Global Change Effects on Biological Interactions: Nutrient Inputs, Invasive Species, and Multiple Drivers Shape Marine Patagonian Communities

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Introduction

Interactions between organisms have been historically recognized as one of the main drivers of the distribution and abundance of species (Paine 1966; Rohde 1984). Organisms interact with others either negatively (one participant is benefited at the expense of a negative impact on the other, e.g., predation and competition) or positively (one species benefits from the presence of another species without harm to the

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latter, e.g., mutualism and facilitation; Halpern et al. 2008; Silliman and He 2018). For a long time, negative interactions were considered the most relevant in determining the structure of biological communities, while positive interactions were underemphasized as their impact on communities was thought to be negligible or even null (Paine 1966; Menge and Sutherland 1987). In recent years, the ecological role of positive interactions has been re-evaluated and considered to be as important as negative ones in structuring communities (Silliman et al. 2011). Indeed, under increasingly stressful environmental conditions, competitive interactions can shift to facilitative ones (Bertness and Callaway 1994; He et al. 2013). This becomes particularly important under the current global change (GC) scenario, as the persistence of populations could depend on the amelioration of harsh conditions provided by other species (Bulleri et al. 2018).

Species are climate-dependent, and they have developed adaptations as a response to natural variations in the Earth's climate system, which include events of change from short (e.g., seasonal cycles) to mid and long timescales (e.g., ENSO episodes, glacial to interglacial transitions; Alheit and Bakun 2010; Overland et al. 2010). Since the 1900s the planet is undergoing one of the largest changes in climate ever experienced (see Helbling et al., this volume), with two particularities: (1) the changes are occurring at extremely accelerated rates, and (2) we, human beings, are in part responsible for it (IPCC 2019). Scientists warned that the likely rate of change over the next century will be at least ten times quicker than any climate shift in the past 65 million years (Ripple et al. 2020). The increase in anthropogenic carbon dioxide (CO_2), methane (CH_4), and halocarbon emissions into the atmosphere is the main driver of these changes, being one of their primary direct consequences of warming and acidification of the aquatic systems (IPCC 2019). Since the late 1900s the Earth's average surface temperature has risen ca. 2 °C, and much of this heat has been absorbed by the ocean. Simultaneously, the pH of ocean surface layers has decreased by approximately 0.02 pH units per decade since preindustrial

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times (Bindoff et al. 2019). As a consequence of warming, the planet has been exposed to other changes, including sea level rise, increased ocean stratification, ocean deoxygenation, decreased sea-ice extent, and altered patterns of precipitation and winds, among others (IPCC 2019). Additionally, marine ecosystems have also been impacted by local and regional pressures, such as increased anthropogenic nutrient input to coastal waters, coastal land use change, extreme climatological events, invasive species, and overexploitation of fish and shellfish species (Halpern et al. 2008; Bennett et al. 2021; Vizzo et al. 2021).

Many studies have provided evidence about the impact of different GC drivers on the physiology, behavior, and ecological traits of single species, which often lead to changes in population structure, distributional range, and seasonal abundance (Rabalais et al. 2009; Häder et al. 2014). These studies are invaluable to understand the mechanisms behind the response of different species to GC, in order to make predictions on the functioning of ecosystems under current and future scenarios. More recently, the impact of GC on species interactions started to be considered (Walther 2010; Cahill et al. 2013; Bates et al. 2017). Evidence showed that GC influences virtually every single species interaction in both bottom-up and top-down directions (Doney et al. 2012). Even if species composition is not altered by GC, it has been observed that the strength or direction of interspecific interactions might change (Harley et al. 2006). Since biological interactions intervene and, in many cases, modulate ecosystem functions (e.g., nutrient cycling, primary and secondary productivity) and services to humankind (e.g., food, nutrient cycling, carbon sequestration and storage; MEA 2005), studies incorporating more complex scenarios, albeit challenging, are extremely necessary.

Coastal areas provide many goods and services such as habitat for many species (Barbier et al. 2011), wave energy dissipation (Gedan et al. 2011) and protection against erosion and storm damage (Shepard et al. 2011; Möller et al. 2014), cycling of land-derived nutrients (McGlathery et al. 2007), and sequestration and storage of atmospheric CO_2 (Duarte et al. 2013; Duarte 2017). In particular, coastal intertidal areas are exposed to strong gradients in physical and chemical factors, such as desiccation, nutrient availability, and tidal exposure (Bertness and Callaway 1994; Helmuth et al. 2006). In these stressful environments many organisms live close to their fundamental niche edges (*sensu* Hutchins 1947; Wethey and Woodin 2008), and thus, any change in environmental conditions (e.g., climate) may directly affect their performance by increasing their levels of physiological stress. Such effects can also be indirect, throughout, for instance, changes in predation rates, competition, and facilitation (Gilman 2017; Lord et al. 2017; Yakovis and Artemieva 2017).

Studies aiming to evaluate the impact of GC on species interactions in Patagonian coastal areas are scarce. The reader will have noticed from previous chapters that even in many cases, little is known about GC effects on single species/groups. Throughout this chapter, we aim to show examples of how different GC drivers affect biological interactions of species inhabiting different coastal ecosystems (i.e., salt marshes, macroalgal beds, open coastal waters) of Atlantic Patagonia. In some of these ecosystems, the impact of GC drivers on organisms from different trophic levels has been well explored, thus providing a good basis to make more robust predictions about potential effects on biological interactions.

Increased Nutrient Inputs in Vegetated Coastal Areas of Patagonia

Anthropogenic activities influence the relative strength of bottom-up (i.e., nutrients) and top-down (i.e., grazers, predators) forces on coastal communities by altering both land-derived nutrient inputs and consumer populations (see Eriksson et al. 2009). As a direct consequence of the growing human population and increased settlement and use of coastal areas (Nixon 1995; Valiela 2006), nutrient inputs to coastal waters have increased worldwide leading to eutrophication (e.g., Valiela et al. 1997), one of the main drivers of change in coastal ecosystems around the globe (Malone and Newton 2020).

Salt marshes are one of the most representative vegetated environments along Patagonian coasts. The loss of salt marshes is almost entirely related to degradation as a result of anthropogenic activities (Pratolongo et al. 2013), in particular land fill, fire practice associated with cattle raising, and eutrophication. There are several studies showing that increased nutrients enhance plant growth and biomass production in Argentinean salt marshes (e.g., Alberti et al. 2010, 2011), and most of them also show that the burrowing crab *Neohelice granulata* could partially counteract these bottom-up effects by exerting a strong top-down pressure through herbivory. In this regard, manipulative experiments showed that nutrient enrichment increases biomass of *Sporobolus* spp. by nearly 50% (Daleo et al. 2008). However, top-down pressure exerted by *N. granulata* decreases plant biomass by around 20% and 40% in *Sporobolus densiflorus* and *Sporobolus alterniflorus*, respectively (Alberti et al. 2007). Although some of these studies were conducted in salt marshes outside Patagonia, their authors proposed that similar processes might be operating in Patagonian salt marshes north of 42° 25′S where this crab species occurs in high densities (Alberti et al. 2007).

Increased nutrient availability (mainly N) may lead to more palatable plants which, in turn, may lead to a higher herbivory pressure (Cebrian et al. 2009). In Patagonian salt marshes, the evidence suggests that the relative importance of nutrients and herbivory might vary given that growth as well as herbivory vary throughout the year. For example, Alberti et al. (2011) showed that increased nutrients also increase the consumption of *S. densiflorus* leaves by *N. granulata* in summer and even to a greater extent in fall. Moreover, the impact of nutrients is not uniform through the salt marsh. The maximum effect of increased nutrients on primary production occurs at mid marsh elevations, while no effects of nutrient additions were observed at low or high marsh elevations, where other factors such as anoxia and high salinities seem to be more limiting for salt marsh plants (Alberti et al. 2010).

Nitrogen enrichment strongly enhances the infection by the fungus *Claviceps purpurea* on *S. densiflorus* (Daleo et al. 2013), which reduces seed production and releases alkaloids that decrease herbivory, as shown in other regions (Fisher et al. 2005; Lev-Yadun and Halpern 2007). Thus, fungus effects on plant community structure, as well as on consumers, could have considerable impacts in Patagonian salt marshes. Additionally, increased salinity decreased plant responses to nutrient addition, probably as a consequence of sodium ion interference with ammonium uptake (Daleo et al. 2015). This antagonistic effect is of special importance, as increases in soil salinity are expected to occur as a result of warming (Lynch and St. Clair 2004) and especially in salt marshes (Silliman et al. 2005).

The relative impact of increased nutrients and crabs on plant growth is partly regulated by the physical features of the salt marshes where interactions take place (Daleo and Iribarne 2009). Increases in sediment aeration and nutrient availability due to crab burrowing activities would be more important in poorly oxygenated soils. On the other hand, crab herbivory impact would be more important in areas with coarse sediments and therefore good substratum oxygenation (Daleo and Iribarne 2009). The latest would be the case of northern Patagonian salt marshes inhabited by *N. granulata*.

Another well-represented vegetated system along Patagonian coasts are macroalgal beds (for a detailed description of these environments, see Horta et al., this volume). As a general pattern, one of the first symptoms of increased nutrient inputs to coastal waters is the change in the composition of the macroalgal assemblage, where opportunistic species take advantage over others. When eutrophication is incipient, the increase in macroalgal biomass can have a positive effect by sequestering excess nutrients (Boyer et al. 2002) and by providing abundant food of high nutritional quality for consumers (Hemmi and Jormalainen 2002). However, as the eutrophication process continues, the excessive growth of opportunistic macroalgae can have several detrimental effects. For instance, the massive canopy may grow over the previously dominant species (perennial algae) impeding their photosynthesis (Smith and Schindler 2009). Advanced states of eutrophication are usually characterized by hypoxic or anoxic events, with the consequent decline of associated organisms including macroalgal grazers (D'Avanzo and Kremer 1994; Fox et al. 2009) and the simplification of the original community structure (Valiela et al. 1997; Fig. 1A, B). Under this scenario of high nutrient supply and reduction of consumer abundance, the systems become bottom-up controlled while top-down control may be negligible (Raffaelli et al. 1998). However, in systems where the hydrodynamic forces are strong, the large tidal flush can partially relieve the effect of eutrophication by diluting and exporting land-derived nutrient loads, as well as biological products, minimizing hypoxia-related stress on the biota (Martinetto et al. 2010, 2011). This is the case of San Antonio bay (SAb; 40° 43′ 37″ S, 64° 56′ 57″ W) where the anthropogenic nutrient concentrations, mainly introduced via groundwater from the septic system of the nearby city of San Antonio Oeste, are among the highest registered worldwide (NO_3^-~ 100 µM, PO_4^{3-}~ 7 µM; Teichberg et al. 2010). At that site, the nutrients remain in the system long enough to be assimilated by macroalgae and support high biomass and diversity of primary producers, but not enough to cause hypoxic or anoxic events (Martinetto et al. 2010, 2011; Fig. 1C).

High biomass of nutrient-rich macroalgae can provide a large amount of food of high nutritional quality to grazers, which would explain the higher abundance of herbivore invertebrates reported in nutrient-impacted areas of SAb (Martinetto et al. 2011; Becherucci et al. 2019). The higher invertebrate abundances would in turn

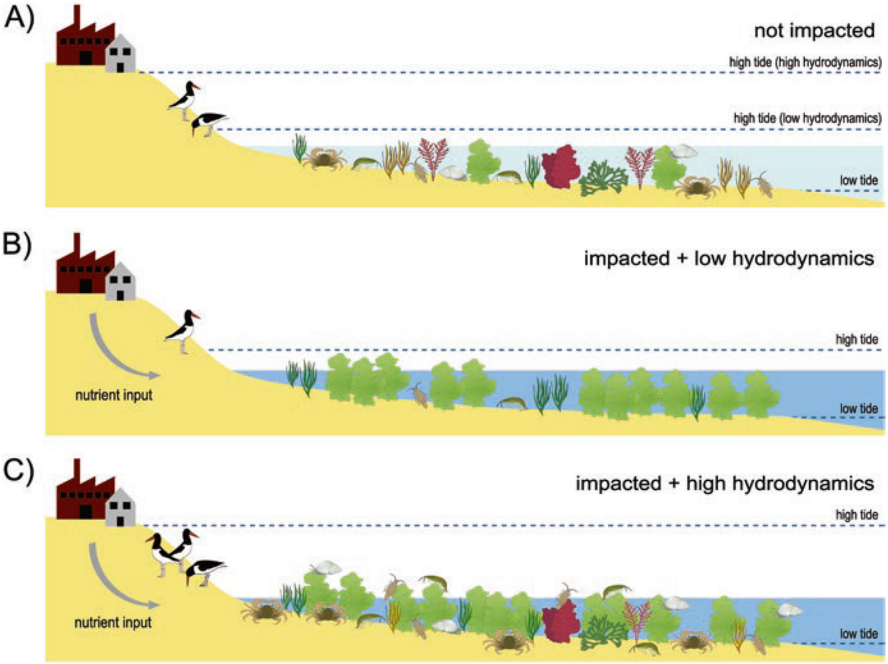

Fig. 1 Responses of the macroalgal community to potential scenarios derived of increases in anthropogenic nutrient input under different hydrodynamic conditions: (**A**) pristine community without nutrient addition; (**B**) anthropogenic nutrient increase under low hydrodynamic conditions, leading to the eutrophication of the system characterized by the overgrowth of opportunistic green macroalgae, anoxic conditions, and a decline of consumer diversity and abundances; and (**C**) anthropogenic nutrient increase under high hydrodynamic conditions as experiencing in Patagonian coasts (e.g., San Antonio bay), where the large tidal flush attenuates the impact of excessive nutrient load, resulting in an increase of both macroalgal and consumer abundances

explain the preference of local and migratory shorebird species for these areas as feeding sites (e.g., oystercatchers and several migratory shorebirds and gulls; Garcia et al. 2010; Martinetto et al. 2010). In fact, some shorebird species changed their foraging strategy from visual-tactile in non-impacted areas to tactile in nutrient-impacted areas, probably prioritizing higher encounter rates with prey of higher nutritional quality that occurs hidden within the macroalgal mats (García et al. 2010).

In nutrient-impacted areas of SAb, herbivores exert a strong pressure on *Ulva lactuca* reducing their biomass by up to 60% (Martinetto et al. 2011). Surprisingly, this macroalga species does not substantially contribute to the intertidal benthic food web (Becherucci et al. 2019). In a manipulative experiment, it was found that increased N supply leads to increased macroalgal biomass only when herbivores were present, which could be related to the additional input of N (mainly NH_4^+) due to excretion (Bracken and Nielsen 2004). Thus, both top-down and bottom-up forces seem to act conjointly in the regulation of macroalgal proliferation in SAb.

Changes in trophic interactions have been reported as a result of higher nutrient inputs in Patagonian intertidal areas. For instance, males of the amphipod *Ampithoe valida* from the Chubut river estuary (i.e., an area exposed to high anthropogenic nutrient inputs) showed higher food consumption rates (FCR) when feeding on macroalgal diets with high nutrient content. By contrast, individuals from intertidal areas less impacted by anthropogenic nutrient inputs showed the opposite behavior: higher FCR when feeding on macroalgae with low nutrient content (Valiñas et al. 2014). Thus, at least in less impacted areas, individuals would be consuming more macroalgae as a way to compensate for the lower quality of the food (Cruz-Rivera and Hay 2000; Duarte et al. 2014). Compensatory feeding mechanisms were also reported in SAb, where it was observed that mesoherbivores increased food consumption rates when the N and C contents of the macroalgae were lower (Martinetto et al. 2011).

Biological Invasions in Vegetated Coastal Areas of Patagonia

In the last decades, the rate of non-native species introduction has increased worldwide, mostly due to increased global trade and transport, leading to widespread changes in the structure and functioning of ecosystems (Seebens et al. 2013; Antón et al. 2019). Many invasive species can benefit some native species (Geraldi et al. 2013; Ramus et al. 2017), although some others can cause extensive negative impacts on native communities (e.g., altering ecosystem functioning, Doherty et al. 2016, or introducing diseases and parasites, Chinchio et al. 2020), and even many of them are responsible for species extinctions (Bellard et al. 2016). In some cases, negative impacts of invaders involve a decrease in the abundances of native species but not on diversity (Antón et al. 2019). This is probably associated with buffering mechanisms conferring ecosystem resistance against exotic species, such as functional redundancy between exotic and native species (García et al. 2014). Anthropogenic disturbance can boost the effects of invasive species on native communities by creating favorable habitats, removing potential predators and competitors, and introducing propagules, thus increasing their chances of establishment in a novel area (Byers 2002; Bertness and Coverdale 2013; Geraldi et al. 2013).

Although there is a large list of species reported as introduced in Patagonian coasts (see chapters by Horta et al., and López Gappa, this volume, Orensanz et al. 2002; Schwindt et al. 2020), only a few are widespread along that range and altered the physiognomy of coastal habitats (Casas et al. 2004; Escapa et al. 2004). This is the case of the barnacle *Balanus glandula*, the reef-forming oyster *Magallana gigas* (formerly *Crassostrea gigas*), the green crab *Carcinus maenas*, and the kelp *Undaria pinnatifida*. The first three have been reported in salt marshes and macroalgal beds of Patagonia, while the invasion of *U. pinnatifida* is mostly restricted to rocky low intertidal and subtidal environments.

The Cases of Balanus glandula *and* Magallana gigas

The barnacle *Balanus glandula* shows a great plasticity as it was found colonizing the branches, roots, and rhizomes of the cordgrass *Sporobolus alterniflorus* (Schwindt et al. 2009; Méndez et al. 2013) in Patagonian salt marshes and also fouling *Magallana gigas* and the endemic crab *Neohelice granulata* (Méndez et al. 2014, 2017). It was proposed that both *M. gigas* and *Sporobolus* spp. would facilitate the establishment of *B. glandula* (Sueiro et al. 2013; Méndez et al. 2015) by increasing habitat structure and complexity and also by enhancing sediment stability (Escapa et al. 2004; Méndez et al. 2015; Fig. 2). In the case of the barnacle-oyster interactions, and based on studies performed with species of similar characteristics in other regions (e.g., Thieltges 2005; Ramsby et al. 2012; Yakovis and Artemieva 2017), barnacle epibiosis could benefit oysters by slowing down desiccation during the low tide and/or by providing camouflage from predators. In addition, since attachment surfaces are a limiting factor in soft-bottom intertidal areas, recruitment on living substrata such as *Sporobolus* spp., *M. gigas*, or *N. granulata* may be beneficial (Foster 1987; Escapa et al. 2004; Méndez et al. 2015). Crabs may also constitute motile vectors speeding the regional invasion of *B. glandula* by contributing the dispersion of their larvae (Méndez et al. 2014; Fig. 2).

The invasion of both *B. glandula* and *M. gigas* in Patagonian salt marshes favors populations of several taxa of invertebrates such as insects, juvenile crabs, isopods,

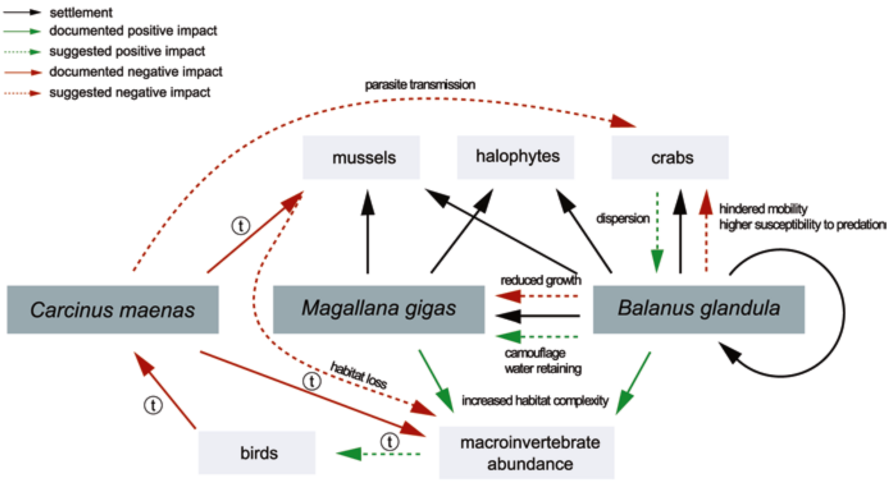

Fig. 2 Schematic representation of documented (solid arrows) and suggested (dashed arrows) interactions mediated by the invasive species *Carcinus maenas*, *Magallana gigas*, and *Balanus glandula* in Patagonian coasts. Trophic interactions are indicated with "t." Both the oyster *M. gigas* and the barnacle *B. glandula* increase habitat complexity benefiting other species by providing refuge. Negative effects of *B. glandula* include limiting mobility and growth of species the barnacles settled-on. The green crab *C. maenas*, which has recently been found to drastically expand in salt marshes of Patagonia, is considered a major threat to these ecosystems by potentially exerting a strong top-down pressure, interfering facilitative mechanisms, and transferring parasites to other organisms

and polychaetes (Escapa et al. 2004; Méndez et al. 2015, 2017), probably by offering protection against predators and alleviating harsh environmental conditions such as heat stress, dehydration, and wave exposure. The physical structure formed by aggregations of *B. glandula* is also important for its own recruitment (Méndez et al. 2017), as barnacle tests serve as substrata for the settlement of conspecific larvae (Qian and Liu 1990; Schubart et al. 1995; Fig. 2). In the case of *M. gigas*, several local and migratory bird species showed higher abundances and feeding rates in oyster-invaded areas, which would be related to the higher abundance of invertebrate prey (Escapa et al. 2004; Fig. 2).

Negative effects have also been reported as a result of *B. glandula* and *M. gigas* invasion. It was proposed that barnacles would increase the risk of dislodgement, reduce growth, or affect feeding activities of oysters as have been shown for other species (da Gama et al. 2008). Moreover, negative effects of the epibiosis of *B. glandula* on *N. granulata* were also suggested (Fig. 2) as barnacles settle on vital zones of the crabs (e.g., walking appendages, ocular peduncles, jaws, and mouth; Méndez et al. 2014) and potentially interfere with their behavior (e.g., walking, feeding, mating). In addition, the elevated contrast of colors derived from the presence of white barnacles growing over brown crabs might also increase their predation risk (Méndez et al. 2014). These potential impacts of *B. glandula* on *N. granulata* deserve further investigation as this crab species exerts a strong top-down control on salt marsh plants and modulates major ecosystem functions (e.g., Costa et al. 2003; Alberti et al. 2007, 2015; Martinetto et al. 2016; Gutiérrez et al. 2018).

The Case of Carcinus maenas

In the chapter by López Gappa (this volume), a detailed description of the biology of the green crab *Carcinus maenas*, along with information about its occurrence in Patagonian coasts, was provided. Regarding biological interactions, this species deserves particular attention as it is listed among the ones that cause an overall decrease in all the ecological attributes (e.g., abundance, richness, diversity) of native communities (Antón et al. 2019). Laboratory feeding trials and diet analysis showed that *C. maenas* preferentially feeds on slow-moving and sessile animals, including mussels that act as foundation species (i.e., species that determines the diversity of associated taxa through non-trophic interactions and plays central roles sustaining ecosystem services; Ellison et al. 2005; Ellison 2019) in the intertidal zone (Hidalgo et al. 2007; Cordone et al. 2020; Fig. 2). Based on these results, the authors proposed that *C. maenas* could interfere in facilitation mechanisms mediated by mussels such as the provision of refuge from predation and the amelioration of environmental stress for a large number of invertebrate species (Silliman et al. 2011; Bagur et al. 2016), as it has been observed in other regions invaded by this species. Also *C. maenas* could negatively affect other crab species through the transmission of the nemertean parasite *Carcinonemertes* sp. that was detected for the first time in Argentina in this species (Cordone et al. 2020; Fig. 2). Moreover, this crab has been reported as a novel prey item of the kelp gull *Larus dominicanus*

(Yorio et al. 2020), highlighting a new trophic interaction in Patagonian coasts (Fig. 2). In a recent publication, the authors refer to an “alarming” increase of *C. maenas* population in rocky salt marshes of Nuevo gulf (Battini and Bortolus 2020), although no numerical data were provided to support this statement.

The Case of Undaria pinnatifida

Local studies showed that *Undaria pinnatifida* can outcompete some native macroalgal species (Casas et al. 2004; Raffo et al. 2012; but see Raffo et al. 2009) and proposed light, nutrient, and substratum limitations over native species as potential explanations (Raffo et al. 2015). For instance, manipulative experiments showed that *U. pinnatifida* fronds reduced the photosynthetic active radiation (PAR) levels up to 75% which could potentially affect the growth of native ephemeral macroalgae (Raffo et al. 2015; Fig. 3). Also, in low intertidal and shallow subtidal areas, the holdfast of *U. pinnatifida* covers a substantial fraction of the bottom, which could reduce the surface available for other species. On the other hand, the lack of a strong top-down pressure would partially contribute to its settlement in Patagonian coasts. Although some gastropods and sea urchin species are able to feed on *U. pinnatifida*, the grazing impact of these species is unlikely to control the macroalga (Teso et al. 2009; Fig. 3). Sewage and domestic water effluents in urban areas may also have

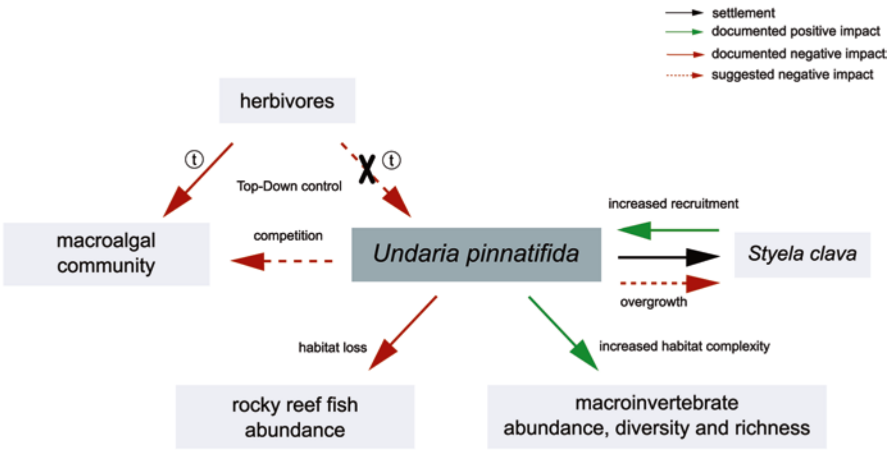

Fig. 3 Schematic representation of documented (solid arrows) and suggested (dashed arrows) interactions mediated by the invasive macroalga *Undaria pinnatifida* in Patagonian coasts. Trophic interactions are indicated with “t.” The invasive success of *U. pinnatifida* in Patagonia is probably caused by competitive exclusion, the lack of a strong top-down control, and the facilitation by other organisms such as the ascidian *Styela clava*. Besides some positive effects on macroinvertebrate species, there is growing concern by some authors about the proliferation of *U. pinnatifida* along the Patagonian coast due to its negative impact on local biodiversity

contributed to *U. pinnatifida* settlement as this macroalga can incorporate nitrate, ammonium, and phosphate from the sewage (Torres et al. 2004).

The complex three-dimensional structure generated by the large *U. pinnatifida* fronds (up to 2 m in length) increases species richness, diversity, and abundance of some benthic taxa (e.g., crustaceans, sea urchins, nemerteans, and polychaetes; Irigoyen et al. 2011a) relative to uninvaded areas (Fig. 3). In intertidal areas of SAb, > 80% of *U. pinnatifida* is attached to the invasive ascidian *Styela clava*, and manipulative experiments proved that the recruitment of the macroalga is higher when the ascidians are present (Pereyra et al. 2017). The authors proposed that *S. clava* would facilitate *U. pinnatifida* settlement via moisture retention and protection from grazers, as was reported in other regions (Thompson and Schiel 2012; Yakovis and Artemieva 2017). Moreover, the erect structure of *S. clava* might improve flow dynamics (Harder 2008), increase spore settlement (Bulleri and Benedetti-Cecchi 2008), and facilitate access to light (e.g., Maida et al. 1994) to the kelp. In a recent study (Pereyra et al. 2021), it was found that recruitment of *U. pinnatifida* is higher on live *S. clava* individuals than on mimics of the ascidians, evidencing that a biologic non-trophic effect would be playing a major role in the facilitation process between the kelp and the ascidian than the structure of the ascidians alone. Authors suggested that the siphonal activity of *S. clava* could provide a more oxygenated environment for kelp sporophytes or could help capture more spores. Moreover, the chemical composition of the tunic may favor the emergence of the macroalgae (Paul et al. 2011). However, when macroalga overgrows, it commonly occludes *S. clava* siphons (Pereyra et al. 2017) which could potentially affect water pumping and filter-feeding activities (e.g., Farrell and Fletcher 2006; Fig. 3). Negative effects on fish abundances in low-relief rocky reefs covered by *U. pinnatifida* were also reported in the region (Irigoyen et al. 2011b; Fig. 3).

Impact of Multiple Global Change Drivers on Open Coastal Areas of Patagonia

The Case of Planktonic Communities

In the chapter by Villafañe et al. (this volume), the authors provided a comprehensive description about the impact of different GC drivers (e.g., increased temperature, acidification, increased nutrient inputs, UVR) on planktonic communities. Some of these studies covered more than one trophic level (i.e., phytoplankton-bacterioplankton, bacterioplankton-phytoplankton-microzooplankton) and/or different cell groups (e.g., by cell size, nano- and microplankton; by taxonomic groups, diatoms, small flagellates, etc.), thus providing some clues about potential effects of GC drivers on biological interactions. For instance, it was observed that under high UVR and nutrient inputs, the structure of the community shifted toward a dominance by nanoplanktonic flagellates, which in turn would negatively impact the heterotrophic picoplankton by increasing bacterivory (Cabrerizo et al. 2018). In the same vein, a simulated warming scenario reduced the total biomass of the microbial community, favoring nanoplankton and bacteria (Moreau et al. 2014). In contrast, increased primary production under different future GC scenarios, mainly modulated by increases in the abundance of larger diatoms, was also reported (nutrients, pH, and UVR, Villafañe et al. 2015; nutrients and pH, Masuda et al. 2021). The responses of phytoplankton communities to GC in terms of favored/negatively impacted cell sizes or dominant groups differ depending on the initial composition of the community, their previous light story, and the intrinsic characteristics of the species. However, in terms of growth rates, most studies show a clear trend of increases of this variable regardless of the GC driver or the combination of drivers considered (i.e., UVR, CO_2, nutrients, DOM, or temperature; see Villafañe et al., this volume).

Global change can also lead to a decoupling of phenological relationships, with important ramifications for trophic interactions, including altered food-web structures and eventually ecosystem-level changes (e.g., Edwards and Richardson 2004). For instance, shifts in the Patagonian wind patterns impact phytoplankton communities, not only by favoring smaller cells but also by delaying their blooms for a lapse of about 2 months (Bermejo et al. 2018; Vizzo et al. 2021). Several studies around the globe document drastic declines in the populations of planktonic predators due to climate-related perturbations with the concomitant disruption of predator-prey relationships (e.g., Winder and Schindler 2004). Unfortunately, there is no information about how grazers can impact phytoplankton communities under GC scenarios in Patagonia or how they can be indirectly impacted by the effect of GC on primary producers (but see Spinelli 2013). More studies on this regard are needed given that the outcome of the phytoplankton-zooplankton interactions is expected to be transmitted to all trophic levels, with potentially severe ecological and economic impacts in the region.

The Case of the Squat Lobster Munida gregaria

Long-term data series indicate that some species from Patagonia increased (while others declined) their abundances during the last decades, and examples linking these trends with GC drivers were largely discussed along the different chapters of Galván et al.; Narvarte et al. this volume. While in some cases the impact on the populations is the direct result of the GC stressors acting on the species, in others, the effects are mediated by bottom-up or top-down processes. For instance, top-down impact caused by commercial fishing may reduce the abundance of predators for small fish species, thus decreasing the top-down pressure on these latest (Boersma and Rebstock 2014). In other cases, bottom-up processes triggered by increased nutrient inputs boost primary production in coastal waters, which may indirectly impact primary consumers.

One clear example of increased population abundances in Patagonia is the case of the squat lobster *Munida gregaria* (Varisco and Vinuesa 2015; Diez et al. 2016; de la Barra 2018). This crustacean is found in the southern end of South America and around the coastline of Australia, New Zealand, and the subantarctic Campbell islands. The species has two morphotypes, the *gregaria* type or pelagic-benthic stage and the *subrugosa* type or epibenthic stage. Pelagic juveniles of *M. gregaria* have been documented in the Atlantic ocean in the 1920s (see Varisco and Vinuesa 2010 and references therein). Nevertheless, the *subrugosa* was the only morphotype recorded in the Atlantic coast (not so in the Beagle channel) over the past decades, until the recent appearance of the pelagic morphotype (i.e., *gregaria*) at the beginning of the 2000s. Strandings of this crustacean species along the coast, as well as operational impacts on the shrimp fisheries (de la Garza et al. 2011), are evidence of a recent population growth which was confirmed by direct and indirect observations. A significant increase in the relative abundance and frequency of occurrence of *M. gregaria* was recorded in 2010 and subsequent years in San Jorge gulf (SJg) and adjacent waters (Varisco et al. 2015) and in San Matías gulf (SMg; de la Barra 2018). Moreover, acoustic studies evidence that the population expansion of *M. gregaria* along the Argentine shelf was promoted by the reappearance of pelagic swarms (Madirolas et al. 2013). Even in places where the *gregaria* morphotype was present (e.g., Beagle channel), an increase in pelagic/benthic ratio was observed (Diez et al. 2016).

Munida gregaria plays a key role in the trophic webs of Patagonian and subantarctic coastal ecosystems for two main reasons: (1) it is an important prey item of several marine mammals (Koen Alonso et al. 2000; D'Agostino et al. 2018), fishes (Sánchez and Prenski 1996; Galván et al. 2008; Belleggia et al. 2017), and seabirds (Scioscia et al. 2014), and (2) as the species obtains energy from pelagic and benthic environments, it thus plays a key role in the coupling of both systems (Funes et al. 2018), aside from being a direct link between primary producers and top predators (Vinuesa and Varisco 2007).

Although several hypotheses have been proposed to explain the increase in the abundance of *M. gregaria* and the reappearance of the pelagic swarms in Patagonian coastal waters, the evidence to date is inconclusive. A combination of the following processes has been proposed: (a) a decrease in top-down pressure (Varisco and Vinuesa 2015; Diez et al. 2016), (b) migrations of *gregaria* morphotype from Beagle channel to Patagonian northern waters (Ravalli and Moriondo 2009), (c) a slight increase in the fecundity of the species (Varisco 2013), and (d) an increase of bottom-up forces. Given the broad spatial scale and dynamics of this expansion, migratory process or local increases in fecundity could hardly explain the observed population growth (Varisco 2013). Thus, top-down and/or bottom-up effects linked to GC are more likely behind the *M. gregaria* expansion.

Skates and four commercial bony fishes (e.g., *Genypterus blacodes*, *Genypterus brasiliensis*, *Acanthistius patachonicus*, and *Salilota australis*) were identified as the main predators of *M. gregaria* in the SJg (Sánchez and Prenski 1996). These species are catalogued as species in retraction either because their frequency of occurrence or population biomass has decreased from the 1970s to date (see Galván

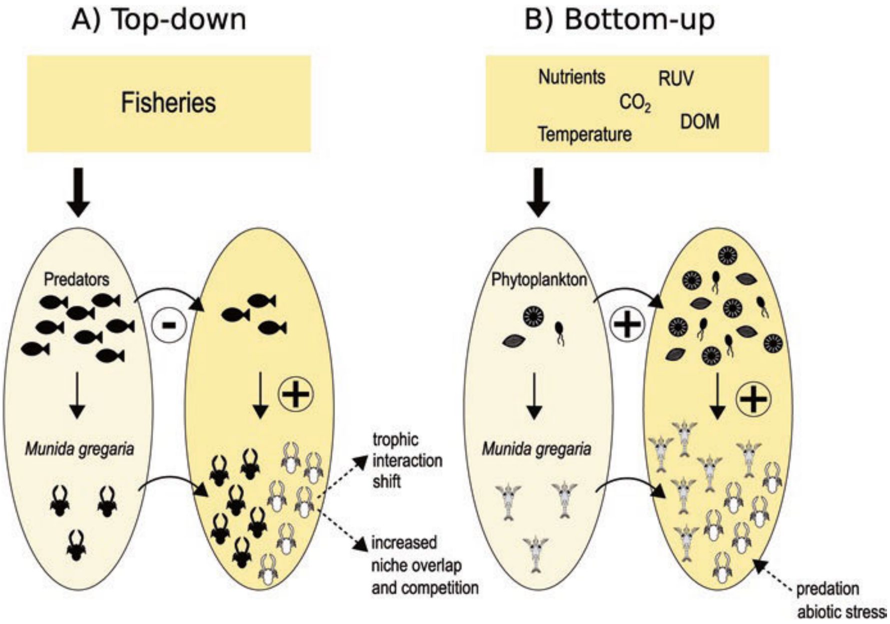

Fig. 4 Main mechanisms proposed to explain the expansion of *Munida gregaria* in Patagonian waters: (**A**) A decrease in top-down pressure on benthic stages of *M. gregaria* (black squat lobsters) leads to a population increase and a subsequent appearance of the pelagic ecotype (white squat lobsters), which potentially explains shifts in trophic interactions as well as increased competition with other organisms of the pelagic realm. (**B**) The increased food availability in the pelagic realm as a consequence of a global-change-induced phytoplankton growth leads to an increase of larval and postlarval stages (gray larvae) as well as the further expansion of the pelagic ecotype

et al., this volume), as a result of commercial fishing or incidental capture (Fig. 4A). Thus, a decrease in top-down pressure on *M. gregaria* has been proposed to explain the expansion of the squat lobster recently observed (Fig. 4A). However, there is evidence contrary to such hypothesis. In the 1980s, the most abundant fish of the assemblage in SJg, the hake *Merluccius hubbsi*, preyed on *M. gregaria* in small quantities (Sánchez and Prenski 1996), but since 2008 the occurrence of squat lobsters in hake's diet increased from < 2% to > 50% (Belleggia et al. 2017), in synchrony with the increase in *M. gregaria* abundance and the decrease in other predator abundances. A similar result was reported at the SMg where *M. gregaria* was not found in the gut contents of hakes collected between 2006 and 2007 (Ocampo et al. 2011) but became the main prey item in samples collected in 2015 (Alonso et al. 2019).

The match between the reappearance of the pelagic swarms and the population expansion of *M. gregaria* could give a clue about some potential advantages that this species would have in the pelagic realm. Different studies reported a positive relationship between large shoals of *M. gregaria* and frontal areas (Diez et al. 2016), as also the presence of shoals in areas of the SJg with increased primary productivity (Varisco and Vinuesa 2010; Ravalli et al. 2013). As mentioned in the previous section, there is a general trend of increased growth rates of phytoplankton communities under different GC scenarios (see Villafañe et al., this volume). Thus, bottom-up processes (i.e., increased food availability) could also explain the increase in the time of residence of *M. gregaria* in the water column, which would further determine the relative abundance of the benthic or pelagic individuals (Varisco 2013; Fig. 4B). However, there are some aspects that we need to take into consideration: (1) as early life stages are the most vulnerable to both predation and abiotic stress (Przeslawski et al. 2015), a larger time that larval stages spend in the plankton before migrating to the bottom could negatively impact the abundance of the squat lobster, and (2) higher prey abundance does not necessarily imply an advantage for consumers. For instance, if food is abundant but of low quality, individuals will not be able to fulfill their metabolic requirements or should invest more time (and energy) to do it (i.e., food compensation mechanisms; Cruz-Rivera and Hay 2000). In such cases, organisms would be allocating less energy to other processes, such as those related to reproduction, which would ultimately affect the reproductive potential of the population.

In addition to the trophic shifts previously mentioned, *gregaria* and *subrugosa* morphotypes have different trophic positions but similar body size (Funes et al. 2018). Pelagic individuals feed mainly on phytoplankton and have a trophic level just over 2 (Varisco and Vinuesa 2010; Funes et al. 2018). Benthic individuals have a trophic level close to 3 and feed on benthic species like crustaceans, foraminiferans, polychaetes, and macroalgae (Romero et al. 2004; Varisco and Vinuesa 2007) and even on fishery discards (Varisco and Vinuesa 2007). An increase in the abundance of pelagic individuals and its consumption by demersal fishes would shorten the food chain length and change the bentho-pelagic dependence of predators. However, also other interactions such as competition for food with pelagic species from similar trophic levels could be triggered, as it was already reported for other squat lobster species. For instance, on the coast of Perú the squat lobster *Pleuroncodes monodon* and the Peruvian anchoveta, *Engraulis ringens* both occur in frontal areas overlapping their trophic niches and spatial distribution (Gutiérrez et al. 2008). In southern Patagonia, it was proposed that pelagic individuals would overlap their trophic niche with the anchovy *Sprattus fueguensis* (Diez et al. 2012), whereas in central and northern Patagonia, a similar situation might be occurring in the pelagic domain with small crustaceans (e.g., euphausiids, pelagic amphipods, and copepods; see table 1 in Botto et al. 2019) and small pelagic fish (Fig. 4B). However, a partial overlap between *M. gregaria* and the Argentine anchovy *Engraulis anchoita* was recently reported in SMg (Luzenti et al. 2021), and authors suggest that the interaction between species could result from an active search and predation of anchovy on squat lobster juveniles.

Perspectives

The reader may have noticed through the chapters of this book that most studies in Patagonian marine systems are based on the direct effects of different GC drivers on individual species or groups (e.g., phytoplankton, intertidal invertebrates), and few studies analyze the effects on biological interactions. In this chapter, we showed that facilitation mechanisms (e.g., settlement, dispersal mechanisms) between sessile invasive species and native fauna are more frequently documented than interference processes. Negative effects of invasive species include top-down pressure and indirect effects on native species by disrupting facilitation by foundation species (e.g., *C. maenas* predation on mussels). Other interference processes were related to decreased habitat suitability (e.g., *U. pinnatifida* and rocky reef fishes) or settlement on vital parts of the individuals preventing its normal performance (i.e., *U. pinnatifida* overgrowing *S. clava*, *B. glandula* growing on crabs).

Also, GC drivers affect trophic interactions through direct and indirect ways. Direct mechanisms include bottom-up processes such as increased macroalgal biomass as a result of land-derived nutrient inputs in coastal areas and increased phytoplankton abundance, a general pattern observed when simulated different future GC scenarios. Yet, these direct effects on primary producers would indirectly benefit primary and in some cases secondary consumers (e.g., invertebrates and birds in macroalgal beds and *M. gregaria* in coastal open waters). In the same vein, top-down pressures mediated by GC processes affect organisms directly by predation (e.g., the invasive crab *C. maenas*, fisheries), but also could have indirect effects through trophic cascades (e.g., *M. gregaria* expansion). Overall, significant changes in the composition and the structure of the communities have been observed in response to all the surveyed GC drivers.

Compared to research done on GC impacts at the species level, studies including multiple species and their interactions are still scarce at a global scale. The Patagonian region in particular is understudied compared to other regions in the world (e.g., Thomsen et al. 2014; Eger and Baum 2020; Reeves et al. 2020). For instance, despite the growing body of literature on the impact of invasive ecosystem engineers in Patagonian coasts reviewed here (see cases of *B. glandula, M. gigas*, and *U. pinnatifida*), the number of studies on this topic still remains very low compared to other world regions (Guy-Haim et al. 2018).

Coastal ecosystems are highly dynamic systems in which all the species are connected through multiple interactions. Therefore, to understand and predict the effects of GC on marine ecosystems of Patagonia and the services they provide, it is essential to know the structure and functioning of their communities. The challenge when predicting the effects of GC lies upon identifying those interactions between species that are most vulnerable to changing climate and other anthropogenic pressures and that, at the same time, are key determinants of the structure and functioning of their community (e.g., foundation species). For these purposes, experimental approaches in combination with observational field data are strongly recommended to develop models aimed to predict future ecosystem changes under different GC scenarios. However, to obtain more robust models and to evaluate the accuracy of their outcomes, it is necessary to count with long-term data series. With few exceptions (e.g., penguins, imperial cormorant, southern right whale; see chapters by Crespo and Quintana et al., this volume), no studies of GC based on long-term data series have been published, and many of the available data series would be not long enough to disentangle the natural variations in climatic variables that operate at mid to long-term timescales (e.g., ENSO episodes) from human-induced climatic effects. Future research therefore should focus on the incorporation of field observations, manipulative experiments, and modeling, which would be the best ecological approach to understand how marine ecosystems as a whole are facing GC in Patagonia.

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