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Undermining the foundation: a brief overview of the effects of a widespread invader on coastal ecosystem engineers

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By creating habitats or influencing the immediate physical environment, ecosystem engineers shape the diversity, function and services provided by ecosystems. Thus, the disruption of these species is relevant given their broad influence on native communities and ecosystems. As such, we review the effects (positive, negative, or neutral) of a widespread invasive species, the European green crab (*Carcinus maenas*) on key coastal ecosystem engineers. We examined the literature and focused on 53 published studies to assess reported impacts on well-known macrophytes, mussels, oysters and clams. Despite the wide range of response variables measured and reported, green crab effects were overwhelmingly negative. These effects were mediated by direct (through consumption and sediment burrowing) or indirect mechanisms (through seed consumption, alteration of habitat quality or effects on related species), and were often context dependent. These conclusions are limited by ongoing green crab expansions where possible impacts have not been yet documented, and by cases of neutral or minor impacts that remain unpublished. Green crab effects often result in disruption rather than the loss of local ecosystem engineers, but they clearly add to the ongoing effects of other global stressors.

KEYWORDS

ecosystem engineer, invader, habitat-modifier, macrophytes, bivalves

1 Introduction and approach

Coastal ecosystems are exposed to multiple anthropogenic stressors, including the arrival of an increasing number of invasive species (Ruiz et al., 1997; Stachowicz et al., 2002; Byrnes et al., 2007; Bailey et al., 2020). While some invaders cause minor changes, others trigger cascading effects that amplify their ecological influence on communities or ecosystems. The extent of these effects depends on the nature of the invader (Capelle et al., 2015) and the species that they target upon establishment. The European green crab

(*Carcinus maenas*) is a voracious omnivorous predator that has been labeled one of the world's 100 worst invasive species (Lowe et al., 2000). This crustacean has spread to most coastal regions, and its diet includes a wide variety of prey (e.g., Ropes, 1968; Cohen et al., 1995; Baeta et al., 2006; Cordone et al., 2022; Fisher et al., 2024) including a key group of species that, given their role, are referred to as ecosystem engineers (Jones et al., 1994). These species create or transform the habitat (autogenic or allogenic engineers, respectively; Jones et al., 1994), enhancing diversity (Romero et al., 2015), and changing the function and services that communities and ecosystems provide (Tsuchiya and Nishihira, 1986; Bos et al., 2007; Barbier et al., 2011; Scherer and Reise, 1981).

Coastal ecosystem engineers encompass plants and animals operating from micro- to macro-benthic communities, but the groups that have gathered the most attention include macrophytes and a wide variety of bivalves (e.g., Gutiérrez et al., 2003; Matheson et al., 2016). We argue that examining the impacts of invasive species on ecologically important ecosystem engineers as a distinct group is timely and meaningful, as these effects may shape the influence that invaders ultimately have on native communities and ecosystems. Hence, using the green crab as an aggressive and widespread model invader (Baeta et al., 2006), this Minireview examines the main habitat-forming or modifier ecosystem engineers this species has come to interact with, the types of studies conducted, the nature of the effects commonly reported – whether direct or indirect and whether positive, negative or neutral–. In doing so, we aim to identify consistent findings across studies, species and regions, and highlight knowledge gaps that warrant further investigation.

We examined the published literature and identified 53 studies (Table 1) describing and quantifying green crab effects on ecosystem engineers. Studies were found through Google Scholar, available academic databases, and online networks (e.g., ResearchGate). We used a series of keywords (and their combinations), including but not restricted to, "*Carcinus maenas*", "invasion", "ecosystem engineer" "foundation species", "seagrass", "saltmarsh", "mollusc", "bivalve", "clam", "mussel", "oyster", "native macrofauna", and "native community", in addition to the species names of known ecosystem engineers, and articles' cross-references. We therefore circumscribed the search of engineers to the groups best represented in the published literature, i.e., macrophytes (seagrass, saltmarsh and macroalgal species) and bivalves (mussels, oysters and clams). Moreover, a key step in the inclusion of a species in the list of ecosystem engineers was the confirmation (by published sources) of its status as such. For some well-researched species (e.g., the blue mussel, *Mytilus edulis*), the number of studies was purposedly limited to avoid unnecessary repetition of relatively well-known effects. In this case, only studies explicitly addressing a green crab effect on the engineer (e.g., reporting rates of interaction rather than simply including the species as part of a community invaded by green crabs) were retained. While most studies refer to invaded regions, a few refer to the effects of green crabs on their native range of distribution.

2 Influence on seagrasses and other macrophytes

Green crabs have a broad diet (Ropes, 1968; Le Roux et al., 1990; Baeta et al., 2006), but their consumption of seagrass tissue is restricted to a few records of clipping and shredding (Neckles, 2015; Howard et al., 2019) or grazing upon tender shoot meristems of eelgrass (Malyshev and Quijón, 2011). Most reported impacts (Table 1) are the result of crab burrowing in the search for shelter or other sources of food, a process by which they damage roots and rhizomes (Prystay et al., 2023), impacting their stability, dislodging, or uprooting entire plants (Davis et al., 1998; Neckles, 2015; Matheson et al., 2016). As an example, in the northwestern Atlantic, green crabs have drastically reduced eelgrass (*Zostera marina*) shoot densities in areas of New Hampshire and Maine (USA), Nova Scotia and Newfoundland (Canada). In New Hampshire, green crabs reduced the survival of eelgrass transplants almost four times compared to green crab exclusions (Davis et al., 1998). In Nova Scotia, eelgrass declines reached up to 75% in a short (4-month) period (Garbary et al., 2014), while in Newfoundland, eelgrass beds saw a milder 27% decline over a 14-year period (Matheson et al., 2016). The latter study also showed that across 20 sites in Placentia Bay, four were found to be devoid of eelgrass due to crab burrowing, with one site experiencing up to a 90% reduction in shoot abundance, due primarily to the digging by large male crabs (Matheson et al., 2016).

Green crab indirect impacts include the consumption of seagrass seeds, limiting or reducing spread potential and the subsequent seasons' survival (Unsworth et al., 2024; Infantes et al., 2016). While seed consumption seems opportunistic, appearing when alternative food is unavailable, at least one study conducted in Sweden reported signs of preference. Compared with two other consumers, a hermit crab and a sea urchin, green crabs consumed 2–7 times more seeds, and a single green crab was recorded to consume 73% of the available seeds over a week-long study period (Infantes et al., 2016). Schooler et al. (2022) also reported green crabs eating over 10 eelgrass seeds per day in Coos Bay, Oregon, USA, a behavior that also impairs the success of restoration seagrass initiatives (Infantes et al., 2016). Green crab activities cause resuspension of fine sediments, which covers eelgrass blades which either suffocates them (Neckles, 2015) or reduces the plant's ability to photosynthesize (Garbary et al., 2014). Green crabs also consume macro- or meso-grazers that feed primarily on algae, causing a feeding release that prompts algal overgrowth on eelgrass beds deterring its condition and growth (Infantes et al., 2016). Similar indirect effects are likely common but have not been documented.

Sediment burrowing has been shown to have a strong effect on at least two saltmarsh species, *Sporobolus foliosa* and *S. alterniflorus* (formerly *Spartina foliosa* and *S. alterniflora*, respectively). In San Francisco Bay, USA, the green crab alone or in combination with stressors like sea-level rise, accounted for at least 60% of the loss of

TABLE 1 Summary of 53 studies reporting the influence of the green crab (*Carcinus maenas*) on prominent ecosystem engineers (EE), grouped as macrophytes (MP), mussels (MU), oysters (OY), and clams (CL).

EE	Location	Species	Response variable	Effect (L/F)	Main findings regarding green crab impacts	Ref
MP	Wales, UK	*Zostera marina*	Shoot biomass	– (L/F)	Eelgrass shoot density was reduced from 7 to 13 times when not protected from green crabs. Crab seed consumption confirmed up to 20 mm in depth in substrate	Baeta et al., 2006
	ME, USA	*Zostera marina*	Shoot biomass	– (F)	Invasion coincided with the near full bed disappearance. Green crab protection caused a 3 × survival increase. Clipping, shredding and digging up to 10–15 cm caused shoot suffocation and dislodging	Bailey et al., 2020
	BC, Canada	*Zostera marina*	Shoot biomass	– (F)	High crab density caused 73–81% eelgrass decline through shoot shredding. Loss of 17.6 shoots d^{-1} caused an estimated 78% decline in blade biomass	Banke et al., 2024
	NL, Canada	*Zostera marina*	Biomass Cover	– (F)	Bed cover declined 27% in 1998–2012, with 4 out of 20 sites cleared, and one showing a 90% decline. Areas with crabs > 5 yrs were most affected. Digging by male crabs covered eelgrass with fine sediments	Barbier et al., 2011
	NS, Canada	*Zostera marina*	Biomass Density	– (F)	~75% decline in density over 4 months. Loss of 4.1 shoots $cage^{-1}$ and 200,000 shoots d^{-1} in a 50,000 m^2 area. Crabs caused bed thinning and bald spots, increasing rhizome shoots and reducing frayed shoots	Bateman, 2017
	PE, Canada	*Zostera marina*	Density Condition	– (L/F)	Adult crabs uprooted 10× more eelgrass shoots than juvenile crabs in laboratory trials and could uproot up to 84% of shoots. Juvenile crabs grazed on the tender tissues of the base of shoots	Battini and Bortolus, 2020
	NH, USA	*Zostera marina*	Density Biomass	– (L)	Moderate crab densities caused a 39% loss of shoot transplants. Crabs damaged shoots during digging, indirectly reducing rhizome chances to develop and grow, and limiting restoration success	Behrens Yamada and Hunt, 2000
	Sweden (Southwest)	*Zostera marina*	Seed numbers	– (L/F)	Daily consumption of 44–59% of eelgrass seeds. One green crab fed an average of 147 seeds in one week. Crab feeding on seeds was ~2x higher than other consumers	Bertness and Coverdale, 2013
	CA, USA	*Spartina foliosa*	Tiller density	– (F)	Crabs caused a decline in marsh cordgrass survival. When protected, a 49–63% cordgrass density increase was recorded. Inundation and green crabs negatively affected marsh success	Bertness and Grosholz, 1985
	CA, USA	*Spartina foliosa*	Tiller density biomass	– (F)	Plots exposed to crabs lost 61 and 66% more stems than partial cages and controls, respectively. In August, crabs caused a 90% stem loss compared to controls. Indirectly, 51% of invertebrates could be lost	Beukema and Dekker, 2014
	NE, USA	*Spartina alterniflora*	Marsh stability	+ (F)	Green crab predation on purple marsh crabs (*Sesarma reticulatum*) caused a grazing/bioturbation relief to salt marshes, improving the success of restoration	Bos et al., 2007
	PE, Canada	*Chondrus crispus (giant strain)*	Frond biomass	0/– (L)	While crabs disrupted and caused minor algal biomass loss (<2%), they were indirectly harmful through consumption of small mussels (used as anchoring mechanism by the algae)	Bruno et al., 2003
MU	Wales, UK	*Mytilus edulis*	Abundance fishery	– (F)	Over 33 months, crabs accounted for fishery losses of 550 kg ha^{-1} (peak losses at 26 kg ha^{-1} d^{-1}). Prevalent sizes were most consumed, with preference for 2.5–3 cm SL. Feeding rates related to temperature	Byrnes et al., 2007
	Netherlands (Southwest)	*Mytilus edulis*	Recruitment Abundance	– (F)	Small crabs consumed 3–9 mussel seed d^{-1}, while large (adult) crabs consumed up to 19 seed d^{-1}. Small sized mussel are at the most risk from predation by crabs and starfish (*Asteris rubens*)	Campbell et al., 2019
	Denmark (Southeast)	*Mytilus edulis*	Coverage Biomass	– (F)	Declines in mussel bed coverage were correlated with green crab presence, with seabed biomass declining by ~4 kg m^{-2}. Tidal action and crab seasonal colonization had the worst effects on coverage	Capelle et al., 2015
	Wales, UK	*Mytilus eduls Ceratoderma edulis*	Abundance Size	– (L)	Large and mid-size crabs preferred and consumed large amounts of mussels and cockles. Feeding rates were size-dependent as crabs ranked prey by profitability	Cohen et al., 1995

(Continued)

TABLE 1 Continued

EE	Location	Species	Response variable	Effect (L/F)	Main findings regarding green crab impacts	Ref
	Germany, Wadden Sea	*M. edulis, L. littorea, H. ulvae*	Abundance Size	– (F)	In seagrass beds, crabs fed primarily on small mussels. Male and female crabs consumed large amounts of molluscs, targeting the most abundant bivalves and large littorinid snails	Cordone et al., 2022
	Portugal, Porto	*M. galloprovincia-lis, Xenostrobus securis*	Abundance Preference	– (F)	Crabs consumed 2x more native (gallo mussel) than invasive mussels, facilitating the invasion of the latter species (*X. securis*). Feeding rates increased with temperature	Crain et al., 2008
	England, UK	*Mytilus galloprovincialis*	Mussel shell chipping	– (L/F)	In the field and laboratory, juvenile green crabs used a distinct technique to damage (marginal mandibular chipping) and access small gallo mussel tissues, causing considerable losses	Crooks, 2002
	BC, Canada	*Mytilus galloprovincialis,* Various clams	Abundance Choice	– (L)	In prey choice trials, crabs consumed up to ~8 ind. d^{-1} of either gallo mussels or varnish clams, consistently choosing the smaller bivalve with thinner shells. Crabs are a threat to these commercial species	Curtis et al., 2012
	Australia (South)	*Xenostrobus inconstans*	Abundance Shell type	– (L)	Male and female crabs consumed ≥ 82.5% of all mussels, which are preferred due to their softer shells. However, crabs are expected to consume any bivalve with shell strengths <140 Newton	Davis et al., 1998
	Australia (Southeast)	*Xenostrobus secures*	Abundance Size	– (L/F)	Due to green crab size (larger than native species), they consumed more mussels as trial periods were extended. Unlike native crabs, green crabs were not outgrown by mussels	Ens et al., 2021
	Argentina (Patagonia)	*P. purpuratus, B. rodrigueii, A. ater*, others	Diet (meta-barcode)	– (L/F)	Based on metabarcode data, crab prey items included primarily bivalves (35.6%) followed by amphipods (13%). Crab expansion is expected to destabilize the food web	Fisher et al., 2024
	Argentina (Patagonia)	*Perumytilus purpuratus and other spp.*	Abundance Preference	– (F)	Newly arrived crabs are the largest benthic predators, so consume most prey available, including *P. purpuratus*, at larger quantities and sizes than any native predator	Floyd and Williams, 2004
	NE, USA	*Geukensia demissa*	Abundance Size	– (F)	Green crabs and native crabs accounted for up to ~31% of small (<36 mm SL) ribbed mussel mortality rates at marsh flats devoid of large adult mussels	Flynn and Smee, 2010
	NE, USA	*Geukensia demissa*	Abundance Size	– (L)	Crabs alone or with a conspecific consumed 17 and 63% of ribbed mussels available in laboratory trials. The largest proportion of mussels consumed were <40 mm SL	Garbary et al., 2014
OY	PE, Canada	*Crassostrea virginica*	Abundance	– (F)	Eastern oyster mortality was highest (74% small oysters) at sites with high crab density. Crab inclusions, controls, and exclusions treatments resulted in 65–87, 14–43, and 1% mortalities, respectively	Gibbons et al., 2024
	PE, Canada	*Crassostrea virginica*	Survival Pairing, Size	– (L)	Crabs fed more heavily on individual Eastern oyster spat (≥50%) than on naturally attached (cemented) oyster spat, collected from aqua-culture operations. Feeding rates were higher on small-sized oysters	Glude, 1955
	PE, Canada	*C. virginica, M. edulis, M. arenaria*	Abundance	– (L/F)	Crabs consumed 83, 75, and 58% of blue mussels, Eastern oysters, and softshell clams available (native crabs consumed ≤33%), without discriminating among size classes	Gonzalez et al., 2024a
	PE, Canada	*C. virginica M. edulis M.arenaria*	Abundance Size	– (L/F)	Overall, crabs preferred small and thinner-shell bivalves, with highest to lowest feeding rates upon softshell clams, blue mussels and Eastern oysters, respectively. Only large-sized crabs fed effectively on oysters	Gonzalez et al., 2024b
	PE, Canada	*Crassostrea virginica*	Abundance, Size	– (L/F)	Crabs of increasing size ranges consumed more Eastern oysters and larger SL. Small oysters (spat) were consumed fastest (within 24 h) and represented the most vulnerable stage	Griffiths et al., 1992
	BC, Canada	*Magallana gigas*	Density Functional response	– (L)	Crabs harmed oyster populations by consuming an average of 3.9 oysters d^{-1}. They used type II functional response, which implies predation attempts at even the lowest prey densities	Griffiths and Richardson, 2006
	CA, USA	*Ostrea lurida*	Abundance Size	– (L)		Grosholz, 2005

(Continued)

TABLE 1 Continued

EE	Location	Species	Response variable	Effect (L/F)	Main findings regarding green crab impacts	Ref
					Crab feeding on Olympia oysters was size-dependent, with small to mid-size crabs feeding the most (58% of oysters available under laboratory conditions).	
	OR, USA	*O. conchaphila, V. philipinarum, M. nasuta, others*	Abundance, Preference	– (L)	Crabs consumed 15–62 Olympia oysters d^{-1}, and this species and the California softshell clam were preferred 4 to 16 times over the bent *Macoma* clams in preference trials	Grosholz et al., 2000
	OR, USA	*Ostrea lurida Magallana gigas* Various clams	Diversity of prey	– (F)	An increase in crab populations has been deemed a threat for multiple bivalves, including Olympia oysters, Pacific oysters, littleneck clams, butter clams, and cockles.	Grosholz and Ruiz, 1995
	Wales, UK	*Ostrea edulis, Crassostrea gigas, M. edulis, C. edule*	Prey preference	– (F)	Crabs showed no preference between the two oyster species, but a strong preference for mussels and cockles over oysters. Profitability (biomass based on size and species) drove prey choices	Gutiérrez et al., 2003
CL	ME, USA	*Mya arenaria*	Abundance	– (F/L)	Crabs were linked to 57–88% loss of softshell clams (crushed/chipped missing or dead), while protected areas had 4.5× more recruits than controls. Crabs caused clams to dig 12% deeper	Hidalgo et al., 2007
	ME, USA	*Mya arenaria*	Abundance Depth	– (F)	Crabs fed heavily on clams located in shallow layers of the sediment, regardless of size. Crab presence was correlated with clam depth in the sediment (as an escape strategy)	Holland et al., 2021
	ME United	*Mya arenaria*	Abundance Depth	– (L)	Crab has non-consumptive effects on softshell clams: their presence drove a 15% increase in clam's burial depth, a strategy that increased clam survival from 29 to 67%	Howard et al., 2019
	NS, Canada	*Mya arenaria*	Abundance Size	– (F)	Crab feeding rates on <17 mm SL softshell clams reached 80% in field cage experiments. Overall consumption rates for field sites were estimated to range between ~3 to 22 softshell clams d^{-1}	Infantes et al., 2016
	NL, Canada	*Mya arenaria, P. magellanicus, M. edulis*	Abundance Choice	– (L/F)	Crab feeding rates were temperature-dependent (4× higher feeding rates on scallops in warmer waters), showing preference for softshell clams and mussels over scallops	Jensen and Jensen, 1985
	PE, Canada	*Mya arenaria*	Abundance Habitat	– (L/F)	Crab feeding rates on small softshell clams were 80–90% regardless of habitat type (sand flat or eelgrass), and were higher than those of native predators of similar size (40–60%)	Jones et al., 1994
	Scotland, UK	*C. edule, Macoma balthica*	Abundance Infauna	– (F)	Crabs fed heavily on cockles (1 out of 2000 reached refuge size), and at higher densities had stronger effects on cockles than Baltic clams. Crab exclusion prompted alternative infaunal predators	Juanes, 1992
	UK	*C. edule, Macoma balthica*	Abundance, Burrowing behavior	– (L)	Crabs increased feeding rates on cockles 15× after exposure to their cues for 5 d. Crab cues also caused Baltic clams to burrow over 2× deeper in the sediment	Kamermans et al., 2009
	Denmark	*C. edule, M. edulis Macoma balthica*	Biomass Abundance	– (F)	Cockle and other bivalves' recruitment level was strongly (negatively) correlated with young crab abundances. Seasonal crab impacts on bivalves lessened following cold winters	Kéfi et al., 2012
	Denmark	*C. edule, M. edulis M. arenaria, M.balthica*	Abundance recruitment	– (F)	Green crabs preferred and caused a ~26% loss of cockle recruitment over one season. Juvenile crabs may prevent the development of large cockle, clam, and mussel beds	Le Roux et al., 1990
	Wales, UK	*Cerastoderma edulis*	Abundance Size	– (L)	Individual crabs consumed <40 cockles d^{-1} in the laboratory, and when given a choice, targeted smaller than expected cockles. Feeding rates also increased sharply with temperature	Lipcius and Hines, 1986
	Wales, UK	*Cerastoderma edule*	Abundance Biomass	– (F)	Crabs and oystercatchers feed on cockles at different times and tide levels, but crabs consume twice as many cockles (2432 g dry flesh $year^{-1}$ linear m^{-1}), especially in smaller size classes	Lowe et al., 2000
	NJ, USA	*Mercenaria mercenaria*	Abundance Distribution	– (L)	Crab feeding rates on small hard clams were highest (up to ~83%) at highly aggregated patches of clams. Feeding rates declined by 50% with the split and separation of patches	Malvé et al., 2024

(Continued)

TABLE 1 Continued

EE	Location	Species	Response variable	Effect (L/F)	Main findings regarding green crab impacts	Ref
	NJ, USA	*Mercenaria mercenaria*	Abundance Distribution Flow speed	– (L)	Crab feeding rates on small hard clams were highest in a clustered pattern and at low flows (5 cm s^{-1}) and declined when spread randomly and exposed to higher flows (15 cm s^{-1})	Malyshev and Quijón, 2011
	CA, USA	*Transennella confusa, T. tantilla*	Abundance Size	– (F)	Compared to controls, exposure to crabs reduced 4x and 2x densities of *T. confua* and *T. tantilla*, respectively. Unlike other prey, crabs preferred larger rather than smaller clams	Malyshev et al., 2020
	Tasmania, Australia	*Fulvia tenuicostata,*	Abundance Size	– (F)	Crabs caused a ~50% reduction in clam abundances, with a strong preference for small clam sizes. Co-occurring sea stars fed on larger clam sizes (i.e. risk of predation across all sizes)	Mascaro and Seed, 2000
	Tasmania Australia	*Katelysia scalarina*	Abundance	– (L/F)	Clam survival was significantly lower in areas invaded by crabs. In experimental trials, survival increased from 8% to 90% in controls and crab exclusions, respectively.	Mascaró and Seed, 2001

In addition to geographic location, target (EE) species, measured response variables, nature of the green crab effects (–: negative; +: positive; 0: neutral), and general approach (L, laboratory; F, field study), a summary of main findings is presented. Unless otherwise specified, "crab" refers to green crab. References (Ref) to each study are cited at the bottom of the Table and presented in full in the Literature Cited section.

saltmarsh stems (in some cases reaching up to 90%; Gonzalez et al., 2024a, 2024b). Meanwhile, on the Atlantic coast Bertness and Grosholz (1985) showed that green crabs indirectly harm the stability of saltmarshes by consuming a second and closely associated ecosystem engineer, the ribbed mussel (*Geukensia demissa*). In sharp contrast, and among the few positive effects of green crabs, Bertness and Coverdale (2013) found that green crab predation on purple marsh crabs (*Sesarma reticulatum*), a grazer and bioturbator that degrades saltmarshes, facilitated the recovery of *S. alterniflorus* marshes. A similar positive mechanism may occur in the southwest Atlantic, where recently established populations of green crabs are becoming likely predators of *Neohelice granulata*. Like the purple marsh crab, *N. granulata* is detrimental to Patagonian marshes (*S. alterniflorus* and *S. densiflorus*), so if predation by green crabs is confirmed to be substantial, it may indirectly benefit these plants as well (Battini and Bortolus, 2020).

Lastly, green, red, and brown macroalgae often appear in the diet of green crabs in variable amounts and proportions (see Ropes, 1968; Le Roux et al., 1990; Griffiths et al., 1992; Baeta et al., 2006). However, no article has yet coined green crabs as primarily herbivore species, so the consumption of macroalgae is most often deemed "occasional" or "secondary" to alternative prey like bivalves. One example is the consumption of proportionally small amounts of a variety of Irish moss (*Chondrus crispus*) in Atlantic Canada (Tummon Flynn et al., 2019). These authors showed that green crabs consume some biomass and physically disrupt the macroalgal fronds. However, the actual impact of the crab is mediated by its consumption of associated blue mussels (*Mytilus edulis*), which this variety of Irish moss uses for anchoring to the sea floor forming entangled clumps (Tummon Flynn et al., 2019; 2020; Gibbons et al., 2024).

3 Influence on bed-forming mussels

Strong green crab consumptive effects upon various species of mussels have been well-documented across various coastal regions, both in correlation-based and experimental studies (Table 1). In the northwest Atlantic, green crabs accounted for roughly 550 kg ha^{-1} of blue mussel losses (*Mytilus edulis*), with a peak daily loss of 25.92 kg ha^{-1} over a 40-month coverage experiment in the Menai Strait (Murray et al., 2007). Similar (but widely variable) impacts have been reported from Denmark, where green crabs reduced blue mussel biomass by ~4 kg m^{-2} (Banke et al., 2024), and from the Netherlands, where small mussel seed was consumed at rates of up to 19 seeds d^{-1} (Kamermans et al., 2009). Green crabs also feed on blue mussels across the Atlantic (Matheson and Mckenzie, 2014; Pickering and Quijón, 2011; Miron et al., 2005), at rates considerably higher than native crab species such as the rock crab (*Cancer irroratus*; Miron et al., 2005). As ectotherms, feeding rates are directly influenced by temperature changes, as shown in Newfoundland (Matheson and Mckenzie, 2014) and the UK (Murray et al., 2007), whereby the latter study reported feeding rates six times higher at 13°C compared to 6°C. Green crabs have also been shown to have negative effects on populations of at least three other closely related species of mussels: the Pacific blue mussel (*M. trossulus*), gallo mussels (*M. galloprovincialis*), and purple mussels (*Perumytilus purpuratus*). In the Northeast Pacific large green crabs prefer and consume large amounts of Pacific blue mussels (Behrens Yamada and Hunt, 2000) and gallo mussels (Curtis et al., 2012), whereas gallo mussels are heavily preferred over invasive bivalves in Portugal (Veiga et al., 2011). Juvenile green crabs are also effective consumers of early (<20 mm shell length [SL]) stages of this species in the northeast Atlantic (U.K.; Morton and Harper, 2008).

Green crabs recently arrived at the southwestern Atlantic (Patagonian coast), where purple mussels and *Brachidontes rodriguezii*, form rocky intertidal beds of "scorched mussels". Green crabs have been observed feeding heavily on purple mussels (Hidalgo et al., 2007; Cordone et al., 2022), but no reports of predation on the second species have been documented yet, although it is likely to occur. In the South Pacific (Australia), green crabs feed heavily on two other mussels: *Xenostrobus inconstans* and *X. securis* (Campbell et al., 2019; Bateman, 2017).

For both male and female green crabs, *X. inconstans* is a preferred prey (> 82% in preference trials) over cockles (*Katelysia peronii*) due to its softer shell (Campbell et al., 2019). Meanwhile, *X. securis* is consumed at higher rates than that of native predators, threatening a potential overconsumption of this species' local populations (Bateman, 2017). Green crabs have also been reported to consume non-indigenous populations of *X. securis* in the Northeast Atlantic (Portugal). However, feeding rates in this region are lower compared to those measured on native gallo mussels, possibly favoring the establishment of *S. securis*. As stated above, one additional mussel known to be predated upon by green crabs is the ribbed mussel (*G. demissa*; Peterson et al., 2014), which is closely associated with saltmarsh species in the Atlantic and Pacific sides of North America (*S. alterniflorus* and *S. foliosa*, respectively). Predation on *G. demissa* becomes important at high predator densities (Peterson et al., 2014) on small mussels (Bertness and Grosholz, 1985; Watt et al., 2011), which reflect prey size preferences (e.g., Kamermans et al., 2009).

4 Influence on bed- and reef- forming oysters

Green crabs are eager consumers of various species of oysters (Table 1), in some cases in much higher proportions than co-occurring native predators (e.g., the rock crab; Miron et al., 2005; Schooler et al., 2022). In the northwest Atlantic, small Eastern oysters (*Crassostrea virginica*) face up to a 74% mortality in coastal sites colonized by high green crab densities (Poirier et al., 2017). Rates of 14–43% Eastern oyster mortality are more common, but those measured in crab exclusion cages are strikingly lower <1% (Poirier et al., 2017). In this region, the greatest impacts on Eastern oysters are due to large (adult) green crabs (Pickering et al., 2017), although these quickly diminish with an increase in oyster size, until a refuge size is reached at about 35 (Miron et al., 2005) or 40 mm SL (Pickering et al., 2017). In the Northeastern Pacific, a related species (the Pacific flat oyster, *Magallana gigas*, formerly known as *Crassostrea gigas*) is consumed by expanding populations of green crabs (Ruesink et al., 2005), at rates of nearly four oysters d^{-1} (Ens et al., 2021). Green crabs in this region have been shown to use a logistic (type II) functional response, which has the potential to be highly detrimental to oyster beds in the absence of alternative prey for the crabs (Lipcius and Hines, 1986). *Magallana gigas* is also present in the southwest Atlantic (Patagonian coast), along with populations of *Ostrea puelchana* (Malvé et al., 2024). Both oyster species are likely to be targeted by green crabs currently expanding in that region, but no studies have quantified these potential impacts yet. Three congeners of the latter species (*Ostrea lurida*, *O. edulis* and *O. conchaphila*) are also heavily consumed by green crabs in the Pacific northwest (Palacios and Ferraro, 2003; Snyder, 2004; Ruesink et al., 2005).

Although green crabs have been reported to consume oysters as well as mussels and clams indiscriminately and irrespective of size (Miron et al., 2005), most studies indicate that this predator shows a preference for mussels and clams over oysters (Mascaro and Seed, 2000; Behrens Yamada and Hunt, 2000; Pickering and Quijón, 2011). This is due in most cases to shell thickness (strength) differences, and therefore profitability (the net energy return beyond effort invested on shell breaking; Juanes, 1992). Profitability also explains the preference of green crabs for small to mid-size oysters and other bivalves (Tan and Beal, 2015; Campbell et al., 2019; Poirier et al., 2017; Matheson and Mckenzie, 2014; Murray et al., 2007; Richards et al., 1999; Mascaró and Seed, 2001). Moreover, Campbell et al. (2019) established that green crabs can consume any bivalves with a shell strength <140 Newtons. Unlike clams (see below), oysters do not have the option of digging into the sediment to reach refuge depths, thus refuge strategies rely on size, shell thickness, and in the case of oyster commercial growth operations (see Poirier and Quijón, 2022), on the physical association with other oysters.

5 Influence on habitat-modifier clams

While suspension and deposit feeding clams do not create physical reefs, they can form dense, widespread beds whereby their engineering activities alter the physical and chemical properties of the local habitat, and green crabs can exert high predation pressure on them (Table 1). The reported impacts of green crabs on clams vary widely and depend on habitat type (see Wong, 2013; Malyshev et al., 2020), even in well-studied species like softshell clams (*Mya arenaria*) and cockles (*Cerastoderma edule*). Early records of green crab impacts on the softshell clam in the northwest Atlantic (Maine, USA), date to the 1950s: Correlative studies linked the green crab with a 50% decline in the clam population over the course of four years (Glude, 1955; Welch, 1968). In the same region, Tan and Beal (2015) found that softshell clam survival was seven times higher when protected from green crabs, whereas further north in Atlantic Canada, green crabs targeted primarily small clams (<17 mm SL) and removed nearly 80% in the field (Floyd and Williams, 2004), about 80% in the laboratory (Malyshev et al., 2020), and 45–58% in hatchery tanks (Miron et al., 2005). In the latter two studies, consumption by native predators was much lower. In response to predation risk (green crab presence or odor cues), softshell clams have been shown to dig 12% (Tan and Beal, 2015) or 15% (Whitlow et al., 2003) deeper in the seafloor, and up to two times deeper in laboratory-prepared sediments (Flynn and Smee, 2010). This behavioral response increases clam survival at least three times relative to shallower sediment layers (Whitlow et al. (2003). The balthic clam (*Macoma balthica*) uses the same escape strategy and digs twice as deep into the sediment when exposed to green crabs (Griffiths and Richardson, 2006).

Another widespread ecosystem engineer, that is heavily preyed on by green crabs in the northeast Atlantic (Wales, UK) is the cockle (*Cerastoderma edule*), with feeding rates following recruitment events of six cockles d^{-1} (Mascaro and Seed, 2000) and 30 cockles d^{-1} (Sanchez-Salazar et al., 1987a) which roughly correspond to 2,360 cockles m^{-2} (Sanchez-Salazar et al., 1987b). Similarly, in the Dutch Wadden Sea, green crabs accounted for

26.1% of juvenile cockle mortality over one recruitment season (Jensen and Jensen, 1985). The preference of green crabs for small-sized softshell clams (Campbell et al., 2019) and cockles (Mascaró and Seed, 2001) is commonly reported. Green crab effects on other clams have also been observed, although not always quantified. Noticeable examples include two related species of *Nutricola* (*N. confusa* and *N. tantilla*), which are part of the diet of green crabs in California, USA (Grosholz, 2005; Grosholz et al., 2000), juveniles of *Katelysia scalarina* and *Fulvia tenuicostata* in Tasmania (Walton et al., 2002; Ross et al., 2004), juveniles of quahogs or hard clams (*Mercenaria mercenaria*) in New Jersey, USA (Quijón, 2024; Quijón et al., 2025), the California softshell clam (*Cryptomya californica*) in California, USA (Palacios and Ferraro, 2003), in addition to varnish clams (*Nuttallia obscurata*) and Manila clams (*Venerupis philippinarum*) both targeted by green crabs in British Columbia, Canada (Curtis et al., 2012). The continued spread of green crabs makes many additional clam species that are considered as ecosystem engineers likely targets for this predator (e.g., *Darina solenoides* and *Ardeamya petitiana*, in the Argentinian Patagonia; Malvé et al., 2024).

6 Common effects, limitations, and further studies

We found that a large majority of the studies reporting green crab effects (51 out of 53) describe a negative influence on ecosystem engineers. In the couple of instances in which neutral or positive effects were reported, these were driven by indirect interactions, in which green crabs targeted herbivores or bioturbator species that were detrimental to ecosystem engineers (e.g., Bertness and Coverdale, 2013). The strength of green crab effects was also variable and difficult to compare given the diverse approaches used and the type of ecosystem engineers studied (i.e., habitat-forming seagrasses and bivalves as opposed to non-habitat forming clam populations). Despite that, some consistent mechanisms became evident. Effects on seagrasses and other macrophytes were primarily mediated by burrowing and sediment disturbance (e.g., Garbary et al., 2014; Gonzalez et al., 2024a), and to a much lesser degree by seed or plant tissue consumption (e.g., Infantes et al., 2016). Likewise, interactions with mussels, oysters and clams were primarily direct (consumptive) effects (e.g., Miron et al., 2005; Campbell et al., 2019), although indirect (non-consumptive) effects were also present (e.g., Flynn and Smee, 2010). The latter was not surprising considering the complexity of oysters and mussels as habitat-forming species (e.g., Cordone et al., 2022), and the ability of clams to engage in escape strategies by e.g. burrowing into the sediment up to refugial depths (Tan and Beal, 2015). As a result, green crabs harm or disrupt (in some cases heavily) local populations of ecosystem engineers, beds or reefs, although there are no reports of losses of ecosystem engineers that could be attributed solely to green crabs. Despite this, green crabs' wide range of effects on such a diverse group of species clearly contributes to ongoing changes driven by other global stressors (Holland et al., 2021). The examination of their combined effects (additive or synergistic in nature; see Crain et al., 2008) clearly warrants further research.

This review is a first approach to the study of green crab effects on ecosystem engineers. So even though this group of key species is taxonomically much wider, we were not fully comprehensive and focused on a subset of the best-known coastal engineers: seagrass, macroalgae, mussels, oysters and clams. This entailed overlooking a series of other ecosystem engineers (e.g., herbivorous and carnivorous gastropods; Quinn et al., 2012; Wells et al., 2023) which play clearly important roles in their ecosystems. We also must point out two intrinsic practical limitations on the study of invasive species like the green crab. First, several populations of this species are currently expanding their ranges or invasion (e.g., Malvé et al., 2024), and therefore, an unknown number of new interactions with local ecosystem engineers may be taking place but have yet to be documented. Second, the limited number of neutral or positive interactions reported here could be partially related to a lack of reporting of this type of result. The finding of "negative impacts" often gathers more attention, as discussed before in the context of other invasive species (e.g., Quijón et al., 2017). However, it applies to the reporting of ecological interactions in general (Weintraub, 2016), where neutral or positive effects have been less consistently published, despite their recognized importance (Bruno et al., 2003). Moreover, among the negative results that are published, there is also a bias towards reporting the outcome of trophic interactions, disregarding non-trophic interactions (including competition), which are often more difficult to quantify or remain simply overlooked (Kéfi et al., 2012). While a large majority of the effects described in this Minireview are direct (consumptive or not), the examination of indirect effects is gaining growing attention. In fact, under a different context, green crabs have already become a useful model species for the study of trait- or behaviorally mediated indirect interactions (Quinn et al., 2012; Vriends et al., 2024). So, it is reasonable to suggest that for each direct effect reported here, there are likely several indirect interactions that may need to be examined, and that are likely to contribute to the function and services provided by these species and their coastal ecosystems.

Author contributions

WB: Writing – original draft, Writing – review & editing, Investigation, Formal Analysis, Data curation. PR-B: Data curation, Investigation, Writing – original draft, Formal Analysis, Writing – review & editing. PQ: Methodology, Data curation, Formal Analysis, Conceptualization, Supervision, Investigation, Writing – original draft, Funding acquisition, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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