Short Communication

Ana Carolina Félix-Loaiza, Lucía Mercedes Rodríguez-Bravo, Rodrigo Beas-Luna, Julio Lorda, Eliot de La Cruz-González and Luis Malpica-Cruz*

Marine heatwaves facilitate invasive algae takeover as foundational kelp

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Abstract: Extreme warming events have diminished kelp ecosystems around the world, but few reports exist about their impacts on invasive species. Warming events along the coast of Baja California from 2014 to 2016 negatively affected kelp forest communities historically dominated by *Macrocystis pyrifera*. We measured changes in the macroalgal community at Todos Santos Islands, Baja California, Mexico between 2018 and 2019. Our results documented a dramatic reduction of *M. pyrifera*, and a concurrent structural shift to invasive kelps dominance, with *Sargassum horneri* and *Undaria pinnatifida* being highly abundant in 2019. This study provides insights about impacts of invasive kelp species on macroalgal community structure under future climate scenarios.

Keywords: climate change; invasion impacts; kelp forests; *Macrocystis pyrifera*; phase shifts.

Kelp forest communities along the Pacific Northwest have recently experienced dramatic climate change related impacts (Beas-Luna et al. 2020). From 2013 to 2016, the California Current System experienced an unusually high and persistent warming event, the "Warm Blob", from Alaska southward to the coast of Baja California. In 2015–2016, this warming event was succeeded by one of the strongest El Niño Southern Oscillation (ENSO) on record (Di Lorenzo and Mantua 2016). It is now widely documented that these marine warming events influenced shifts in distribution and abundance of at least 165 taxonomic groups (e.g. Lonhart et al. 2019), canopy kelp biomass was significantly reduced (Cavanaugh et al. 2019) and community structure switched to a less complex system, characterized by species with warmer affinities (Arafeh-Dalmau et al. 2019).

Miller and Engle (2009) hypothesized that changes in the cover and/or density of *M. pyrifera*, caused either by climate change phenomena (e.g. ENSO events and marine heatwaves), or biologically driven changes (e.g. sea urchin overgrazing), could facilitate conditions for the recruitment of new populations of opportunistic non-native invasive species. As climate change effects would be more evident in kelp forests near the southern portion of the California Current (Beas-Luna et al. 2020), there is a need to understand how novel species will influence the structure and function of coastal marine ecosystems in this area.

Kelp forest communities near their southern distribution limit along the coast of southern California, USA and Baja California, Mexico, where *Macrocystis pyrifera* (Linnaeus) Agardh is the historically predominant structuring and foundational native species (Schiel and Foster 2015), have seen an increase in the spread and presence of non-native *Sargassum horneri* (Turner) Agardh (Marks et al. 2015; Riosmena-Rodríguez et al. 2012), and *Undaria pinnatifida* (Harvey) Suringar (Aguilar-Rosas et al. 2004; Silva et al. 2002) over the past decades. Both species are originally from Asia, but are now distributed in locations along the coast of California and Baja California (Aguilar-Rosas et al. 2004; Marks et al. 2015). *Undaria pinnatifida* and *S. horneri* are considered invasive species because they compete for space with native macroalgae and, once established, can induce changes in community composition and species diversity

***Corresponding author: Luis Malpica-Cruz,** Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico; and ECOCIMATI, A.C., Av. Del Puerto 2270, 22880, Ensenada, BC, Mexico, E-mail: lmalpica@uabc.edu.mx. https://orcid.org/0000-0003-0750-1652
Ana Carolina Félix-Loaiza, Lucía Mercedes Rodríguez-Bravo, Rodrigo Beas-Luna and Eliot de La Cruz-González, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico. https://orcid.org/0000-0002-7266-3394 (R. Beas-Luna)
Julio Lorda, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico; and Tijuana River National Estuarine Research Reserve, 301 Caspian Way, 91932, Imperial Beach, CA, USA, E-mail: jlorda@uabc.edu.mx. https://orcid.org/0000-0002-4293-7518

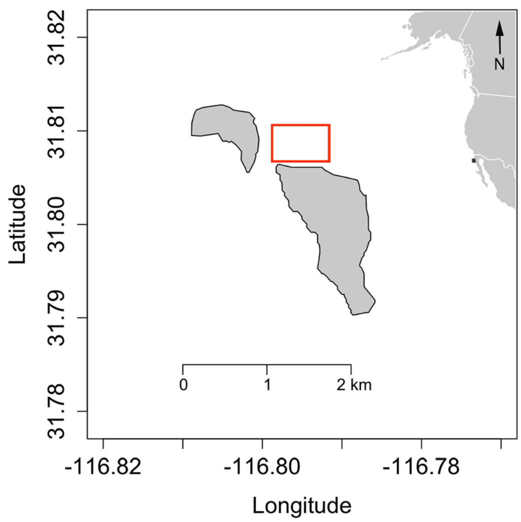

Figure 1: Map showing northern and southern Todos Santos Islands. Red square highlights the sampling area. Black square in inset map indicates location of Todos Santos Bay in Baja California, Mexico.

(James 2017). Here, we report the local presence and discuss potential impacts of *U. pinnatifida* and *S. horneri* at Todos Santos Islands, Baja California, Mexico.

Todos Santos Islands are located off the northwest coast of Baja California, Mexico, approximately 120 km south of the border between the USA and Mexico (Figure 1). Its surrounding waters harbor a temperate ecosystem representative of the Southern California Bight, with seasonal northwest winds that promote coastal upwelling, primary productivity and a rich and diverse trophic chain (Lynn and Simpson 1987). We evaluated shifts in the kelp community on a rocky reef at ~10 m depth between the northern and the southern Todos Santos Islands (Figure 1). We surveyed four 30 × 2 m underwater transects using SCUBA in May 2018 and June 2019. On each transect we measured the density (individuals m^{-2}) of *U. pinnatifida*, *S. horneri* and *M. pyrifera* larger than 15 cm.

Between 2018 and 2019 we documented a dramatic population reduction of *M. pyrifera* in our study site, as the species declined from a mean of ~ 0.7 individuals m^{-2} in 2018 to 0 individuals m^{-2} in 2019 (Figures 2 and 3). In this same site and time period, we also observed a threefold increase in the density of *S. horneri*, and *U. pinnatifida* going from absent in 2018 to ~ 4 individuals m^{-2} in 2019 (Figure 2). Aerial views of the study site show kelp canopy well extended to the water surface in 2018, while there was a total absence of canopy and exposure of bottom rocks in 2019 (Figure 3).

In Baja California, the marine heatwave from 2013 to 2016 led to a dramatic loss of *M. pyrifera* biomass (Arafeh-Dalmau et al. 2019; Cavanaugh et al. 2019) and significant changes to fish, algal and invertebrate communities (Arafeh-Dalmau et al. 2019; Beas-Luna et al. 2020). Marine heatwave events started to diminish in the summer of 2016 and were less intense through 2017. Satellite-derived data from Arafeh-Dalmau (2019) reported that, by spring and winter of 2017, kelp biomass at Todos Santos Islands had recovered to seasonal values observed before the warming events. However, Cavanaugh et al. (2019) found that, while native kelp biomass started to recover at different sites along southern Baja California, the decline continued from 2017 to 2018 at Todos Santos Islands and adjacent areas. Additionally, Arafeh-Dalmau et al. (2019) reported a threefold reduction in the number of *M. pyrifera* fronds before and after the warming events at Todos Santos Islands based on *in situ* surveys. Differences in the impact reported for native kelps at Todos Santos Islands could be explained by methodological differences to estimate *M. pyrifera*, (i.e. biomass vs. fronds), and the different specific study sites assessed. Regardless, this widespread

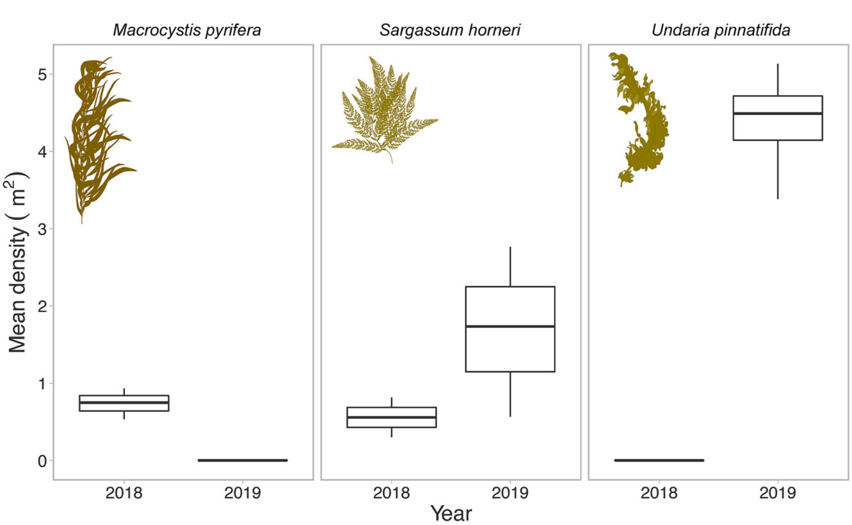

Figure 2: Density changes of native *Macrocystis pyrifera* and two invasive kelp species between 2018 and 2019 at Todos Santos Islands, Baja California, Mexico. Lower and upper box boundaries represent the 25th and 75th percentiles, respectively, the line inside box the median, and lower and upper error lines the 10th and 90th percentiles, respectively.

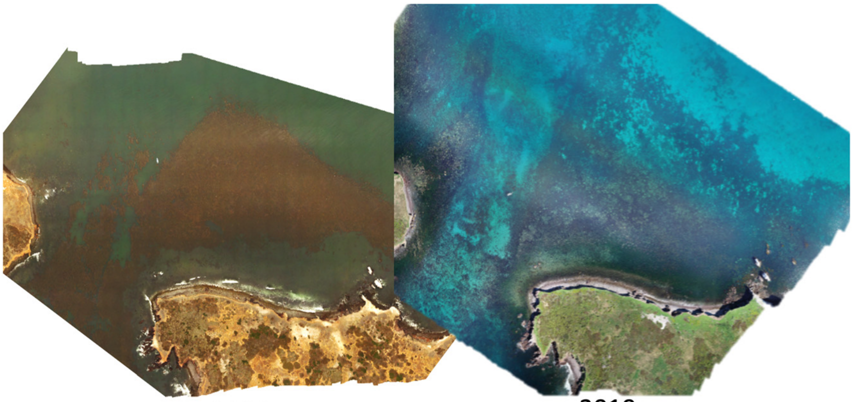

Figure 3: Composite images using AUV (drone) photography from Todos Santos Islands channel reef at 30 m altitude showing presence and absence of native *Macrocystis pyrifera* canopy between 2018 (native dominated) and 2019 (invasive dominated). Orthomosaic composed from ~ 191 images, each image overlapping 80% with the neighboring photos, and with a resolution of 1.29 cm pix^{-1} using Photoscan.

native kelp canopy decline could have further facilitated invasion pathways in this benthic community, specifically for our study site.

Invasive macroalgae such as *S. horneri* have been observed to proliferate after disturbances that decrease the abundance or alter the distribution of native macroalgae (Sullaway and Edwards 2020). *Undaria pinnatifida*, an opportunistic species, grows best in absent or scarce canopy areas (James 2017). Due to its constant recruitment capacity, *U. pinnatifida* has an enhanced invasive potential and would thrive when conditions are suitable (≤15 °C) in open canopy areas, thus establishing persistent populations (Thornber et al. 2004). Arafeh-Dalmau et al. (2019) reported changes to the structure of subcanopy species with a high presence of *U. pinnatifida* after the 2013–2016 marine heatwave at Todos Santos Islands and other locations along the coast of Baja California. Similarly, the 2014–2016 marine heatwave appears to have facilitated the establishment of *S. horneri* populations in areas where *M. pyrifera* populations were previously present (Marks et al. 2015). Indeed, under laboratory and controlled field experiments it has been found that light limitation – such as that produced by these low canopy-forming invasive kelps – can hinder recruitment and juvenile survival of *M. pyrifera* (Beckley and Edwards 2021; Sánchez-Barredo et al. 2020).

The decrease in abundance of *M. pyrifera* coupled with favorable growth conditions for both *U. pinnatifida* and *S. horneri* during and after the 2014–2016 marine heatwave events likely resulted in the increased abundance observed in this study. It is yet unclear how persistent these seeming population shifts will be, but these warming events in addition to other future climate conditions such as ocean acidification (Shlenger et al. 2021) may be the onset of more profound macroalgal community structure shifts at Todos Santos Islands as, once established, both of these species can compete for space with native canopy-forming algae. Furthermore, given the influence of *M. pyrifera* as bio-engineers of their surrounding environment, changes to this foundational species would likely result in a novel community of understory algae, sessile species and mobile predators (Schiel and Foster 2015). Over the past decade, kelp forests and the ecosystem services they provide have deteriorated drastically. Future climate change scenarios suggest a challenging future for these temperate ecosystems. Thus, understanding response mechanisms of novel species interactions will inform adequate management strategies. Hence, further monitoring should be carried out to evaluate the long-term change of macroalgal community structure and its consequences for ecosystem functioning and services, particularly the presence and abundance of invasive kelps in the region. Such studies should focus on better understanding annual lifecycles of the invasive kelps, as well as the impacts of shifts in food availability and novel energy pathways to herbivores and throughout higher-level consumers.

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Data availability: The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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Ana Carolina Félix-Loaiza
Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico

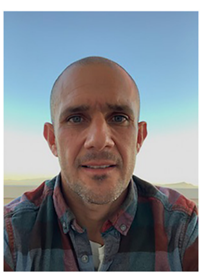
Ana Carolina Félix-Loaiza is a laboratory assistant in the Fish Culture Conservation Laboratory at UC Davis. Scientific diver with experience in ecological monitoring of reefs, estuaries and kelp forests. Worked as a field and laboratory assistant in MExCal, ECODEL, ICMME, and the aquaculture laboratory at Universidad Autónoma de Baja California studying the combined effects of fisheries and climate change on *Panulirus interruptus*. She holds a bachelor's degree in environmental sciences from UABC with a dissertation focusing on the nutritional effects of invasive algae as diet of *Mesocentrotus franciscanus*.

Lucía Mercedes Rodríguez-Bravo
Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico

Lucía Mercedes Rodríguez-Bravo is a research specialist in the Red Sea Research Center at King Abdullah University of Science and Technology. She is interested in marine ecology, global change biology, climate change marine introduced species, and phycology. She has a B.Sc. in marine biology from the University of California San Diego and a M.Sc. in coastal oceanography from Universidad Autonoma de Baja California. She is also a scientific diver with experience in ecological monitoring of coral and rocky reefs and kelp forests.

Rodrigo Beas-Luna
Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico
https://orcid.org/0000-0002-7266-3394

Rodrigo Beas-Luna is a professor at UABC´s Facultad de Ciencias Marinas. He combines field observations, lab work, and quantitative tools to better understand the functioning of temperate marine ecosystems. He is interested in how climate change influences ecosystem dynamics and how to overcome these threats to enhance resilience. He studied biology at the Universidad de Guadalajara, has a Master's degree in marine ecology from CICESE, a Ph.D. in ecology and evolutionary biology from UC Santa Cruz, and was a postdoc at Hopkins Marine Station at Stanford University.



Julio Lorda
Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico
Tijuana River National Estuarine Research Reserve, 301 Caspian Way, 91932, Imperial Beach, CA, USA
jlorda@uabc.edu.mx
https://orcid.org/0000-0002-4293-7518

Julio Lorda is a professor at Universidad Autónoma de Baja California and an adjunct researcher at the Tijuana River National Estuarine Research Reserve. He is interested in ecology, conservation and management of coastal ecosystems. Throughout his career he has worked in different coastal ecosystems such as temperate kelp forests, coral reefs, coastal wetlands, and rivers in the northern and southern hemispheres. His areas of research have ranged widely, including population and community ecology, parasitology, invasions ecology, biogeography, climate change and management.

Eliot de La Cruz-González
Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico

Eliot de La Cruz-González is a laboratory assistant at the Fish Culture Conservation Laboratory at UC Davis, and Certified scientific diver with 4 year experience in ecological sampling campaigns in sub-tidal and intertidal marine environments. He has experience working in the genetics laboratory at Ensenada's Center for Scientific Research and Higher Education. Bachelor's degree in oceanography with a dissertation on community ecology of subtidal temperate rocky reefs and kelp forests, responses to environmental variability, and interactions between native and invasive species at the marine sciences faculty, Autonomous University of Baja California.

Luis Malpica-Cruz
Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, 22860, Ensenada, BC, Mexico
ECOCIMATI, A.C., Av. Del Puerto 2270, 22880, Ensenada, BC, Mexico
lmalpica@uabc.edu.mx
https://orcid.org/0000-0003-0750-1652

Luis Malpica-Cruz is an oceanographer with expertise in marine ecology, conservation and management of natural resources. He has a Master's degree in marine ecology from the Center for Scientific Research and Higher Education of Ensenada, and a PhD in biology from Simon Fraser University. As researcher at Universidad Autónoma de Baja California, he studies aspects of resilience of marine social-ecological systems, in particular the dynamics of fisheries systems, trying to understand the impact of natural and anthropogenic stressors on targeted species, their ecosystems and on the local fishing communities that depend on them.