

Using satellite-derived sea surface temperature to predict the potential global range and phenology of the invasive kelp *Undaria pinnatifida*

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Received: 5 January 2015 / Accepted: 18 August 2015 / Published online: 23 August 2015
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Abstract Understanding the temperature tolerances and phenology of an invasive species is essential to predicting its potential range and impacts on receiving environments. *Undaria pinnatifida* is a kelp species native to Northern Asian waters where it has a winter annual growth cycle. At some introduced sites *U. pinnatifida* can persist year-round, which potentially exacerbates its impacts. In this study we synthesise information on the global distribution and phenology of *U. pinnatifida* and use satellite-derived sea surface temperature (SST) measurements to investigate how distribution and phenology relate to temperature regime. These relationships are used to predict the potential global range and phenology of *U. pinnatifida*. The overall thermal limits of *U. pinnatifida* were considered to be the areas where the range in SST minima overlaps with the range in SST maxima for existing populations. *Undaria pinnatifida* was found to occur in regions with maximum temperatures

of 13.5–29.5 °C and minimum temperatures of 0.1–15.5 °C. The SST regime differed between native and introduced locations, and between locations with year-round and annual populations. All locations with year-round populations had a maximum SST < 20 °C, whereas annual populations had maximum SST > 20 °C; a finding consistent with the reported thermal parameters for *U. pinnatifida* gametogenesis. These results demonstrate that extensive areas of the world's coastline have SST regimes suitable for *U. pinnatifida* colonisation and are potentially at risk from invasion. When considered in combination with additional environmental factors influencing distribution success, this type of prediction mapping provides a valuable tool for invasive species management.

Keywords Invasive species · Wakame · Seaweed · Biological invasion · Niche shift · Distribution

Introduction

Ecological niche modelling is widely used to predict the potential distribution of invasive species (e.g. Peterson and Vieglais 2001). However, it is increasingly clear that invasive species can alter their niche at invaded locations. For example, they may occupy different climatic niche ranges at invaded locations (Broennimann et al. 2007) and when exposed to new environmental conditions, the growth and life cycle patterns of introduced populations can diverge from

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those displayed by native populations (Lockwood et al. 2007; Simberloff 2013). Divergent species traits can, in turn, exacerbate the impacts these species have on receiving environments (Mack et al. 2000). Therefore, understanding what drives variations in species life cycles at introduced sites is fundamental to predicting range expansions and the concurrent impacts, biotic and abiotic, of invasive species.

In the marine environment, algae comprise a significant component of invasive species (Schaffelke et al. 2007) and water temperature is a primary factor which influences both their distribution and life cycle patterns (Lobban and Wynne 1981; Breeman 1988, 1990). Broad temperature tolerances allow invasive species to spread over wide introduced ranges (Dukes and Mooney 1999; Nyberg and Wallentinus 2005; Williams and Smith 2007; Poloczanska et al. 2013). Some of the most high risk invasive algal species in the world, such as *Caulerpa taxifolia* (M. Vahl) C. Agardh, 1817 and the large brown seaweeds *Sargassum muticum* (Yendo) Fensholt, 1955 and *Undaria pinnatifida* (Harvey) Suringar, 1873 have adventive distributions which extend beyond those anticipated from looking at water temperatures in their native range (Aguilar-Rosas and Galindo 1990; Floc'h et al. 1991; Chisholm et al. 2000; Nyberg and Wallentinus 2005).

Undaria pinnatifida is native to Northern Asian waters (Kang 1966; Funahashi 1973; Yamada 1980). It has a wide temperature tolerance and is invasive to several regions around the world (Hay and Luckens 1987; Sanderson 1990; Piriz and Casas 1994; Fletcher and Manfredi 1995; Campbell et al. 1999; Cecere et al. 2000; Silva et al. 2002; James et al. 2014; Minchin and Nunn 2014). In its native range *U. pinnatifida* has an annual life cycle comprised of a macroscopic sporophyte phase in winter and a microscopic gametophyte phase in summer (e.g. Koh and Shin 1990). The sporophyte growth cycle aligns with cooler winter temperatures and senescence of the visible sporophyte occurs *en masse* as temperatures reach 24–27 °C; at these temperatures the growth rate of gametophytes also slows and the small male and female germlings adopt a resting phase (Tamura 1966; Saito 1975; Dieck 1993; Morita et al. 2003b; Gao et al. 2013). We found no reports in the literature of *U. pinnatifida* populations persisting year round within its native range. At some introduced locations however *U. pinnatifida* does not adhere to a strictly winter annual life cycle,

with successive generations of sporophytes being observed year-round in parts of New Zealand, South England, Argentina, Australia, California, and on the French Atlantic coast (Hay and Luckens 1987; Floc'h et al. 1991; Hay and Villouta 1993; Fletcher and Farrell 1999; Casas et al. 2008; Martin and Bastida 2008; Zabin et al. 2009). While these year-round populations can still exhibit a high degree of seasonality in the abundance of adult *U. pinnatifida* (Hay and Villouta 1993; Brown 1999; Casas et al. 2008; Martin and Bastida 2008), unlike native populations, there is no autumnal hiatus, and adult individuals are present year-round. The maximum summer sea surface temperatures at these introduced locations range between 15 and 19 °C and it has been hypothesised that at these temperatures macroscopic sporophytes are able to recruit and be present year-round (Hay and Villouta, 1993; Stuart 2004; Thornber et al. 2004; Schaffelke et al. 2005).

Undaria pinnatifida is a pervasive and proficient invasive species (e.g. Wallentinus 2007). It can form dense assemblages which dominate light, space and nutrient resources, altering the structure and character of marine environments (Sinner et al. 2000; Stuart 2004; Raffo et al. 2009; Irigoyen et al. 2011a, b). It can also disrupt aquaculture activities and foul vessel hulls and other marine structures (Fletcher and Farrell 1999; Cecere et al. 2000; Verlaque 2007). In regions where *U. pinnatifida* can persist year-round these impacts are likely to be greater than in areas where it is only seasonally present (Thornber et al. 2004; Raffo et al. 2009; Irigoyen et al. 2011a, b). Consequently, predicting the potential range and phenology of introduced *U. pinnatifida* populations is key to predicting the potential impacts of invasion.

This paper provides a global synthesis of the current distribution of *U. pinnatifida* and investigates how both the distribution and phenology of *U. pinnatifida* are related to water temperature regimes. Following validation against reported temperatures from the literature, temperature regimes were quantified for all reported locations where *U. pinnatifida* is found using satellite-derived measurements of sea surface temperature (SST). This allowed comparison of temperature ranges between all native and introduced populations, as well as between locations with differing phenologies (winter annual vs. year-round persistence). These temperature relationships were then used to predict the potential range and phenology of *U. pinnatifida*

globally. This study differs from typical niche modelling approaches (e.g. Peterson and Vieglais 2001) as we use satellite-derived sea surface temperature data to predict both the range and phenology of an invasive algal species on a global scale. The approach used has value in not only assessing the potential range of an invasive species, but also the likely levels of impact associated with different phenologies at different locations.

Methods

Compilation of global distribution and phenology information

Information on the current distribution and phenology of *U. pinnatifida* populations was synthesised based on a systematic review of population studies on *U. pinnatifida*. Literature was searched through the University of Auckland Library system including the use of databases such as NZ Science, Scopus and Google Scholar. Japanese, South American and French literature was searched using Google Scholar, the Hokkaido University Collection of Scholarly and Academic Papers (HUSCAP) and the Archive Institutionnelle de l'Ifremer. Some Japanese, Spanish and French research papers were available with only the abstract in English. Some of the Spanish and French papers could be translated using online translation tools and many of the more recent publications are printed entirely in English. Research articles were sought pertaining to the distribution and life cycle patterns of *U. pinnatifida* both within and outside its native range, effort was concentrated on adventive populations with a representative set of native sites selected. Worldwide distribution information was collated for the time period from 1981 to 2014, using the search terms “*Undaria pinnatifida*”. Material published on the physical composition of *U. pinnatifida* tissue, medicinal and nutritional properties surrounding *U. pinnatifida* were omitted from this review. Information for this paper was derived from 69 published articles, four student research theses, six books, six published government agency commissioned technical reports, two extracts from conference proceedings and the Global Invasive Species Database.

From each study, the location, and when available, the phenology of *U. pinnatifida* populations and

temperature regime at the location was recorded. Phenology was classified as being annual; one main recruitment pulse and macroscopic sporophytes not present throughout the year, or year-round; multiple recruitment pulses and some macroscopic sporophytes present throughout the year. Locations were considered to be distinct spatially if they were recorded as comprising discrete populations. In total, *U. pinnatifida* was reported from 51 locations worldwide (Table 1; Fig. 1) and information was available on the phenology of populations at 25 locations. Information on the annual temperature regime (i.e. SST minima and maxima) was available at 25 of the locations (Table 1).

Native sites where temperature information was available encompassed the geographical limits of the species and its temperature tolerances, and were therefore considered sufficient to enable accurate predictions. The endemic range of *U. pinnatifida* has its southern boundary in the centre of Mie Prefecture, southern Honshu, Japan (Morita et al. 2003a), although it has been introduced further south in Asian waters for mariculture (Uwai et al. 2006). The northern limit of distribution is southern Russia, Primorye region, Peter the Great Bay (Skriptsova et al. 2004) giving a latitudinal range of ~34–42°N (Table 1).

Global temperature data

Temperature data reported in the literature from field studies were collected using a range of methods, sampling frequencies, and over varying temporal and spatial scales, making it difficult to compare among studies and locations. Therefore, in order to predict the temperature limits for *U. pinnatifida* worldwide, satellite-derived sea surface temperature (SST) data was used to provide a consistent and standardised approach to estimating temperature regime for all identified *U. pinnatifida* locations. Because *U. pinnatifida* typically grows in shallow water or near the surface (e.g. Saito 1975), sea surface temperature was considered an appropriate proxy for temperature at a site. Satellite-derived SST data has previously been shown to be adequate at inferring broad-scale benthic climatology at depths less than 10 m (Smale and Wernberg 2009). *Undaria pinnatifida* field studies define water temperature regimes by the yearly maxima and minima values, which typically define

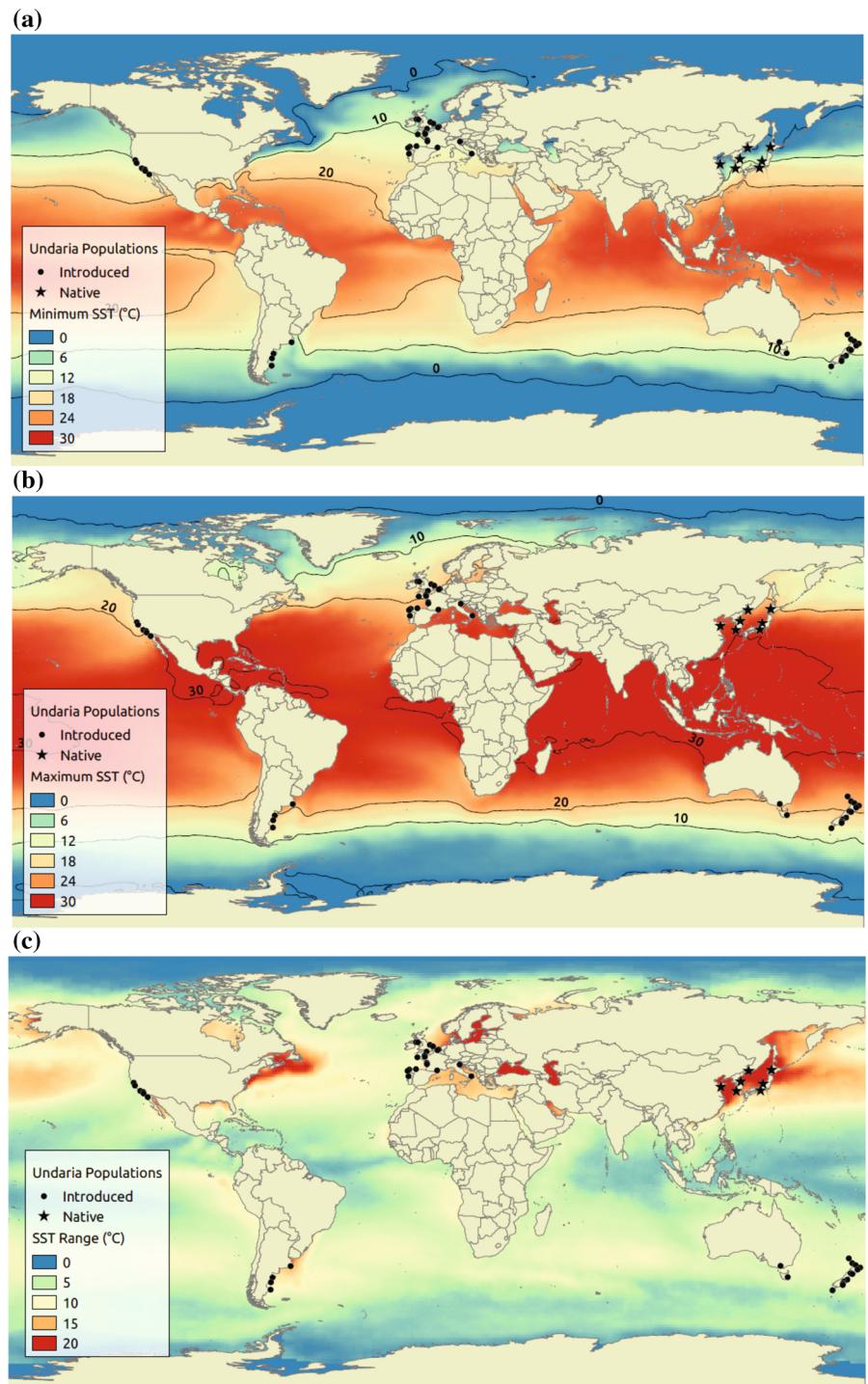
Table 1 Summary of locations for all known adventive *U. pinnatifida* populations around the world and seven representative native sites: reported (where available) and satellite-derived sea surface temperature (SST) data for each site and reported (where available) and predicted phenology for each population

Location, Country	Latitude	Longitude	Native	Reported SST			Reported phenology	Reference	Satellite-derived SST			Predicted phenology
				Max	Min	Range			Max	Min	Range	
<i>Asia</i>												
Hokkaido, JP	43.189893	141.251188	Y	22.0	4.9	17.1	Annual	Yamada (1980)	23.72	2.49	21.23	Annual
Toyama Gulf, JP	37.302676	137.774462	Y	25	4	21	Annual	Akiyama and Kurogi (1982)	27.81	8.31	19.50	Annual
Ise Bay, JP	34.544025	136.750354	Y	27	7.9	19.1	Annual	Morita et al. 2003a	29.47	15.47	14.00	Annual
Qingdao, CN	36.053590	120.431593	Y	—	—	—	Annual	Zhang et al. (1984)	27.93	3.28	24.65	Annual
Ohori, KR	38.214212	128.601402	Y	24	5	19	Annual	Koh and Shin (1990)	25.55	4.39	21.16	Annual
Wando Island, KR	34.298197	126.768815	Y	—	—	—	Annual	Oh and Koh (1996)	29.40	9.94	19.46	Annual
<i>Russia</i>												
Peter the Great Bay, RU	42.784130	131.844980	Y	24	0	24	Annual	Skripsova et al. (2004)	23.56	0.07	23.49	Annual
<i>Europe</i>												
Belfast Lough, IR	54.718016	-5.678269	N	—	—	—	Unknown	Minchin and Nunn (2014)	16.02	6.22	9.80	Year round
Stranraer, UK	54.634947	-4.875575	N	—	—	—	Unknown	Minchin and Nunn (2014)	16.02	6.04	9.98	Year round
Grimsby, UK	53.551751	0.102460	N	—	—	—	Unknown	Minchin and Nunn (2014)	17.39	4.93	12.46	Year round
Norwich, UK	52.942139	1.370913	N	—	—	—	Unknown	Minchin and Nunn (2014)	18.28	5.14	13.14	Year round
Oosterschelde, NL	51.640839	3.669530	N	—	—	—	Unknown	Gittenberger et al. (2010)	19.48	4.49	14.99	No prediction
Zeebrugge, BE	51.364209	3.190896	N	—	—	—	Unknown	Minchin and Nunn (2014)	19.48	4.49	14.99	No prediction
Port Hamble, UK	50.793042	-1.283595	N	—	—	—	Year round	Fletcher and Farrell (1999)	18.09	7.01	11.08	Year round
Jersey, UK	49.193328	-2.135674	N	—	—	—	Unknown	Minchin and Nunn (2014)	18.08	7.96	10.12	Year round
St Malo Bay, FR	48.638163	-2.022883	N	20.2	5.1	15.1	Year round	Castic-Fey et al. (1999)	18.92	8.34	10.59	Year round
Ushant, FR	48.445895	-5.100536	N	18	10	8	Year round	Floc'h et al. (1991)	19.10	9.90	9.21	Year round
La rochelle, FR	46.122384	-1.167701	N	—	—	—	Unknown	Minchin and Nunn (2014)	22.31	9.70	12.61	Annual
Royan, FR	45.591965	-1.122521	N	—	—	—	Unknown	Minchin and Nunn (2014)	22.92	10.27	12.65	Annual
Lagoon of Venice, IT	45.452067	12.338397	N	26	5	21	Annual	Curiel et al. (2001)	28.01	8.33	19.67	Annual
Gijon, ES	43.574275	-5.658425	N	—	—	—	Unknown	Minchin and Nunn (2014)	21.88	12.02	9.85	Annual
A coruna, ES	43.381306	-8.416311	N	—	—	—	Unknown	Minchin and Nunn (2014)	20.33	12.18	8.16	No prediction
Port la Nouvelle, FR	43.015754	3.069691	N	—	—	—	Annual	Floc'h et al. (1991)	24.75	11.72	13.03	Annual
Serre de outes, ES	42.827128	-9.136431	N	—	—	—	Unknown	Minchin and Nunn (2014)	20.34	12.60	7.75	No prediction
Taranto, IT	40.468518	17.202162	N	—	—	—	Unknown	Cecere et al. (2000)	27.44	13.07	14.37	Annual
Aveiro, PT	40.461433	-8.754597	N	20	13	7	Unknown	Araújo et al. (2009)	20.43	12.95	7.48	No prediction

Table 1 continued

Location, Country	Latitude	Longitude	Native	Reported SST		Reported phenology	Reference	Satellite-derived SST			Predicted phenology
				Max	Min			Max	Min	Range	
<i>The Americas</i>											
San Francisco, US	37.780227	-122.384239	N	-	-	-	Unknown	Zabin et al. (2009)	15.58	9.923	5.66
Monterey, US	36.605305	-121.890716	N	19	11	8	Year round	Thomber et al. (2004)	17.00	10.80	6.21
Santa Barbara, US	34.402919	119.68829	N	21	12	9	Unknown	Thomber et al. (2004)	19.02	12.00	7.02
Los Angeles, US	33.960572	-118.463442	N	-	-	-	Unknown	Silva et al. (2002)	21.08	13.09	7.99
Catalina Island, US	33.29969	-118.315499	N	-	-	-	Unknown	Silva et al. (2002)	21.08	13.09	7.99
Baja California, MX	31.848835	-116.624591	N	24	12	12	Unknown	Aguilar-Rosas et al. (2004)	22.35	14.16	8.19
Nuevo Gulf, AR	-42.777249	-64.998165	N	19	9	10	Year round	Casas et al. (2008)	19.24	9.15	10.09
Ria Descado, AR	-47.772096	-65.783227	N	13.5	4.5	9	Year round	Martin and Bastida (2008)	16.22	5.95	10.26
Camarones Bay, AR	-44.723517	-65.645667	N	-	-	-	Unknown	Casas et al. (2008)	18.27	7.84	10.43
Mar del Plata, AR	-38.039905	-57.526017	N	21	7	14	Unknown	Meretta et al. (2012)	21.60	6.74	14.84
<i>Australasia</i>											
Rangaunu, NZ	-34.838589	173.321148	N	24	14	10	Unknown	James et al. (2014)	22.46	15.09	7.37
Hauraki Gulf, NZ	-36.838283	174.750300	N	24	12	12	Annual	James and Shears (2013)	21.95	14.02	7.93
Tauranga, NZ	-37.649712	176.158530	N	20	13	9.7	Unknown	Jessop (2006)	22.90	14.11	8.18
Port Phillip Bay, AU	-37.968758	145.005703	N	24	8	16	Annual	Bite (2001)	20.57	12.26	8.31
Gisborne, NZ	-38.672743	178.016541	N	-	-	-	Unknown	Hunt et al. (2009)	21.58	13.79	7.79
Napier, NZ	-39.468909	176.922369	N	-	-	-	Unknown	Hunt et al. (2009)	20.72	12.85	7.87
Marlborough Sounds, NZ	-41.254883	174.017655	N	18	11.8	6.2	Year round	Brown (1999)	19.40	11.38	8.02
Wellington, NZ	-41.289584	174.789994	N	18.7	10.2	9.5	Year round	Hay and Villouta (1993)	19.40	11.38	8.02
Tasmania, AU	-42.583053	147.967128	N	20	10	10	Year round	C. Sanderson Pers Comm	18.76	11.37	7.38
Lytleton, NZ	-43.616657	172.717496	N	-	-	-	Year round	Thompson and Schiel (2012)	16.92	8.75	8.17
Timaru Harbour	-44.383762	171.266501	N	16.5	8	8.5	Year round	Hay (1990)	16.44	7.83	8.60
Oamaru, NZ	-45.106363	170.979169	N	17	7	9	Year round	Hay and Villouta (1993)	15.56	7.54	8.02
Moeraki, NZ	-45.353389	170.845341	N	-	-	-	Year round	Stuart (2004)	15.56	7.54	8.02
Otago, NZ	-45.849455	170.838529	N	16	7	10	Year round	Hay (1990)	15.56	7.54	8.02
Snares Islands, NZ	-48.032813	166.599995	N	-	-	-	Unknown	Hunt et al. (2009)	13.54	8.69	4.85

Fig. 1 Global distribution of *U. pinnatifida* in relation to global patterns in annual minimum (a), maximum (b) and range (c) in sea surface temperature (°C). Native (star) and introduced (circle) populations are shown



the survivable limits for different life history stages of *U. pinnatifida* (e.g. Morita et al. 2003a, b). Therefore, we characterise the SST regime using global maxima and minima values.

National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation (OI) SST V2 time series data were obtained from NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, via their web site

(<http://www.esrl.noaa.gov/psd/>). Weekly average SST values are available on a 1° global grid from 1990 to 2013. Minimum and maximum weekly averages from each year were used to provide an estimate of the long-term minimum and maximum temperatures. Mean yearly minimum and mean yearly maximum grids were then calculated based on annual minimum and maximum values from 1990 to 2013. The 90th percentile of yearly maxima and 10th percentile of yearly minima were calculated as an additional estimate of maximum and minimum temperature for each location. This resulted in two global estimations of yearly maximum SST (mean maximum and 90th percentile maximum) and two global estimations of yearly minimum SST (mean minimum and 10th percentile minimum).

To determine which of the satellite-derived estimates of SST minima and maxima best predicted the SST regime at coastal locations; these were compared to the reported SST minima and maxima values from the literature (see additional details in Fig. 2 legend). The 10th percentile minima better represented literature minima than the mean of yearly minima, with a higher R^2 and lower mean absolute error (10th percentile minima: $r^2 = 0.710, p < 0.001$, MAE = 1.61 °C vs. Mean yearly minima: $r^2 = 0.700, p < 0.001$, MAE = 2.09 °C). In contrast, there was little difference in how well the 90th percentile maxima

or mean yearly maxima represented the literature maxima (90th percentile maxima: $r^2 = 0.789, p < 0.001$, mean absolute error (MAE) = 1.50 °C vs. Mean yearly maxima: $r^2 = 0.799, p < 0.001$, MAE = 1.54 °C). Therefore, for consistency the 10th percentile values were used to represent SST minima (Fig. 1a) and 90th percentile values were used to represent SST maxima (Fig. 1b) in all subsequent calculations. SST range was calculated as the difference between the 90th percentile maximum and 10th percentile minimum (Fig. 1c). In general, the strong concordance between satellite-derived SST and measured temperature data (Fig. 2) meant that SST regime could be reliably estimated for all locations where *U. pinnatifida* has been reported. Minimum satellite-derived temperatures were, however, often higher than minimum temperatures reported in the literature. This is most likely due to greater terrestrial influence on inshore temperature values that are not captured in the larger-scale satellite-derived data. For example, Ise Bay and Toyama Gulf, Honshu in Japan have recorded annual minimums of 7.9 and 4.0 °C respectively, whereas satellite-derived minimum temperature values were 15.5 and 8.3 °C respectively. Both of these sites have high freshwater and snowmelt input from local mountains, which likely results in cooler recorded temperatures inshore compared to satellite-derived values.

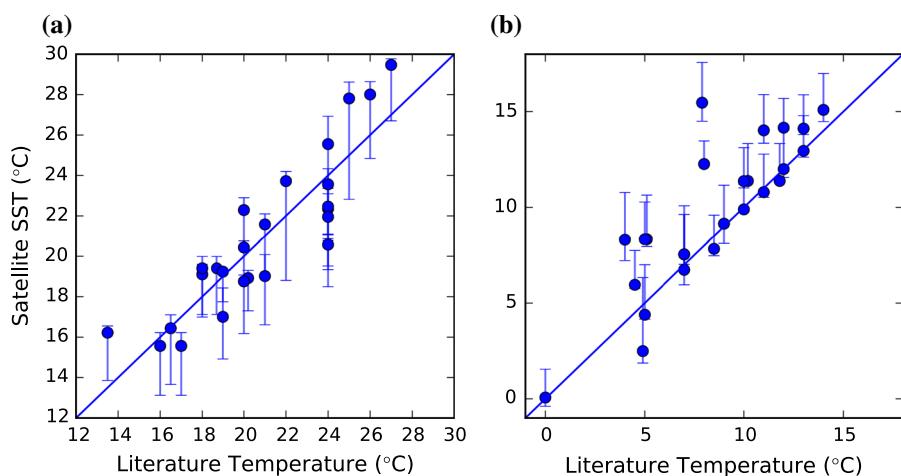


Fig. 2 Satellite-derived estimates versus literature records of maximum (a) and minimum (b) sea surface temperature at *U. pinnatifida* study locations. Each point represents a study on *U. pinnatifida* where the maxima and minima temperature has been reported for a location (Table 1). The error bars on the satellite-

derived measurements represent the range of maximum (a) and minimum (b) annual values observed across the time series (1990–2013). The points indicate the 90th percentile for maxima and 10th percentile for minima. Diagonal line depicts a 1:1 relationship

Sea surface temperature calculations were done in Python using the netCDF4 library to access data and the Pandas library (McKinney 2010) for aggregation. Sea surface temperature metrics (maximum, minimum and annual range) were compared between native and introduced populations, and between populations with year-round and annual presence of sporophytes using a Welch's *t* test in Python statsmodels v0.6.0. This test was used as it allows for different variances in the underlying populations by adjusting the degrees of freedom.

Using satellite-derived SST to map global distribution and phenology

The potential global range where SST regimes are likely to support *U. pinnatifida* populations was estimated based on the SST regimes for existing populations and the global grids of 90th percentile maximum SST and 10th percentile minimum SST from OISST V2 (as outlined above). The overall thermal limits of *U. pinnatifida* were considered to be the area where the range in SST minima for existing populations overlaps with the range in SST maxima for existing populations. Areas with SST maxima and minima outside of these ranges were considered to be too hot or too cold for *U. pinnatifida* to establish viable populations. Within the predicted thermal range of *U. pinnatifida*, phenology was predicted based on the reported differences in SST regime between populations with year-round and annual presence of sporophytes. Due to separation in the ranges of SST maxima between year-round and annual populations, a small area was classified as having no prediction for phenology. The results were interpolated to 0.125° latitude × 0.125° longitude for display as a global map of thermal limits and predicted phenology.

Results

Global distribution and temperature regimes

Sea surface temperature regime in the native range of *U. pinnatifida* is characterised by a large annual range (Table 1; Fig. 1) with temperatures commonly fluctuating by 20–25 °C annually, ranging from 0.1 °C in the winter, to 29.5 °C in the summer (Fig. 3). Introduced *U. pinnatifida* populations occur at locations

with a variety of temperature regimes (Figs. 1, 3), but overall have a narrower annual temperature range (c. 7–15 °C) compared to native populations (Table 1; Figs. 1, 3; Literature: $t = -6.64$, $df = 8.10$, $p \leq 0.001$; Satellite-derived: $t = -7.83$, $df = 7.47$, $p \leq 0.001$).

Maximum temperatures at locations within the native range are significantly higher than at introduced locations, based on both literature and satellite-derived temperature values (Literature: $t = -4.08$, $df = 11.15$, $p = 0.002$, Satellite-derived: $t = -6.81$, $df = 9.16$, $p \leq 0.001$). There are however a few introduced locations, such as the Lagoon of Venice, Italy (8.3–28.0 °C) and Baja California, Mexico (14.6–22.4 °C), that have similar maximum temperatures to native populations. Minimum temperatures among the introduced locations were quite variable (0.1–15.5 °C) and typically higher than those from native locations (Fig. 3). Based on reported data in the literature this difference in minimum temperatures was significant ($t = 3.58$, $df = 6.27$, $p = 0.011$), but there was no significant difference based on satellite-derived data ($t = 1.75$, $df = 6.63$, $p = 0.125$).

Variation in phenology

All *U. pinnatifida* populations reported within the native range had a winter annual life cycle, whereas introduced populations had a mix of annual and year-round presence of sporophytes (Table 1). There were clear differences in temperature regime between locations with annual and year-round presence of sporophytes, and these patterns were consistent based on both the literature and satellite-derived temperature values (Fig. 4). Based on satellite-derived temperature data there was no difference in minimum temperature between populations with annual and year round presence ($t = -0.43$, $df = 12.01$, $p = 0.676$), but annual populations had significantly higher maximum temperatures than year round populations ($t = 8.07$, $df = 14.06$, $p \leq 0.001$). Consequently, locations with annual populations also had a greater range in temperature (Fig. 4, $t = 4.93$, $df = 10.88$, $p \leq 0.001$). All *U. pinnatifida* populations known to have an annual life cycle for which reported temperatures were available in the literature had reported maximum temperatures ≥ 22.0 °C and satellite-derived maximum temperatures ≥ 20.6 °C. All year-round populations had reported maximum temperatures ≤ 20.2 °C

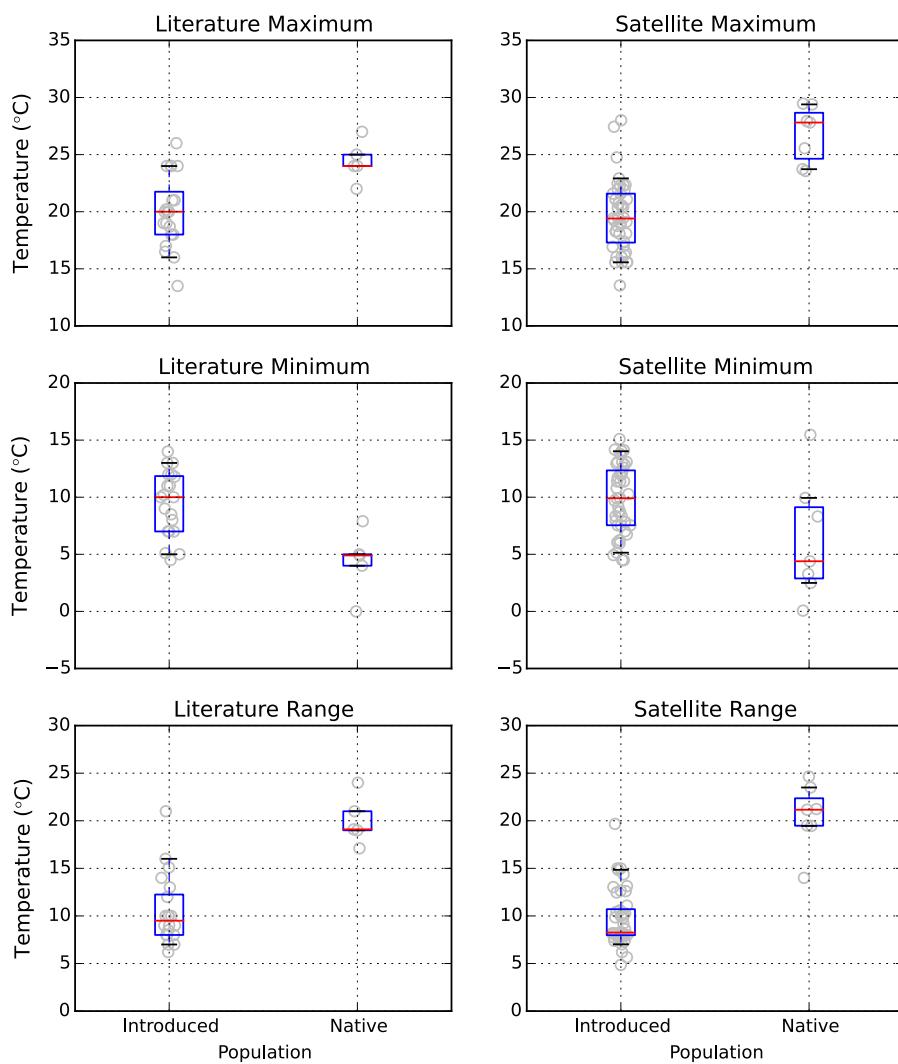


Fig. 3 Comparison of temperature regimes (minimum, maximum and range) between native and introduced populations of *U. pinnatifida* based on literature records (*left*) and satellite-

derived estimates (*right*). The *box* shows the interquartile range (25–75th percentiles, with horizontal *red line* as median) and the *whiskers* show the 5–95th percentiles

and satellite-derived maximum temperatures ≤ 19.4 °C (Fig. 4).

Prediction of global distribution and phenology

Based on the above analysis of the reported distribution, the thermal limits of *U. pinnatifida* were estimated to be where maximum temperatures were between 13.5 and 29.5 °C and minimum temperatures were between 0.1 and 15.5 °C. To predict the potential global distribution of *U. pinnatifida* these were conservatively adjusted, such that areas with maxima

greater than 30 °C or minima greater than 16 °C were deemed too hot to support *U. pinnatifida* populations, and areas where maxima was less than 13 °C or minima less than 0 °C were deemed too cold to support *U. pinnatifida* populations (Fig. 5). Within these thermal limits, populations were characterised as having a year-round phenology where maxima were ≤ 19.4 °C, and as having an annual phenology where maxima were ≥ 20.6 °C (Fig. 5). Phenology was not predicted for areas with maxima between 19.4 and 20.6 °C, and these sites are referred to as having unknown phenology. For the 26 locations where *U.*

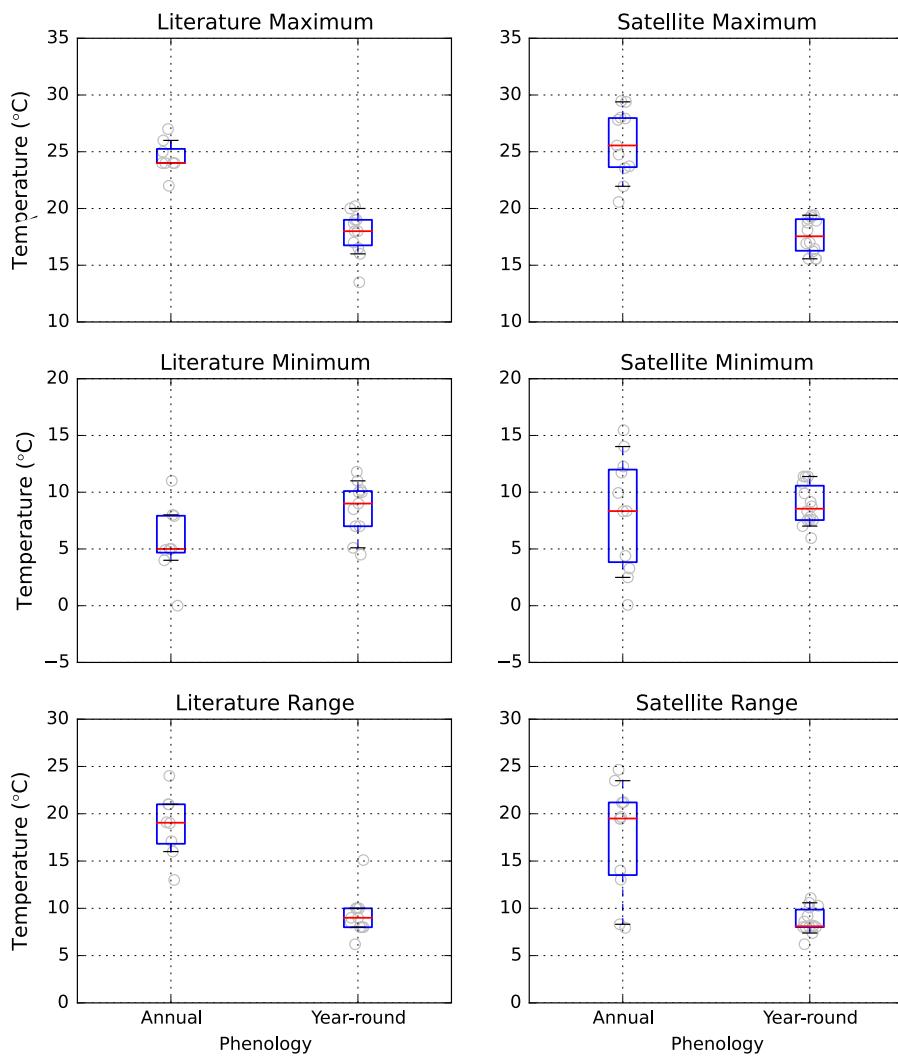


Fig. 4 Comparison of temperature regimes (minimum, maximum and range) between annual and year-round life cycle patterns of *U. pinnatifida* based on literature records (*left*) and satellite-derived estimates (*right*). The *box* shows the interquartile range (25–75th percentiles), with horizontal *red line* as

median) and the *whiskers* show the 5–95th percentiles. Note: literature values are only shown for a subset of the populations where temperature information was available, whereas satellite-derived estimates are given for all locations where phenology information was available (Table 1)

pinnatifida populations occur, but the phenology is currently not recorded in the literature, 12 were predicted as annual, 9 were predicted as being year-round, and for 5 locations no prediction was made (Table 1; Fig. 5).

Based on the global temperature data set, large stretches of the world's coastline were found to have temperature regimes suitable for *U. pinnatifida* establishment (Fig. 5). Prediction bands for the two different phenologies covered a relatively similar

extent and the current distribution of *U. pinnatifida* is relatively evenly split between these two bands. Notable areas with suitable temperatures where *U. pinnatifida* has not yet been documented include the east coast of North America and the west coasts of South America and Africa. The phenology in each of these areas would be predicted to vary along the coast in relation to SST with year-round populations at higher latitudes and annual populations at lower latitudes.

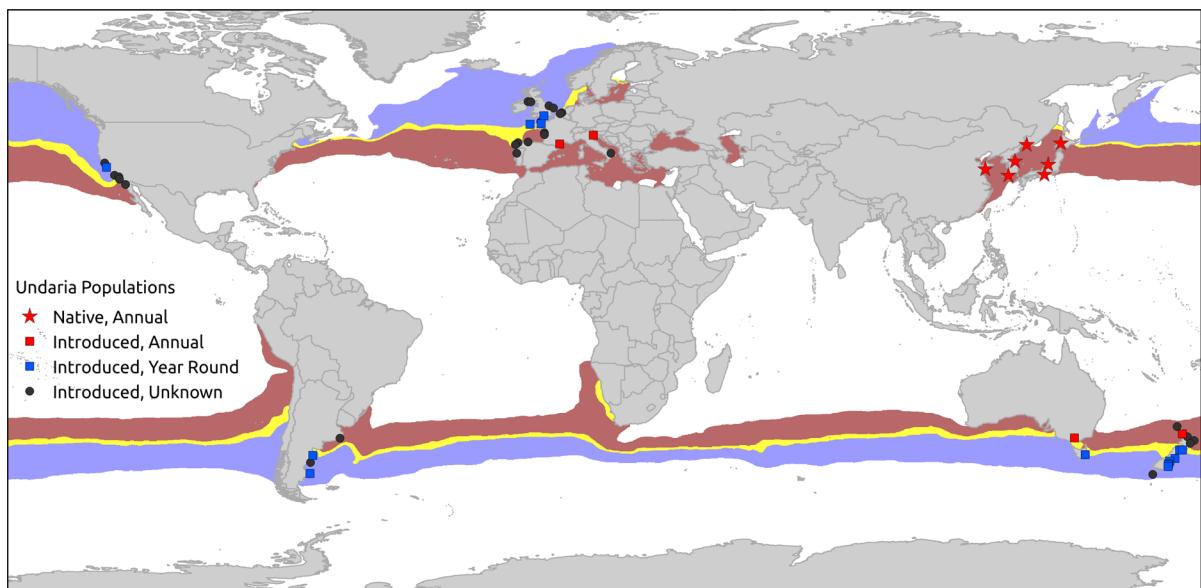


Fig. 5 Potential global range and phenology for *U. pinnatifida* based on satellite-derived sea surface temperature (Blue area predicted to support year round sporophyte presence, Red area predicted to support annual sporophyte presence, Yellow no prediction). The predicted phenology for locations where *U. pinnatifida* is present, but the phenology is not documented (black symbols), is given in Table 1

Undaria pinnatifida has not been recorded at locations where maximum temperatures exceed 29.5 °C or where temperatures drop below 0 °C. This is consistent with the critical temperature limits known to kill all life stages of *U. pinnatifida* (Tamura 1966, Saito 1975; Dieck 1993). Sites with annual temperature regimes falling inside the lethal limits (0–30 °C) must include a period of time during the year where temperatures are between 10 and 20 °C in order to support effective reproduction (Saito 1975; Lobban and Wynne 1981; Bite 2001; Morita et al. 2003a and references therein; Thornber et al. 2004; Kohtio 2008).

Mature *U. pinnatifida* sporophytes are tolerant of a wide range of temperatures (5–27 °C) and following the maturation of the sporophyte, the release and germination of zoospores can occur at temperatures between 5 and 25 °C (Saito 1975; Floc'h et al. 1991; Castic-Fey et al. 1999; Petrone et al. 2011). Zoospores then grow into gametophytes. Although gametophytes may continue to grow at temperatures as high as 27 °C and may survive at temperatures of 0–29 °C (Saito 1975; Dieck 1993), gametophyte maturation and gametogenesis take place at temperatures between 5 and 20 °C (Saito 1956a, b; Lobban and Wynne 1981; Pang et al. 2008) and the optimal temperature range

Discussion

Over the past 32 years *U. pinnatifida* has gained an extensive global distribution and now occurs across a variety of temperature regimes (Fig. 1). *Undaria pinnatifida* was found to be limited to sites where maximum water temperatures are between 13.5 and 29.5 °C and where minimum water temperatures are between 0.1 and 15.5 °C. In its introduced range *U. pinnatifida* exhibits variable seasonal growth patterns, displaying a winter annual phenology at some locations, consistent with native populations, and a persistent year-round phenology at other locations. Our findings are consistent with the hypothesis that the seasonality of the macroscopic sporophyte population is dependent on the local temperature regime, specifically the maximum annual sea surface temperature (Saito 1975; Hay and Villouta 1993; Stuart et al. 1999). Based on satellite-derived temperatures, where summer maxima exceeded 20.6 °C, populations exhibited a winter annual phenology, whereas at locations where summer maxima were below 19.4 °C, populations were classified as being year-round, meaning that some adult sporophytes were present throughout the year.

for maturation of gametophytes is between 10 and 20 °C (Saito 1956a, b; Morita et al. 2003a and references therein; Brown 1999; Bite 2001; Thornber et al. 2004; Kohtio 2008). This upper temperature threshold is consistent with our finding that in locations where summer temperatures exceed 20 °C populations experience a summertime hiatus and are therefore largely restricted to a winter annual life cycle. Locations which experience a narrow annual water temperature range with a summer maximum below 20 °C may allow gametogenesis to occur recurrently during the year; for warmer locations the amount of time during the year when temperatures remain above 20 °C will affect the persistence of *U. pinnatifida* populations. *Undaria pinnatifida* sporophytes have a maximum lifespan of around 6–8 months, (Hay and Luckens 1987; Castic-Fey et al. 1999; Morita et al. 2003b) so a recruitment period of four months or longer, or multiple recruitment pulses per year can result in a year round presence of macroscopic sporophytes.

Peaks of sporophyte recruitment and growth in introduced populations consistently occur when temperatures are between 10 and 17 °C (Casas and Piriz 1996; Castic-Fey et al. 1999; Kohtio 2008; Thornber et al. 2004; Jessop 2006). Consequently, even year-round populations typically experience seasonal variations in growth and reproduction in coincidence with this temperature range (Hay 1990; Hay and Villouta 1993; Thornber et al. 2004; Casas et al. 2008). Factors such as light and nutrient availability vary with seasons and years and also affect the resulting size and abundance of plants at different times of year (Dean 1998; Stuart et al. 1999; Choi et al. 2007). However, our results suggest that temperature is an underlying regulator of whether populations are able to persist year-round. It is therefore expected that inter-annual variation in *U. pinnatifida* phenology will occur in regions where maximum summer temperatures are around 20 °C; during cooler years (max. SST < 20 °C) populations would be expected to persist year-round, whereas in years when temperatures exceed 20 °C populations would be expected to experience a hiatus in recruitment.

The relationships between both the distribution and phenology of *U. pinnatifida*, and sea surface temperature, allowed prediction of the thermal distributional limits of *U. pinnatifida* and its expected phenology globally. The satellite-derived SST data was generally

effective in predicting overall SST regimes at locations where *U. pinnatifida* occurs, due to the confirmed relationship between the SST regimes reported in the literature and those predicted from satellite-derived data. Satellite-derived estimates of SST minima were higher than reported SST minima for a number of locations, such as those around Japan where snowmelt may influence recorded water temperatures (Coastal Oceanography Research Committee, Oceanographical Society of Japan 1985). Inshore SST can be highly variable across small scales (e.g. Yamada 1980; Morita et al. 2003a) as it is more frequently influenced by terrestrial and climatic factors than offshore SST and therefore can show greater fluctuations than oceanic waters (Thomas et al. 2002). Adventive *U. pinnatifida* populations commonly occupy shallow water and artificial marine structures (Fletcher and Manfredi 1995; Floc'h et al. 1991, 1996; Verlaque 2007) where these small-scale temperature fluctuations are not captured at the relatively coarse resolution of the satellite-derived data (Smale and Wernberg 2009). Nevertheless, the relationship between satellite-derived and literature SST values in the present study was considered strong enough to allow the use of satellite-derived estimates as a standardised measure of SST regime to make broad-scale predictions for distribution and phenology of *U. pinnatifida*.

All populations known to be year-round had satellite-derived maximum SST ≤ 19.4 °C, whereas all of the annual populations had satellite-derived maximum SST ≥ 20.6 °C. Due to this separation in maximum temperatures, no predictions of phenology were made for locations where maximum SST fell between 19.4 and 20.6 °C. This approach allows for the fact that we do not know the critical temperature within this range that would determine the realised phenology, that the duration of time spent above a critical temperature will also be important, and that maximum SST for any given location will vary inter-annually such that populations within this range could have a variable phenology from year to year. It is also important to note that within the broad prediction bands for annual and year-round populations, local-scale variation in SST (e.g. associated with shallow sheltered embayments or marinas) will ultimately influence the distribution and phenology of *U. pinnatifida*. For example, within the range where *U. pinnatifida* is expected to occur year-round, local-scale factors could result in summer maximum

SST > 20 °C, which would be predicted to result in an annual population. Therefore, while this method provides a global prediction of regions where SST regimes are suitable for *U. pinnatifida* and defines temperature limits for the likely phenology of populations at some sites, additional information on local SST regimes is important for small-scale predictions of both distribution and phenology. Within the designated thermal limits the realised distribution of *U. pinnatifida* will also depend upon suitable receiving conditions for survival, for example; habitat, salinity, water motion and nutrient levels must all be appropriate (e.g. Lobban and Wynne 1981).

The ability to predict the potential phenology of new populations has implications for understanding impacts at invasion sites. Whether generations of *U. pinnatifida* sporophytes are overlapping or discrete and whether the life history is strictly annual or not, has important consequences for the success of *U. pinnatifida* populations, its impact on native flora and fauna, and its influence on marine community structure. For example, if macroscopic stages only appear in winter when fewer native kelp species are reproductively active, *U. pinnatifida* might compete less directly with native species (Valentine and Johnson 2004); whereas if generations are persistent and overlapping throughout the year, the potential for negative effects on native species is much greater (Thornber et al. 2004; Thompson and Schiel 2012). Such impacts have been documented in the Nuevo Gulf, Argentina where persistent *U. pinnatifida* populations dominate reef sites year-round and impact on community structure and composition, excluding some native species (Raffo et al. 2009; Irigoyen et al. 2011a, b). This study predicts many populations, particularly around Northern Atlantic Europe, could have populations which persist year-round, potentially putting native benthic communities at greater risk from the impacts of *U. pinnatifida* invasion at these sites.

Understanding how temperature affects *U. pinnatifida* phenology and mapping temperatures and temperature ranges allows large-scale predictions of where *U. pinnatifida* can survive and the probable life cycle patterns of populations within these regions. This study identified a number of large regions where temperature regimes are suitable, but *U. pinnatifida* has not yet been documented. These sites include the

east coast of North America and the west coasts of South America and Africa. Mapping these regions where temperatures are suitable for *U. pinnatifida* survival is only the first step in defining particular coastal locations which may be at risk from *U. pinnatifida* invasion. Further research is needed to understand additional local factors which may determine areas within these broad regions which are at risk from invasion. As well as suitable receiving conditions, in order for *U. pinnatifida* to successfully colonise a new site it requires a transport mechanism or vector for introduction, so factors such as the proximity of shipping ports and marinas need to be considered to determine the actual likelihood of *U. pinnatifida* invasion.

Understanding differences in temperature regimes between native and introduced populations is vital when making predictions about the potential distribution of an invasive species. A species in its native range will likely have a reported distribution which is relatively complete, while a species colonising new areas may spread beyond known temperature limits (e.g. Chisholm et al. 2000). The present example revealed how sea surface temperature regimes generally differ between sites of native and introduced *U. pinnatifida* populations. Incorporating different species traits into more traditional ecological niche modelling provides a further advance in predicting invasive species distributions and likely impacts (Guisan and Thuiller 2005). In this case, incorporating *U. pinnatifida* phenology, lead to the novel finding that these differences in temperature regime can result in different life cycle patterns, which can ultimately influence the magnitude of invasion impacts.

This type of approach to modelling species distribution will be of increasing importance under a changing climate regime as the potential distribution of invasive species is also likely to change (Sutherst 2000; Stachowicz et al. 2002; Wernberg et al. 2010). Understanding how the functional attributes of species, such as phenology, may vary under such scenarios will greatly increase the value in such projections.

Acknowledgments We would like to thank Auckland Council and Waikato Regional Council for supporting this research. We would like to greatly acknowledge all the authors of the many interesting and valuable papers used as the basis for this article and to thank the two anonymous reviewers of this paper.

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