper due the page limits.

Abbreviations

MaxEnt: maximum entropy; SST: sea surface temperature; GBIF: Global Biodiversity Information Facility; OBIS: Ocean Biogeographic Information System; WoRMS: World Register of Marine Species; GMED: Global Marine Environment Datasets; PSS: practical salinity scale; ROC: receiver operating characteristic; AUC: area under the ROC curve.

Authors' contributions

HS: study design, data collection, statistical analysis, species distribution modelling, writing the paper. ZB: environmental data interpretation, species distribution modelling, review of the paper. MJC: study design, statistical analysis, writing of the paper. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The dataset supporting the conclusions of this article is included within the article (and its Additional file 1).

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