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Management of natural *Ulva* spp. blooms in San Quintin Bay, Baja California: Is it justified?

Pablo Jorgensen · Silvia E. Ibarra-Obando · José D. Carriquiry

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Abstract According to Zertuche-González et al. (2009), *Ulva* spp. blooms, favored by oyster cultivation, are likely displacing subtidal meadows of *Zostera marina* in San Quintin Bay, Baja California. The authors propose a partial removal of the seaweed to reduce the risk of eutrophication and eelgrass displacement in the bay. We warn about the removal of *Ulva* spp. biomass by raising six arguments that emphasize the necessity of a historical and ecosystem-based management for San Quintin Bay. First, processes other than competitive exclusion by *Ulva* spp. blooms more likely explain changes of *Z. marina* subtidal meadows in the past decade. Second, there is no consistent evidence that oyster cultivation is promoting blooms of *Ulva* spp. and the loss of eelgrass. Third, the removal of *Ulva* spp. biomass is based on experiences of heavily anthropogenically eutrophic systems, while San Quintin Bay is not. Fourth, the proposed course of actions to restore eelgrass meadows ignores general historical baselines of estuarine and coastal systems by confusing what it means to be “pristine.” Fifth, despite the important experimental evidence indicating strong top–down control in temperate seagrass meadows, Zertuche-González et al. (2009) underestimated the capacity of consumers in structuring dynamics of vegetated soft-bottom communities in San Quintin Bay. Sixth, *Ulva expansa* may exert positive effects on seagrass ecosystem properties and functions. Instead, we propose protection against the propagation of unsustainable practices in the bay, and the reintroduction of large consumers that are now absent in this ecosystem. An ecosystem-based analysis of the role of *Ulva* spp. on eelgrass dynamics is needed.

Keywords *Zostera marina* · *Ulva* bloom · Grazer control · Oyster culture · Seagrass management

Based on the occurrence of recent *Ulva* spp. blooms in San Quintin Bay, Zertuche-González et al. (2009) proposed the partial removal of the seaweed to reduce the risk of eutrophication and the displacement of subtidal meadows of *Zostera marina* in the bay. At the moment, a company dedicated to the culture of oysters in San Quintin Bay has applied for permissions to harvest *Ulva* spp. in the bay and exploit it as agricultural fertilizer, among other uses (Juan Guerrero, personal communication). Here, we warn about the removal of *Ulva* spp. as a management practice without a well-founded ecological analysis explaining the causal mechanisms leading to macroalgal blooms, as well as assessing more accurately the potential impacts of the activity on the ecosystem. We raise six arguments that emphasize the necessity of a historical and ecosystem-based management of coastal lagoons along the Pacific coast of Baja California.

Ulva had a minor role in the displacement of subtidal *Zostera marina* meadows

Zertuche-González et al. (2009) concluded in their abstract that “*Ulva* may be displacing the seagrass *Zostera marina*

P. Jorgensen (✉)
El Colegio de la Frontera Sur (ECOSUR),
Km 5.5 Ave. del Centenario,
Chetumal, Quintana Roo C.P. 77014, Mexico
e-mail: pjorgensen@ecosur.mx

S. E. Ibarra-Obando
CICESE,
Carretera Ensenada-Tijuana no. 3918, Zona Playitas,
Ensenada, Baja California C.P. 22860, Mexico

J. D. Carriquiry
Instituto de Investigaciones Oceanológicas,
Universidad Autónoma de Baja Calfornia,
Apdo. Postal # 453, Ensenada, Baja California C.P. 22860,
Mexico

subtidal beds." These authors based their conclusion on the overlap existing between the areas that experienced the largest decreases in eelgrass cover in San Quintin Bay between 1987 and 2000 (Ward et al. 2003) and the location of extensive mats of *Ulva* spp. during the period 2004–2005 (Zertuche-González et al. 2009). However, the occurrence of the notoriously large *Ulva* spp. mats and the extensive reduction of eelgrass cover are clearly out of phase. This time lag is important because there are no previous evidences that *Ulva* spp. were present in such high abundances during the period in which the subtidal eelgrass meadows significantly decreased.

Proximate reports of macroalgal abundance are scarce. Macroalgal biomass in San Quintin Bay was quantified across a depth gradient within eelgrass meadows of the Bahia Falsa arm (hereafter BF) during the period June to December, 1982. *Ulva* spp. (including species of the former *Enteromorpha* genus) dominated mean total algal biomasses, peaking at up to 124 g DM m^{-2} at the beginning of autumn (Ibarra-Obando and Aguilar-Rosas 1985). Even higher mean biomass values of *Ulva expansa* occurred within eutrophic meadows during summer (2001, 150 g DM m^{-2}) and winter (2002, 127 g DM m^{-2}), without symptoms of stress to eelgrass derived from reduced photosynthesis (Jorgensen et al. 2007). Eelgrass biomass, density, growth, and other sensitive variables of eelgrass stress (e.g., leaf length and number of leaves, root, and rhizome biomass, etc.) were uncorrelated with macroalgal biomass, which had been used as a controlling variable (predictor) (Jorgensen et al. 2007). This correlative approach did not allow Jorgensen et al. (2007) to categorically identify the causal mechanisms that control eelgrass abundance, and it cannot be ruled out that *Ulva* spp. blooms may be affecting eelgrass fitness. In fact, comparable ulvoid mats have been shown to reduce *Z. marina* shoot density in areas lacking significant anthropogenic eutrophication in the northeastern Pacific (Nelson and Lee 2001).

Ulvaceans forming drift mats were shown to potentially cause sizeable gaps in the seagrass canopy in experiments where the macroalgal biomass was manipulated. After 3 months, the inclusion in cages of *Ulva intestinalis* biomasses that reflected naturally occurring blooms in New South Wales (Australia; a 15-cm thick algal mat, ~4,500 g WM m^{-2} or ~450 g DM m^{-2}), reduced the biomass of mixed seagrass meadows to ~25% of the seagrass biomass present in the exclusion treatment (Cummins et al. 2004). In Washington State (USA), the removal of *Ulvaria obscura* masses in plots within the edge of subtidal eelgrass meadows determined an increment of 32% in eelgrass density in comparison with the density of meadows where *U. obscura* accumulated naturally (mean, 144 g DM m^{-2}; Nelson and Lee 2001). However, *U. obscura* likely outcompete eelgrass only when found in gaps or at the edges of meadows (Nelson and Lee 2001). The interactive effects of nutrients, *Ulva* spp. biomass, and brant-simulated herbivory on density, biomass, and growth rate of four intertidal eelgrass meadows in San Quintin Bay are being analyzed by an ongoing project. Mean eelgrass aboveground and belowground biomass, eelgrass density, and eelgrass shoot growth rate were not significantly reduced in the addition of ~2,000 g WM m^{-2} of *Ulva* spp. (mainly *U. expansa*) after a 4-month period (three-way factorial ANOVA, α=0.05) (Abella et al., unpublished data). However, main effects of *Ulva* addition on intertidal eelgrass descriptors were likely overshadowed by the very strong (significant) effect of the herbivory simulation treatment (Abella et al., unpublished data).

The report of high mean spring values of *Ulva* biomass in 2004 and 2005 in San Quintin Bay should be seen as a cause of concern for the stability of its eelgrass meadows (Zertuche-González et al. 2009). However, *Ulva* spp. does not seem to have triggered major declines of *Z. marina* subtidal meadows within the bay between 1987 and 2000, in part because there is no evidence that *Ulva* spp. blooms occurred when the cover of subtidal eelgrass meadows was significantly reduced. Moreover, the greatest reductions in subtidal eelgrass cover took place in a relatively large zone influenced by the San Simon River delta (Fig. 1) during a series of storms and flooding that occurred in the winter of 1992–1993. These events were responsible for a "significant portion of the loss of eelgrass cover at San Quintin Bay" (Ward et al. 2003). Ward et al. (2003) reported that sediment loads "buried entire beds of intertidal and subtidal eelgrass that were adjacent to the river delta in zone 3 and portions of beds that were in the path of sediments carried by tidal and river currents between the river delta and bay mouth in zones 4 and 5" (Fig. 1). Sediment loading from this flooding event decreased water depth in the bay resulting in an increase in intertidal areas and reduction in the original coverage of subtidal meadows (Ward et al. 2003). While continuous as well as sparsely distributed intertidal seagrass meadows of *Z. marina* or *Ruppia maritima* in zone 3 had a net increase of 157 ha, the net loss of subtidal meadows in this area was 322 ha, which represented 71% of the total loss of subtidal meadows in the bay (Table 1).

It might be noted that relative short-term (2–3 years) macroalgal blooms may be caused by remineralization of nutrients following storm events. It could be possible that the combination of flooding and a short-term bloom would push the system past a tipping point, favoring ulvoids. Similarly, nutrient enrichment from agriculture practices involving the use of N and P fertilizers in the vicinity of the San Simon River Delta could also have favored macroalgal bloom development after the storm events [for fertilizer use in San Quintin Valley, see Aguirre-Muñoz et al. (2001); nutrient discharge from fertilizer is about five times domestic

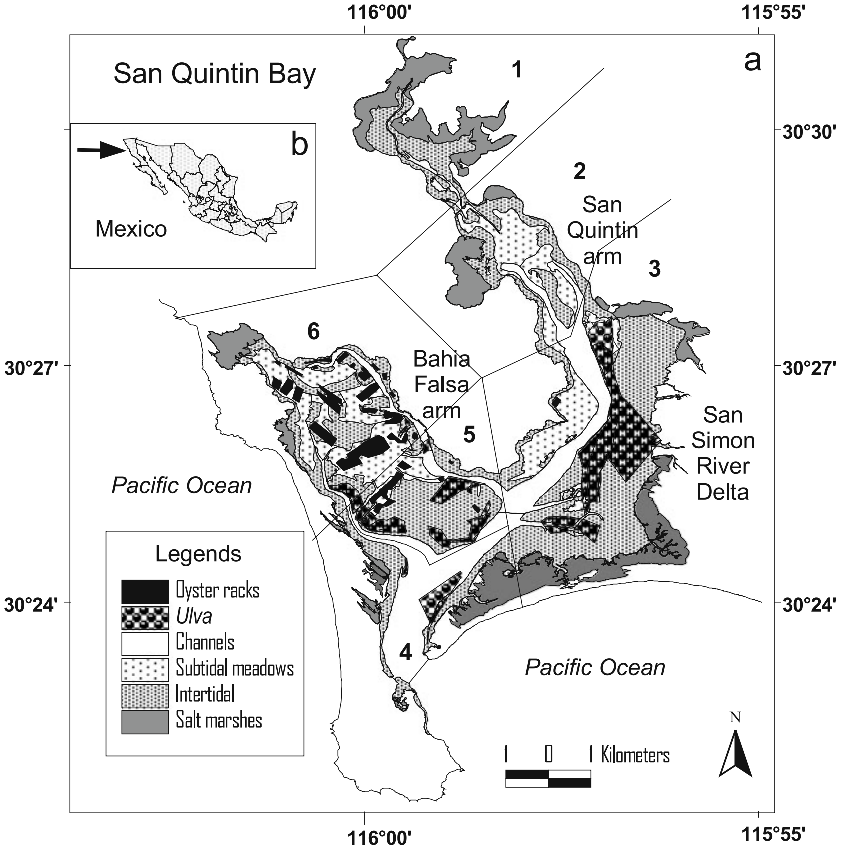

Fig. 1 Distribution of *Ulva* spp. mats, subtidal eelgrass of *Zostera marina*, racks for oyster cultivation, and other major habitats within San Quintin Bay (**a**), Mexico (**b**). Distribution of intertidal areas, subtidal meadows, and salt marshes were adapted from Fig. 1 of Ward et al. (2003). The map of the bay was divided in six zones, following Ward et al. (2003). The location and extension of the racks was estimated from Fig. 2 of Ward et al. (2003). The area occupied by large mats of *Ulva* spp. was estimated from Fig. 1 of Zertuche-González et al. (2009)

waste discharge]. However, this is speculative, since none of these processes were described for San Quintin Bay. The cause of submerged eelgrass meadow loss away from the river delta remains uncertain because of the lack of historical information (Ward et al. 2003).

Considering the major impacts that flooding has on eelgrass distribution and the bathymetric and litoral configuration of the bay (Ward et al. 2003, 2004), the potential negative effects of *Ulva* spp. based on past eelgrass distribution should be assessed by comparing present distributions with 1992–1993 post-flooding maps of San Quintin Bay habitats. For instance, by comparing more recent data of *Ulva* spp. distribution (measured in 2004–2005) with seagrass distribution maps of 1999 and

Table 1 Extension (ha) of San Quintin Bay major habitats in 2000 as estimated from Ward et al. (2003)

Category	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
Intertidal						
Saltmarsh	281 (−11)	127 (−1)	307 (+24)	159 (−18)	0 (0)	83 (+15)
Mudflat	19 (−33)	37 (+11)	452 (+15)	154 (+63)	121 (+104)	102 (+67)
Seagrass	138 (+60)	174 (+73)	518 (+157)	17 (−27)	202 (−91)	133 (−36)
Subtidal						
Seagrass	25 (−23)	175 (−37)	137 (−322)	3 (−23)	84 (−22)	463 (−30)
Channel	17 (−3)	58 (−47)	237 (+36)	287 (−12)	161 (+8)	93 (0)
Total	480	571	1,651	620	568	874
Ulva spp.	0	0	265	20	120	26
Racks	0	0	2	0	15	66

The bay was divided in six zones, following the map of Ward et al. (2003). The area covered by racks used for oyster culture was calculated assuming an impact area of 5 m around the center of each rack (see Ward et al. 2003). Spatial changes in habitat distribution between 1987 and 2000 are indicated *within parentheses*. The area occupied by large mats of *Ulva* spp. in May 2004 was estimated from Zertuche-González et al. (2009). Intertidal areas include mudflats and exposed seagrass meadows (≥0.0 m MLLW), while submerged meadows were classified as those <0.0 m MLLW

2000, it can be seen that *Ulva* mats mostly overlap with intertidal *Z. marina* and *R. maritima* meadows and intertidal mudflats (Fig. 1). Hence, the maps of *Ulva* spp. distribution in 2004–2005, at most, reflect the recent displacement of intertidal seagrass meadows but not the subtidal eelgrass meadows, as Zertuche-González et al. (2009) claimed in their paper. In fact, we contend that the inverse relationship between *Ulva* spp. and eelgrass cover and abundance reported by Ward et al. (2003) and interpreted by Zertuche-González et al. (2009), as evidence of the role of *Ulva* spp. in the loss of eelgrass meadows in the bay, was explained by the existence of large mats of *Ulva* spp. covering intertidal areas in 2000 (Ward et al. 2003).

There is no evidence that oyster cultivation is promoting *Ulva* spp. blooms or that oyster cultivation reduced eelgrass cover in the period 1987–2000

According to Zertuche-González et al. (2009), the recent increase in *Ulva* spp. biomass in San Quintin Bay is related to excretion of ammonium by oysters under culture. However, the distribution of *Ulva* spp. is inconsistent with the location of racks used for oyster rearing (Table 1 and Fig. 1). An important fraction of *Ulva* spp. biomass in BF is trapped around oyster racks and was not quantified by Zertuche-González et al. (2009). The extent to which this biomass is responding to ammonium excreted by oysters is uncertain and was not assessed by these authors. The contribution of ammonium excreted by bivalves may represent an important fraction of DIN fluxes, particularly during El Niño years (Hernández-Ayón et al. 2004). However, during non-El Niño years, fluxes of DIN are controlled by external inputs of new nitrogen from the adjacent ocean by upwelling-induced water advection and tidal mixing (Hernández-Ayón et al. 2004).

Beyond the relative importance of nutrients excreted by oyster for *Ulva* spp. growth, it seems apparent that the biomass of *Ulva* trapped around oyster racks constitutes an important source of C and N to the bulk organic matter of sediments in BF and the nutrition of resident macrofauna (Table 2 and Fig. 2). In spite of the putative impact of *U. expansa* on the food web, there is no evidence of negative impact of oyster culture on eelgrass distribution. Conversely, the analysis of eelgrass distribution in San Quintin Bay from satellite images between 1987 and 2000 indicated an apparent increase of eelgrass inside areas that potentially may suffer the negative impact of oyster culture, despite the considerable increase in the number of oyster racks (57–484) over the 13-year period (Table 1; Ward et al. 2003). Similarly, the biomass of eelgrass in the intertidal zone of BF nearly doubled between 1982 and 2005 (Ibarra-Obando et al. 2007).

The suggested removal of *Ulva* spp. biomass is based on experiences of heavy anthropogenically eutrophized systems

The comparison of San Quintin Bay with systems affected by cultural eutrophication may lead to risky, unfounded management practices. Removal of *Ulva* spp. biomass may be adequate as a short-term management practice to reduce eutrophication stress in systems receiving large land-derived anthropogenic inputs of nitrogen where water exchange is limited, such as Sacca di Goro (Cellina et al. 2003) and several other embayments in Europe and the East Coast of North America (references in Zertuche-González et al. 2009). However, in the Northeast Pacific, productivity in relatively unpolluted coastal lagoons such as San Quintin Bay is regulated by strong wind-forced upwelling events associated with the California Current System (Alvarez-Borrego 2004). Maximum upwelling events occur in spring and summer but become stronger during La Niña years and relaxed during El Niño years (Bakun and Nelson 1977). Hence, productivity and biomass in San Quintin Bay show strong interannual variability in response to ocean cycles, such as the El Niño Southern Oscillation phenomenon, or even longer term cycles (Alvarez-Borrego 2004; Caso et al. 2007; Ibarra-Obando et al. 2007).

In San Quintin Bay, green tides are dominated by *U. intestinalis*, *Ulva clathrata* (formerly *Enteromorpha intestinalis* and *E. clathrata*) and *U. expansa* (Aguilar-Rosas et al. 2005). *Ulva intestinalis* and *U. expansa* are in the same functional-form group but most likely are not functionally redundant. Differential salinity tolerances and

Table 2 Annual C and N percent contribution of phytoplankton, *Ulva expansa,* and *Zostera marina* to deposited particulate organic matter within shallow subtidal eelgrass meadows of zones 2 (San Quintin arm, SQ), 3 (base Y, BY), and 6 (Bahia Falsa arm, BF; for details see Jorgensen 2006), estimated through the concentration-weighted mixing model of Phillips and Koch (2002)

	BY			BF			SQ		
	Phyto	*Ulva*	*Zostera*	Phyto	*Ulva*	*Zostera*	Phyto	*Ulva*	*Zostera*
C	56	16	28	38	47	15	47	00	53
N	54	16	30	36	48	16	45	00	55

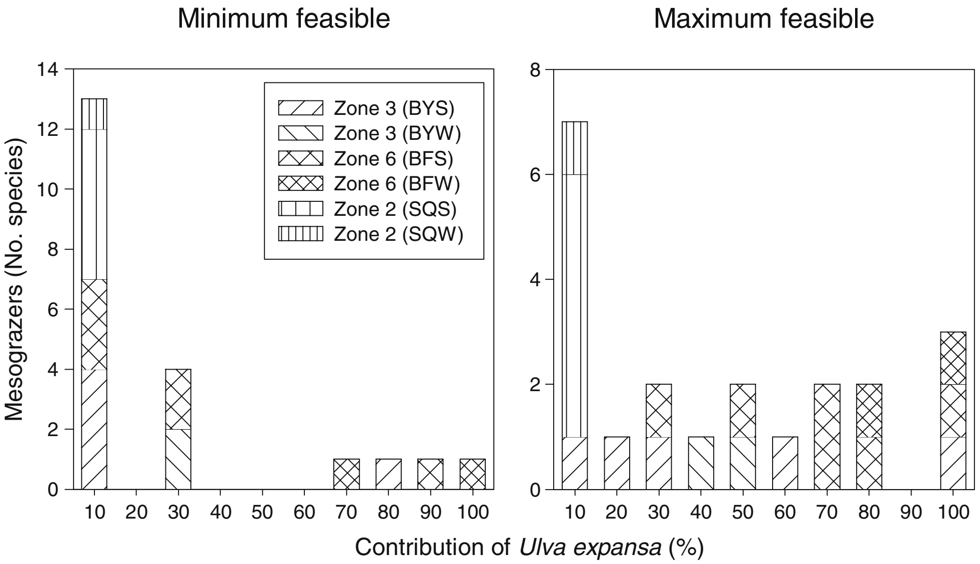

Fig. 2 Histograms of minimum and maximum feasible contributions of *Ulva expansa* as food source to mesograzer taxa in subtidal meadows of *Zostera marina* in zones 2 (San Quintin arm, SQ), 3 (base Y, BY), and 6 (Bahia Falsa arm, BF) in summer 2001 and winter 2002 (W) (for details see Jorgensen 2006). All of the possible combinations of the food sources contributing to a consumer were estimated through IsoSource, a linear mixing model based on mass balance equations recommended when the number of potential food sources is greater than the number of tracers +1 (Phillips and Gregg 2003)

N requirements likely determine zonation and successional patterns between both dominant macroalgae. *Ulva intestinalis* preferentially grows in the intertidal zone and is favored over *U. expansa* where, or when, salinities drop below 25 ppt; also, it is a better competitor for limiting N (or when N is supplied in rapid pulses; Fong et al. 1996). Conversely, *U. expansa* occupies the low intertidal and subtidal zones and is able to take up (and sequester) N and grow more quickly when N is in excess over a longer term and when salinity is near to oceanic values (Fong et al. 1996). Hence, the phase shift to a cool period that started with the strong La Niña 1999 (see Goericke et al. 2005) should naturally favor eelgrass (see long-term series in Ibarra-Obando et al. 2007) and also green tide development of *U. expansa* (Jorgensen et al. 2007). In contrast, repeated El Niño conditions registered during the period 1987–2000 in the northwest coast of Baja California are characterized by low ocean productivity and marked increases in winter rainfall (Caso et al. 2007), which may have favored *U. intestinalis* blooms in the zones more affected by terrestrial runoff. Under this scenario, it seems apparent that *Ulva* removal makes little sense in naturally productive systems such as San Quintin Bay, especially since changes in benthic vegetation are a consequence of relative long-term oceanographic processes and historical changes in food web structure (see next point).

The unrealistic "pristine" status of San Quintin Bay: importance of a historical baseline

Zertuche-González et al. (2009) suggested San Quintin Bay was in a pristine state prior to the loss of subtidal eelgrass meadows that occurred during the period 1987–2000. It is interesting to note, however, that eelgrass cover was estimated to be ~20% almost 50 years ago (Barnard 1970), nearly half that of 1987–2000 [compare maps based on aerial photographs and benthic surveys in Barnard (1962, 1970) and Dawson (1962); with maps based on satellite images in Ward et al. (2003) or based on airborne digital multispectral videography in Ward et al. (2004)]. In their conception of what is supposed to be pristine, Zertuche-González et al. (2009) tacitly perceive as the natural "baseline" a system where large vertebrates were extirpated (see Jackson 2001). Uncontrolled exploitation of natural resources in San Quintin initiated more than 150 years ago, long before scientific research began in the bay. Prior to 1850, abundant populations of sea otters were completely exterminated by American and Russian hunters (Barnard 1962). The green turtle (*Chelonia mydas*), a key herbivore that feeds largely on eelgrass and macroalgae (López-Mendilaharsu et al. 2005), was supposedly abundant in San Quintin Bay but was harvested to local extinction by residents (Barnard 1962). Moreover, since the 1960s, San Quintin began to be appreciated by international waterfowl hunters that preyed principally on brants. In addition, non-game birds such as the American egret and grebes were shot as well for target practice, both during open and closed hunting season (Barnard 1962). Uncontrolled harvesting of a large herbivore and detritus feeder gastropod (*Megastrea undosa*) continues nowadays (P.J., personal observation). Similarly, sea otters (*Enhydra lutris*), large geese (*Anser*, *Branta*, and *Chen* spp.), and other highly valuable resources were depleted by prehistoric populations in some systems such as San Francisco Bay (Lotze et al. 2006). Trends of long-term degradation occurred in estuaries and near-shore marine systems worldwide, with damage being particularly severe over the last 150–300 years (Lotze et al. 2006).

Overexploitation and habitat destruction have been responsible for the large majority of historical changes taken place in seagrass meadows, coral reefs, and kelp forests (Jackson et al. 2001; Lotze et al. 2006; Pandolfi et al. 2003). The loss of diversity and complexity increase the vulnerability of these systems to recent increases in sedimentation, turbidity, eutrophication, and species invasion, giving way to algal blooms, among other undesirable effects (Lotze et al. 2006). Hence, the reduction of exploitation and habitat protection should be a major management priority to regenerate resilience of estuarine and coastal ecosystems (Jackson et al. 2001; Lotze et al. 2006). Conservation efforts in some areas during the twentieth century led to partial recovery of some groups such as pinnipeds, otters, or birds (Lotze et al. 2006). However, most of the time, "…scientific debate revolves around species far down the original food webs, and former top predators and grazers are forgotten or ignored" (Jackson 2001).

The role of consumers in controlling vegetated soft-bottom communities in San Quintin Bay

According to Zertuche-González et al. (2009), harvesting of *Ulva* spp. biomass might reduce the possibility of green tide development through the decay of macroalgae in the subsequent cycle. This suggestion is in part based on their assumption that consumers in the system do not have an important impact on diminishing the biomass of *Ulva* spp. However, the effects that consumers have on biomass control and ecosystem function are particularly strong in marine benthic communities (Shurin et al. 2002). Herbivory pressure may be crucial at the colonization and early life-history stages of macroalgae (Lotze et al. 2001). Meta-analysis of experiments combining both nutrient and grazer control of opportunistic primary producers highlight the interdependence of top–down and bottom–up control of benthic marine communities, indicating that impacts on nutrient supply and food-web structure must be managed together (Burkepile and Hay 2006; Eriksson et al. 2007; Hughes et al. 2004). A simple trophic cascade model usually predicts the effect of consumers in benthic marine communities (Shurin et al. 2002). Trophic cascades were recently demonstrated in temperate eelgrass meadows of San Quintin Bay (Jorgensen 2006) and on a small shelter bay on the Swedish west coast (Moksnes et al. 2008). In these systems, grazing invertebrates (mesograzers) within eelgrass meadows consume and thus control the biomass of opportunistic algae that could outcompete eelgrasses for light. Small fish predators, however, control mesograzers' abundance and therefore release the algae from grazing pressure, with the resultant negative effects on seagrasses under eutrophic conditions.

In San Quintin Bay, the trophic cascade results in alternating high and low abundance of the bay pipefish at the highest level, through mesograzers (mainly amphipods), to basal producers at the lowest trophic level (epiphytes vs. eelgrass) (Jorgensen 2006; Jorgensen et al. 2007). In the Swedish west coast, the trophic cascade involves *Ulva* spp. (formerly *Enteromorpha* spp.) blooms (besides epiphytes), among the opportunistic algae that compete with eelgrass (Moksnes et al. 2008). The latter work shows that an amphipod (*Gammarus locusta*) can readily adjust their density and biomass to control the temporal bloom of *Ulva* spp., which is favored by water column nutrient enrichment when predation rates are low. Amphipoda is the numerically dominant macroinvertebrate taxa in eutrophic subtidal eelgrass meadows of San Quintin Bay (Barnard 1970; Jorgensen 2006). When released from predation pressure amphipods attained >30,000 ind. m^{-2} during summer (Jorgensen 2006) and should exert a strong grazing pressure over *Ulva*. However, when small predators are abundant, amphipod's biomass is reduced, further increasing the biomass of ephemeral algae. Both studies have demonstrated that the increase in opportunistic algal blooms and the loss of eelgrass may be linked to the local ecological extinction of large predators by overexploitation, which release the small predators from predation pressure and trigger the depression of key mesograzer populations (Jorgensen 2006; Moksnes et al. 2008).

Macroalgal species in naturally occurring ulvoid blooms in the Northeastern Pacific (Washington State, USA) may display, however, a tradeoff between resource competitive ability and herbivory resistance in agreement with the "keystone predator" model (Nelson et al. 2008). Higher consumer pressure in the subtidal than in the intertidal zone may determine compensatory shifts in abundance of grazing-resistant *U. obscura*, in detriment of the grazing-susceptible *U. lactuca* (Nelson et al. 2008). Such a compensatory response of *Ulvaria* could dampen the cascading predator impact on algal biomass (Shurin et al. 2002). Nonetheless, *U. obscura* was not reported for San Quintin Bay where green tides in the subtidal are dominated by *U. expansa* (Aguilar-Rosas et al. 2005; Jorgensen et al. 2007), while *U. intestinalis* usually form green tides in the intertidal zone (Ibarra-Obando and Aguilar-Rosas 1985). Resistance to grazing pressure was not assessed for *U. expansa*. Its preferential occurrence in the subtidal zone and its higher N content, in comparison with *U. intestinalis* (Fong et al. 1996), may suggest that *U. expansa* produce chemical deterrents against herbivores (see Nelson et al. 2008). Nonetheless, the high N content in *U. obscura* was associated with the production of dopamine as the herbivore deterrent, which has never been reported from any marine alga other than *U. obscura* (Van Alstyne et al. 2006).

The foliose thallus of *Ulva* is expectably more palatable than most other morphological macroalgal thallus (e.g., coarsely branched macroalgae, leathery or rubbery macroalgae, and calcareous algae). *Ulva* allocate less production to low digestible structural materials, and several co-generic species do not likely contain constitutive or inducible anti-herbivore chemical defenses and are usually used as control foods in feeding studies (Jormalainen and Honkanen 2008; Van Alstyne et al. 2001). An activated chemical defense mechanism was recently described for several *Ulva* species along the northwest coast of USA. However, the activated compound does likely not deter feeding of mesograzers, even at concentrations much higher than that would be found in most macroalgae (Van Alstyne et al. 2001). Hence, it can be expected that *U. expansa* in San Quintin Bay be highly susceptible to grazing by amphipods.

Hyale nigra and *Erichthonius brasiliensis* constituted ~80% of the amphipods within eelgrass meadows in San Quintin Bay (Barnard 1964). *H. nigra* is a nestling species that have little contact with the sediment and is strongly associated with eelgrass leaves, and feeds on macrophytes, associated debris, or epiphytes. *E. brasiliensis* is mainly a detritus feeder that lives in tubes attached to *Z. marina* or coarse particles over the sediment (Barnard 1964). Generalist and mobile species of the genus *Hyale* in Australasia usually preferred *Ulva* to several other macroalgae, including its host seaweed (Taylor and Steinberg 2005). Likewise, *Ulva* was shown to be the preferred food item for other vagile amphipod species (including *H. nigra*) in no- or multi-choice feeding assays (Kraufvelin et al. 2006; Paul et al. 2006). *H. nigra* was shown to consume *Ulva* sp. at rates that more than doubled those of the other four macroalgae in no-choice feeding assays (Paul et al. 2006). Moreover, the presence of tubes of amphipods attached to *U. expansa* fronds within eelgrass meadows (P.J., personal observervation) and the high density of amphipods in eelgrass meadows where *U. expansa* is abundant indicate that the macroalga may also function as host (and food source) for the more sessile amphipod *E. brasiliensis*. During summer, the mean density of amphipods (adults and juveniles) in subtidal eutrophic meadows in the area of confluence of the two arms of the bay (hereafter BY) and BF was about two orders of magnitude greater than in nitrogen limited meadows of the San Quintin arm (hereafter SQ; Jorgensen 2006).

The hypothesis that *U. expansa* is highly palatable to several mesograzers in San Quintin Bay is congruent with the recent quantification of energy flows of the food web of subtidal eelgrass meadows through C and N stable isotope analysis. Numerically dominant benthic invertebrates in eutrophic eelgrass meadows of San Quintin Bay incorporated an important fraction of *U. expansa* into their tissues (Jorgensen 2006; Jorgensen et al., unpublished data). The minimum feasible contribution of *U. expansa* to the diet of three of eight mesograzer taxa in BF was equal or greater than 70% of the total C and N assimilated, as estimated by mixing models applied to C and N stable isotope data (Fig. 2; Jorgensen 2006). Amphipods assimilated between 22% and 73% and 60% and 79% of their C and N content from *U. expansa* during summer and winter, respectively. In synthesis, *U. expansa* biomass (which can form thalli up to 2 m in diameter) not only provides refuge against predators but may also serve as a valuable food resource for relatively sessile and mobile mesograzers. Although mesograzers' control over primary producers was demonstrated only for epiphytes (Jorgensen 2006), the association of dominant amphipod herbivores consumes and assimilates large quantities of *U. expansa*. High assimilation of *U. expansa* would indicate algal digestibility by a diverse association of mesograzers and a system susceptible to strong cascades (Hall et al. 2007).

Ulva expansa may have positive effects on San Quintin Bay seagrass ecosystem properties and functions

Ephemeral drift macroalgae are widely recognized by their negative effects on seagrasses by overshading, oxygen depletion, or toxic ammonium concentrations (e.g., Cummins et al. 2004). Light limitation through overshading of macroalgal mats on seagrasses (particularly on shoot recruits) is usually the most likely explanation for the reduction in eelgrass shoot density (Hauxwell et al. 2001; Huntington and Boyer 2008). However, there may be positive effects of macroalgal mats on seagrass ecosystem properties and functions (plant diversity, plant productivity, nutrient cycling, trophic transfer efficiencies, and energy flux) whose net effect at any given time or location may be difficult to predict (Huntington and Boyer 2008).

At the moment, only one published study on San Quintin Bay simultaneously quantified and correlated water column and sediment properties, benthic primary producers, and primary and secondary consumer abundances (Jorgensen et al. 2007). In this study, individual patches of *U. expansa* reached up to ~350 g DM m^{-2}, and mean biomass of *U. expansa* was shown to surpass the biomass of eelgrass within continuous subtidal meadows. However, eelgrass biomass, density, and growth (among other eelgrass stress-sensitive variables) were uncorrelated with macroalgal biomass, set as one of several controlling variables (predictors) (Jorgensen et al. 2007). Vegetative shoot density was inversely related to epiphyte biomass on eelgrass leaves, indicating potential competitive interactions between eelgrass and its epiphytes for light availability (Jorgensen et al. 2007). Since the foliose thallus of *U. expansa* likely reduces predation pressure of the pipefish on the mesograzer-controlling epiphyte loading on eelgrass leaves (Jorgensen et al. 2007), it is possible that these subtidal meadows may benefit from the occurrence of

U. expansa. Drifting mats of *U. expansa* may also promote higher densities and diversity of epifauna (and higher grazing pressure over epiphytes) by enhancing immigration of peracarids (e.g., amphipods) and other mesograzers with no (or limited) larval dispersal abilities by passively transportation in algal patches (Arroyo et al. 2006). Moreover, drift algae may benefit the eelgrass by outcompeting epiphytes from their leaves (Irlandi et al. 2004).

Additionally, it was shown that *U. expansa* provides fresh or decomposing nutritional source of energy and nutrients for the food web, increasing the value of seagrass meadows as feeding or nursery grounds for transient juvenile fish, including some commercially exploited species (Jorgensen 2006; Jorgensen et al., unpublished data). These transient fish feed selectively on eutrophic eelgrass meadows when juveniles, before they migrate to the rocky shores at the end of the summer and autumn (references in Jorgensen 2006). Ontogenetic migration of transient fish may represent an important fraction of macroalgal production leaving the system. Similarly, *Ulva* spp. biomass may represent an important source of nutrients and carbon for the dry ecosystems of the Baja California Peninsula, as it was demonstrated in similar upwelling systems in Peru (Catenazzi and Donnelly 2007). Drifting *Ulva* mats lying on the intertidal zone subsidize N-limited plants in the salt marsh in Southern California (Boyer and Fong 2005).

Final comments

Model competition outcomes between *Z. marina* and *Ulva* in a coastal lagoon in Italy predicted that *Z. marina* can survive only when environmental circumstances constrain the biomass of *Ulva rigida* below 150 g DM m^{-2} (Lagoon of Venice; Coffaro and Bocci 1997). Since mean spring values of *Ulva* biomass in 2004 and 2005 clearly exceeds the critical value from which the macroalga is predicted to outcompete eelgrass (297.4 and 347.3 g DM m^{-2}), recent reports of *Ulva* biomasses in San Quintin Bay may be seen as a cause of concern for the stability of its eelgrass meadows. Based on these facts, it appears that the removal of *Ulva* biomass must not be discarded as an option for the conservation of eelgrass meadows in San Quintin Bay.

Harvesting of benthic algae could be useful to remove excess nitrogen from the water column under some situations (Cellina et al. 2003). However, the weakness of arguments and evidences supporting subtidal *Z. marina* meadow displacement by *Ulva* spp. (among other questions raised here) makes unlikely that the harvesting of the macroalgae is advisable in subtidal eelgrass meadows of San Quintin Bay. Subtidal continuous eelgrass meadows in San Quintin Bay are likely resilient to macrolagal disturbance. Lack of light reaching the substratum among large eelgrass shoots and potentially high amphipod abundance of subtidal meadows in BY and BF (Jorgensen et al. 2007) may jointly prevent macroalgal growth and may serve as a barrier to drifting mats of ulvoid algae in the subtidal (see Eriksson et al. 2007; Nelson and Lee 2001). Harvesting of extensive mats of *Ulva* layering on the intertidal may be beneficial in view of the impressive cover and biomass that *Ulva* spp. may reach during spring in the zone (Fig. 1; Zertuche-González et al. 2009) and the beneficial effects of the experimental removal of macroalgae biomass on seagrass abundance demonstrated in other systems. However, more experimental studies are needed to justify commercial practices in this naturally productive ecosystem. Furthermore, as Valiela et al. (1997) clearly pointed, “to propose collecting macroalgal biomass as a means to remove nutrients, we will need to find effective, affordable techniques, estimate effective harvest rates, and devise a suitable harvest regime, and we need to explore the inevitable consequent effects on water quality.”

The harvest of macroalgal biomass will probably be associated to a series of physical disturbances (e.g., boat anchoring, boat propeller scarring, hull grounding, and human wading), shown to affect seagrass meadows (Eckrich and Holmquist 2000; Hammerstrom et al. 2007). Thus, is it reasonable to incur the chance of unfortunate consequences for the ecosystem, associated with the harvest of *Ulva* biomass in a naturally eutrophic system, where eelgrass cover was shown to be much lower in the past? Beyond the claimed benefits of macroalgal harvest, we envision, as a better solution, more protection against the development of unsustainable practices in the bay and the reintroduction of large consumers that become extinct (or ecologically extinct) in the past. Finally, we urge the multidisciplinary scientific community working in the highly productive marine ecosystems of the Northwest Pacific coast of Mexico to avoid neglecting the experimental and historical evidences of the key role of consumers in driving and shaping marine benthic communities.

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