*Ecology*

*Article*

*Title:* Consumer- and seaweed-specific impacts of invasion-mediated changes to detrital subsidies on rocky shores

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**Abstract**

Detrital subsidies such as leaf litter, animal carcasses, and marine wrack can profoundly shape recipient habitats by influencing resiliency and productivity. Species introductions and climate-driven range shifts alter the quantity and quality of these subsidies in donor habitats, thereby potentially influencing recipient communities. Such impacts might be particularly important when detrital shifts alter detritivore feeding and performance. Attempts to identify a general theory predicting the consequences of invasive species on detritivores have been challenging, in part because most theories have been based on the study of microbes or consumers of living prey. Further, two recent meta-analyses disagree about the impacts of invasive plants on detritivore populations. Here, we examined the potential impact of a human-mediated shift in macroalgal detrital subsidy from native kelp, *Macrocystis pyrifera,* to invasive Devilweed, *Sargassum horneri,* on recipient rocky shores, with an emphasis on exploring species-specific impacts. We assessed consumer performance on single species diets or on a mixture in no-choice assays, and we assessed feeding preference in choice assays. Additionally, we examined the impacts of this shift on grazing of native benthic seaweeds by an intertidal consumer assemblage. Replacing Kelp with invasive Devilweed had consumer-specific impacts on performance – suppressing growth of Red abalone (*Haliotis rufescens*) but enhancing growth of Black turban snails (*Tegula funebralis*). The effect of mixed diets on consumer growth also displayed consumer-specificity. Also, replacing native Kelp with invasive Devilweed increased grazing of native benthic seaweeds by a realistic detritivore assemblage, but only on the habitat-forming brown seaweed, *Silvetia compressa.* Thus, invasion-mediated changes in detrital wrack composition had consumer- and seaweed-specific impacts. Such species-specificity could underlie disagreements about the impact of species invasions on detritivore populations and could impede our ability to identify a general theory about how species invasions will impact recipient communities via detrital pathways.

**Introduction**

Ecosystems are connected through fluxes of organisms, energy, materials, and information from donor systems that can alter species abundances and interactions in recipient food webs (Polis and Hurd 1996, Nakano et al. 1999, Ostfeld and Keesing 2000, Talley et al. 2006, Gratton et al. 2008, Greig et al. 2012). For example, detrital subsidies can modify key ecological processes (e.g., competition and predation; Yang 2006, Piovia-Scott et al. 2011, Kenny et al. 2017), generate trophic cascades (Polis and Hurd 1996, Polis et al. 1997, Nakano et al. 1999, Jefferies 2000), and stabilize food webs (Takimoto et al. 2002). Changes to these donor communities via species introductions and range shifts are likely to change detrital subsidies and the habitats that rely on them (Zhang et al. 2019).

Detrital food webs may better resist perturbations because of donor control and trophic diversity in recipient habitats (Odum 1969, Neutel et al. 1994, Moore et al. 2004). Changes in community taxa composition of donor habitats arising from species introductions and climate-mediated range shifts may lead to changes in detrital subsidies that could destabilize these recipient ecosystems (Collins and Baxter 2014). For example, species shifts in donor systems may change the quantity and quality of detrital supply leading to consequences on populations of recipient primary consumers (i.e., detritivores), and the species they interact with (Yang 2006). Identifying a general theory about how species invasions affect recipient detritivores and their communities would improve our ability to predict future environmental change (Yang et al. 2010). Unfortunately, there is a lack of consensus about how species invasions will impact detritivores, from both theoretical and meta-analytical perspectives. Clearly, there is a need to better understand how human-mediated changes to donor ecosystems influence recipient detritivores and their communities.

Such human-related impacts are likely to be seen and mediated by detritivores in recipient ecosystems because they are ubiquitous (Ostfeld and Keesing 2000, Yang 2006) and early responders to subsidies (Moore et al. 2004, Levin et al. 2006). These detrital shifts could impact detritivores in at least two ways. First, compositional shifts in donor systems could modify consumer performance. For example, a mixed diet of low and high quality detritus can stimulate grazing but reduce lipid content of consumers (Larrañaga et al. 2020). The direction of these impacts will be influenced by the relative quality of the subsidy before and after these shifts. Second, compositional shifts in donor systems could shift feeding to/from resident resources in recipient habitats (Duggins et al. 1989, Bustamante et al. 1995, Parker and Hay 2005). In particular, if novel subsidies are less preferred by recipient consumers, the arrival of novel subsidies may shift consumption onto resident resources/species. Both altered consumer performance and preference could change the strength of interactions between recipient consumers and the species they interact with (Polis and Strong 1996).

Predicting detritivore response to novel resources is challenging given that 1) most theories have focused on predicting responses of native decomposers (i.e., microbes) and consumers to novel resources and 2) these theories disagree with each other. For example, microbial studies generated the Home-Field Advantage Hypothesis (HFA; Bocock et al. 1960, Gholz et al. 2000, Pugnaire et al. 2023) which predicts that microbes will underutilize novel resources, primarily because of a lack of evolutionary history. In contrast, the Prey Naiveté Hypothesis (Cox and Murray 2006, Carthey and Banks 2014, Papacostas and Freestone 2019) predicts that consumers will prefer novel resources because a lack of evolutionary history limits the ability of prey to defend against novel consumers.

Further, two meta-analyses have been unable to resolve these discrepancies. In the first, invasive plants had weakly negative or neutral impacts on detritivore abundance in three ecosystems (wetlands, woodlands, and grasslands; McCary et al. 2016). In contrast, a second meta-analysis found that leaf litter from invasive plants increased detritivore abundance in recipient habitats (Zhang et al. 2019). The uncertainty about invasion impacts on decomposers extends to consumers of seaweed detritus (i.e., detritivores). For example, one meta-analysis found no overall effect of seaweed invasions on density, biomass, and growth of consumer species (Maggi et al. 2015). Another meta-analysis found that arthropods, but not mollusks, had reduced preference for non-native red seaweeds (Swantje et al. 2017).

We tested the impacts of a seaweed invasion on growth and preference of rocky intertidal detritivores in the Southern California Bight. The native wrack in this system is largely composed of California Giant Kelp, *Macrocystis pyrifera* (Hereafter, “Kelp”; Hayes 1974, Dugan et al. 2003, VanBlaricom and Kenner 2020). Kelp is a nutritious, high preference food for various organisms including abalone (*Haliotis cracherodii*) and Black turban snails (*Tegula funebralis*; Leighton and Boolootian 1963). Kelp forests, especially along leeward shores of the Channel Islands, have been invaded by *Sargassum horneri* (Hereafter, “Devilweed”), since 2003 (Marks et al. 2015, Kenner and Tomoleoni 2020). As such, we expect that wrack will increasingly include Devilweed as donor Kelp forests are invaded. Thus, it is important to understand how this novel wrack subsidy will impact recipient detritivores and their communities.

To test how shifts towards Devilweed impact consumer performance, we fed snails (Black abalone, Black turban snails) Kelp, Devilweed,or a mixture of both, and measured soft tissue growth and behavior (self-righting times). To test if Devilweed changed feeding, we offered several rocky intertidal wrack consumers a choice between native Kelp and invasive Devilweed. Lastly, we offered an assemblage of wrack consumers foods made from native benthic seaweeds and either Kelp or Devilweed to determine if replacement of Kelp with Devilweed shifts grazing onto native seaweeds.

**Methods**

*Study organisms*

Striped shore crabs (*Pachygrapsus crassipes*), Blue banded hermit crabs (*Pagurus samuelis*), Black turban snails (*Tegula funebralis*)Black abalone (*Haliotis cracherodii*) are, or were, abundant seaweed consumers and wrack detritivores along rocky shores of southern California (Morris et al. 1980, Barry and Ehret 1993, Aquilino et al. 2012). For example, Black abalone consume benthic seaweeds and are subsidized by Kelp detritus (VanBlaricom and Kenner 2020). Additionally, Black abalone were historically important seaweed consumers prior to declines related to disease and overharvesting (VanBlaricom 1993, Altstatt et al. 1996, Raimondi et al. 2002). Although Black abalone densities have started to recover on some of the Channel Islands, densities remain at least an order of magnitude below historic levels (Raimondi et al. 2002, Miner et al. 2006). We included all of these species in this study as they represent a typical assemblage of rocky intertidal detritivores in areas receiving detrital inputs of the invasive Devilweed. Furthermore, we included Red abalone (*Haliotis rufescens*) – a local consumer of detrital kelp and kelp detritus in one of the assays (see below).

*Devilweed prevalence surveys*

To confirm that Devilweed is present and to determine the relative contribution of Devilweed to wrack, we surveyed large wrack piles deposited on two beaches at two sites on San Nicolas Island in January 2020 (33.27335° N, 119.57629° W, 33.28310° N, 119.53557° W) and measured the proportion of the wrack pile surface area Devilweed represented. We adopted this qualitative metric of because our time at these sites was limited and surveying pile and Devilweed surface area (as opposed to total biomass) allowed us to quickly survey a large amount of wrack. At each site, we selected the first 20 large (>1 m) wrack piles encountered along a haphazardly placed 50 m transect. We measured the longest length and width of the pile each wrack pile and Devilweed individuals on the surface of the piles. We calculated the area of Devilweed and piles using the equation for an ellipse (*A=πab*), where “a” and “b” are one half the length and width. For each pile, we calculated the sum area of all Devilweed individuals and divided by the area of the pile to estimate the proportion of wrack that consisted of Devilweed. Using this method, the relative contribution of Devilweed to wrack for a large pile could be estimated in minutes as opposed to hours.

*Performance Assays*

To understand how shifting wrack composition affects the performance of rocky shore detritivores, we measured the growth of juveniles of two wrack consumer species [Turban snails and Red abalone (*Haliotis rufescens*)] on diets of Kelp, Devilweed, or an equal mixture of the two. We used Red abalone as a proxy for Black abalone because of logistical challenges of conducting research with endangered Black abalone. For example, most captive Black abalone are mature adults that might not respond to diet changes because of their large size and slow growth. We justify using a congener as a proxy species because both abalone species 1) consume brown seaweeds (Leighton and Boolootian 1963, Winter and Estes 1992, Nelson et al. 2002), 2) have similar growth rates (Ault 2009), and 3) share some overlap in habitat (Díaz et al. 2000, Neuman et al. 2010). Because Devilweed reduces Kelp abundance in subtidal habitats but does not extirpate it across short time scales (Sullaway and Edwards 2020), the mixture treatment is the most ecologically realistic.

We collected Black turban snails (shell length = 6-10 mm) from Sunset Cliffs Natural Park (SCNP, 32.71972° N, -117.25725° W; SC permit #11084). We used lab-reared, juvenile Red abalone from a single cohort (May 2017) provided by NOAA Fisheries Southwest Fisheries Science Center (hereafter, “SFSC”; shell length = 45-60 mm). All organisms were transported to San Diego State University’s Coastal and Marine Institute Laboratory (CMIL) and placed in plastic containers (190 x 160 x 110 mm) with mesh (2 mm openings) covers. The performance assay began March 5, 2020. At this time, all containers were completely submerged in tanks with 14°C recirculating, aerated water with a pH of 7.75. Due to facility closures caused by the COVID-19 pandemic, we transported all organisms to a temporary recirculating seawater system setup on March 19, 2020. The experiment continued at this location until the termination on April 17, 2020 (i.e., six weeks after the start). Here, the water temperature was maintained at 15°C. Because artificial seawater was used at this facility, the pH was more basic (range from 8.4-8.7). We monitored ammonia and ammonium daily during this period and used these data to determine dates of partial water replacements (conducted on March 28 and April 1, 2020; 30% and 80% volume replacement, respectively).

Animals were offered one of four diets (Kelp*,* Devilweed*,* a ~1:1 mixture of Kelp and Devilweed, or starvation; n=20). Seaweed was offered *ad libitum*. We included the entire thallus (i.e., stipes, blades, and pneumatocysts) to account for tissue-specificity in performance/ preference. We assessed diet-related impacts on performance by calculating the change in dry soft tissue mass of the animals. Final dry tissue mass was calculated by weighing the tissue after dissecting it from the shell, freezing the tissue at -80°C, and freeze-drying it for 24 hours. To estimate initial dry tissue mass, we subsampled 20 animals from each species at the start of the experiment and calculated a regression of shell length to dry soft tissue mass. Because the relationship between maximum shell length and dry tissue mass was strong and linear for both Turban snails (R2 = 0.89, F(1,18)=148.20, p<0.001)and Red abalone(R2 = 0.89, F(1,18)=160.71, p<0.001)*,* we used these regressions to estimate starting soft tissue biomass, non-lethally.

In addition to growth, we assessed how diet impacted abalone self-righting times (n=20). Because abalone are extremely vulnerable to predators when their ventral tissues are exposed, such assays can inform environmental influence on predator-prey interactions (e.g., slow righting time suggests an increased vulnerability to predators; Baldwin et al. 2007, Lachambre et al. 2017). During righting tests, abalone were placed, dorsal side down, in 15°C seawater. We measured the time it took Red abalone to flip over so that the dorsal side of their shell faced up. These tests were conducted until abalone corrected their orientation or 4 minutes passed. We conducted these assays at the start and end of the performance assay.

*Preference Assays*

To understand how shifting wrack composition affects feeding preferences, we offered rocky intertidal consumers a choice of Kelp and Devilweed. Kelp was collected as fresh wrack from Ocean Beach (32.75380° N, -117.25284° W) and benthic Devilweed was collected by snorkel from the jetty at Mission Bay in San Diego (32.76158° N, -117.24521° W). Non-abalone animals were collected from SCNP and transported to CMIL and held in flow-through seawater. Adult Black abalone (held under ESA Permit #19571-2R) were held in chilled, flow-through seawater at SFSC. Separate feeding choice assays were conducted with each of the four primary consumer species (Shore crabs, Hermit crabs, Turban snails, and Black abalone). This assay was conducted with captive Black abalone because choice assays were non-lethal to animals, and we focused on preference rather than growth.

To standardize hunger level and to motivate our animals to feed, all animals were fed *Ulva spp.* for three days and then starved for two days prior to the preference assays. All feeding assays were conducted in June 2019, with the exception of Black abalone (August 2019). We offered 3 Turban snails (n=14), 3 hermit crabs (n=14), or a single shore crab (n=15) a choice of Devilweed and Kelp in plastic containers (190 x 160 x 110 mm). Container walls included six 35mm holes lined with mesh (2 mm openings) to improve water exchange. Black abalone were housed individually in 280 x 230 x 180 mm mesh-lined (5 mm openings), PVC-framed cages with a Plexiglas® floor. We offered animals an equivalent biomass of Kelpand Devilweed that had been anchoredwith binder clips (mean ± SE: 7.5 ± 0.4 g for Hermit crabs, 7.5 ± 0.3 g for Shore crabs, 6.5 ± 0.3 g for Turban snails, 21 ± 0.4 g for Black abalone). All replicates were paired with no-consumer controls to account for changes in mass unrelated to consumption (Dolecal and Long 2013). Individual replicates were stopped when either ~3/4 of either seaweed was consumed, or six days had passed. All remaining seaweed and seaweed fragments were blotted dry and weighed. We adjusted for autogenic growth using the equation Ti (Cf /Ci) – Tf, where Ti and Tf represent the seaweed masses of the experimental treatments and Cf and Ci represent the seaweed masses in control treatments before (i) and after (f) the assay (Sotka and Hay 2002, Dolecal and Long 2013).

*Native Benthic Seaweed Assay*

To understand if shifts in wrack composition cause intertidal detritivores to change consumption of native benthic seaweeds, we offered an assemblage of intertidal consumers a choice of native benthic seaweeds in the presence of either Kelp or Devilweed. To create realistic assemblages of wrack consumers, we surveyed the abundance of rocky intertidal detritivorous invertebrates at SCNP in August 2019. We recorded all snails and crabs found within a 0.50 x 0.50 m quadrat that was flipped end over end and parallel to shore (n=10). This procedure was repeated in the low, mid, and high intertidal zones. Although this technique accurately sampled Turban snails and Hermit crabs, it did not sample mobile Shore crabs. To determine a realistic number of animals to add to our experiments, we multiplied field densities by the floor area of the plastic containers used in the assay. This resulted in the addition of three Turban snails and three hermit crabs to each replicate. Because mobile Shore crab densities are difficult to measure, we added a single individual to each replicate. We recognize this approach creates an assemblage with relatively more abundant Shore crabs and therefore might overestimate their role.

We offered animals a choice between three artificial foods (see below) made from native benthic seaweeds (*Ulva spp., Silvetia compressa,* and *Centroceras clavulatum*),and a wrack seaweed (either Devilweed or Kelp). Because we were unable to collect all of our seaweeds at the same time and we were concerned about changes to palatability while maintaining seaweeds in the lab, we fed animals artificial, agar-based foods made from freeze-dried, homogenized seaweeds. We note that this process maintains chemical traits while removing morphological traits that may also impact palatability. Following methods adopted from previous studies (Bolser and Hay 1996, Thornber et al. 2008, Dolecal and Long 2013), we mixed homogenized freeze-dried seaweed (5.6% w:v) into a heated agar solution (2.0% w:v). This mixture was poured into polypropylene petri dishes (50 mm) and allowed to cool for ~30 min. The agar-foods were blotted dry, weighed, and offered to the consumer assemblage.

We secured the petri dishes containing agar-based foods in random order along the length of containers with mesh covered tops (330 x 190 x 108 mm container with 2 mm mesh opening; n=20 and n=10, for grazing treatments and controls, respectively). Because our previous experiments found negligible autogenic growth in agar-based foods not exposed to consumers, we reduced the number of controls to one control for every two experimental replicates. These assays began simultaneously on November 11, 2019. After ~36 hours, all artificial foods were removed, blotted dry, and reweighed. We calculated changes in mass using the previous formula.

**Statistical Analyses**

To test the effect of all diet treatments including seaweeds (i.e., all but “starved” treatment) on final dry tissue mass, we used an ANOVA with detritivore species and diets as main effects, and their interaction. We tested the effect of diet treatment on individual species (Red abalone and Black turban snails) using Linear Mixed Effects Models (LMEM) with diet as the main effect and estimated initial dry masses as a random effect to account for differences in starting mass. Starvation treatments were used for reference but were not included in the model. To test the effect of diet on changes in self-righting times of abalone, we used a LMEM with self-righting time difference (before treatment – after treatment) with diet as the main factor and replicate number as a random factor to account for within-subject variability and repeated measures.

For preference assays, we compared changes in seaweed mass, corrected for autogenic growth, using Paired t-tests for each consumer species (Devilweed vs. Kelp). For the native benthic seaweed assay, we compared overall grazing (native benthic seaweeds + wrack) using a paired t-test and tested for interactions using ANOVA. We used a LMEM to investigate the effects of wrack species and native benthic seaweeds on consumption. The model included wrack treatment (native or invasive) and native benthic seaweed species (*Ulva spp., Silvetia compressa,* or *Centroceras clavulatum*) as fixed factors, and their interaction. We also included a random factor for replicate number because seaweed choice was not independent within replicates. All statistical analyses and visualizations were conducted using the R Programming Language (R Core Team, 2023). Linear and mixed effect models were conducted using the R base and ‘nlme’ packages. Necessary assumptions were met for statistical analyses and post-hoc tests were conducted as needed.

**Results**

*Devilweed prevalence survey*

Wrack piles on San Nicolas Island were dominated by Giant kelp (*M. pyrifera*), but also included Feather boa kelp (*Egregia menzisii*), Surf grass (*Phyllospadix spp.*), and Devilweed (*S. horneri*). Devilweed was present on 28% of wrack piles (11 of 39 piles), where it constituted 3 ± 1% of the surface cover of those piles.

*Performance*

Diet influenced detritivore tissue growth (ANOVA: F3,152=15.773, p <0.001). However, detritivore species and diet interacted to influence detritivore tissue growth (F3,152=15.238, p<0.001), thus, we analyzed detritivore species separately to understand how each diet impacted growth. After controlling for estimated initial dry tissue mass, Devilweed diet influenced Red abalone and Black turban snail growth, but in opposing directions. Replacing Kelp with Devilweed suppressed Red abalone tissue mass by 25% (E= -0.6144, SE= 0.1903 t=-3.228 p = 0.002), but increased Turban snail tissue mass by 31% (E=0.0064, SE= 0.0028 t=2.314 p = 0.024). Interestingly, the effect of the mixed diet treatment (i.e., offering consumers Kelp and Devilweed in a 1:1 ratio) was also consumer-specific. For Red abalone, a mixed diet had an intermediate effect on tissue mass compared to animals in the no-choice treatments fed one of the species (i.e., Kelp or Devilweed only diets). In contrast, Turban snails fed mixed diets grew similar to Devilweed-only treatments and better than Kelp-only treatments (Fig.1). Because no choice was ever fully consumed, any mixed-diet effect could not be attributed simply to the loss of a higher quality food. Consistent with Devilweed suppressing Red abalone growth, there was a trend for Devilweed to increase the amount of time it took Red abalone to right themselves (Fig. 2). However, after controlling for differences in initial righting time, this effect was not statistically significant (F2,57=2.091, p=0.133).

*Preference*

Detritivores displayed species-specific feeding preferences for wrack seaweeds. Black abalone and Turban snails consumed 111% and 158% more Kelp than Devilweed (Fig. 3a and 3b: t=4.5053, p<0.001 and t= 5.7152, p<0.001, respectively). Although these two detritivores preferred Kelp, both species consumed some Devilweed (One sample t-test, t=4.782, p<0.001 and t=2.105, p=0.055, for Black abalone and Turban snails, respectively). Shore crabs fed similarly on the two wrack species (Fig. 3c, t=0.0739, p=0.9422). In contrast, Hermit crabs preferred Devilweed (Fig. 3d, t=-3.7593, p=0.002). This apparent preference was driven, at least in part, by a complete avoidance of Kelp (One sample t-test, t=0.147, p=0.89).

*Native Benthic Seaweed Assay*

In the presence of foods made from native benthic seaweeds, replacing native wrack species (Devilweed for native Kelp) reduced grazing on wrack by 134% (t=7.5289, p<0.001). This reduction was not associated with a change in overall grazing rates (i.e., the sum of grazing on wrack and native benthic seaweeds; 5.97 ± 0.22 g and 5.22 ± 0.20 g for native and invasive wrack type, respectively; t-test, t = -1.261 p = 0.215), suggesting consumers shifted grazing onto native benthic seaweeds in the presence of Devilweed wrack. This suggestion was confirmed by the discovery that feeding on artificial foods made from native benthic seaweeds depended on wrack type (interaction: ANOVA, F3,152=17.116, p<0.001). Including Devilweed wrack increased grazing on *Silvetia* (M=0.75, SE=0.28, p=0.0265), but did not affect feeding on the two other benthic native seaweed (p>0.05; Fig. 4).

**Discussion**

Invasion mediated changes in wrack composition had both consumer- and seaweed-specific impacts.Replacing Kelp with invasive Devilweed had species-specific performance impacts that suppressed Red abalone growth but enhanced Black turban snail growth. This is consistent with recent findings that suggest a diet of Devilweed negatively affects growth and survival of Red abalone (Bauer et al. 2023). The effect of mixed diets on consumer growth also displayed consumer-specificity (Red abalone displayed intermediate growth on mixed diets whereas Turban snail growth on mixed diets was high and indistinguishable from Devilweed). Also, replacing Kelp with Devilweed increased grazing of native benthic seaweeds by a realistic detritivore assemblage, but only on the brown seaweed, *Silvetia compressa*.

Detritivore-specific performance impacts of an invasive seaweed on different intertidal snails are consistent with detritivore-specific population-level impacts of invasive plants. Such specificity has been observed within several taxonomic levels including Phylum and Superorder. For example, leaf litter detritus from plots invaded by an annual invasive *Impatiens glandulifera*  had higher densities of leaf litter dwelling Acari (Phylum Arthropoda, Subphylum Chelicerata) but did not show differences in springtail densities (Phylum Arthropoda, Subphylum Hexapoda) relative to leaf litter from uninvaded plots (Rusterholz et al. 2014). Similarly, vegetated plots containing invasive giant knotweed (*Reynoutria* spp.) had reduced densities of detritivorous isopods (Superorder Peracarida, Order Isopoda) but similar densities of detritivorous amphipods (Superorder Peracarida, Order Amphipoda), relative to uninvaded plots (Kappes et al. 2007). The detritivore-specific impacts on growth we observed indicates that we observed variation at a more specific taxonomic level (i.e., within the Subclass Vetigrastropoda).

Detritus from invasive plants could have within-Subclass, detritivore-specific impacts in the presence of native detritus via several pathways. First, detritivores may differ in their attraction to or preference for detritus from invasive plants (Mews et al. 2006). However, because both Black abalone and Turban snails strongly preferred Kelp in choice assays, the differing impact of a mixed diet of detrital Kelp and Devilweed on their performance was likely unrelated to behavioral differences that resulted in consumption of proportionally different amounts of invasive seaweed. Second, detritivores may be differentially impacted by how detritus from invasive plants modifies abiotic conditions (Rodil et al. 2008). For example, invasive seaweeds may release allelopathic chemicals into seawater or may modify abiotic factors like pH or oxygen (Lapointe et al. 2018, Bauer et al. 2023). However, this shouldn’t lead to detritivore specificity as they would likely have a general impact on both species. Finally, detritivores may differ in post-ingestive processes that influence their ability to assimilate or detoxify detritus from invasive plants (Frost et al. 2005). This appears likely in our system because Devilweed-only diets suppressed Red abalone but enhanced Turban snail growth. Interestingly, because both species preferred Kelp, this apparent post-ingestion impact in mixed diet treatments was associated with a relatively small amount of Devilweed. This suggests that a) Devilweed positively impacted Turban snails (e.g., it provided a key limiting nutrient for Turban snails), b) Devilweed negatively impacted Red abalone (e.g., it was toxic to Red abalone), or both.

In addition to direct effects on detritivore performance, shifts in detrital subsidies may shape recipient primary producer communities indirectly (David et al. 2017). For example, replacing detritus from Kelp to Devilweed increased feeding on foods made from native seaweeds in intertidal habitats, but only on the most preferred seaweed (i.e., *Silvetia compressa*). We hypothesize that when detrital shifts involve a reduction in detritus palatability like this, consumers in recipient habitats will increase consumption of more palatable living, native plants/seaweeds. Because the relative palatability of non-native and native seaweeds is variable, for example, arthropods feeding on red seaweeds display a preference for native species, but mollusks do not (Swantje et al. 2017), it may continue to be challenging to predict the impacts of detrital shifts on recipient communities. Further, because these plants or seaweeds also differ in their palatability, detrital shifts may have plant or seaweed-specific impacts.

Such impacts may be particularly common for rocky shore consumers that directly and indirectly affect community dynamics and structure by influencing seaweed abundance, diversity, and productivity (Sousa 1984, Aquilino and Stachowicz 2012, Rhoades et al. 2018). Therefore, changing wrack that shifts consumption onto habitat-forming species like *S. compressa* (Sapper and Murray 2003, Whitaker et al. 2010, Graham et al. 2018), may have additional community level impacts. For example, *S. compressa* understories inhabited by diverse algae, sessile and mobile invertebrate communities that are protected from desiccation during tidal emersion will suffer from *Silvetia* reductions (Sapper and Murray 2003, Truong et al. in press).

Although our native benthic seaweed assay including consumers with a preference for Kelp (Turban snails), a preference for Devilweed (Hermit crabs), or a lack of a preference for these two wrack species (Striped shore crabs), replacing Kelp with Devilweed reduced grazing on wrack and shifted grazing *Silvetia compressa* for this consumer assemblage. This shift could be explained simply by Turban snails shifting onto native benthic seaweeds when they were offered a less preferred wrack species. Additionally, interactions with heterospecific consumers may have modified consumption in this assay. The complexity of these interactions will likely make it difficult to predict the impacts of Devilweed and other non-native species, on invaded, naïve ecosystems and the communities they subsidize.

Kelp forests are in decline in many regions globally, being replaced by non-native species that may not serve the same ecological roles (Layton et al. 2020). For example, Australian kelp forests with the habitat-building kelp, *Ecklonia radiata*, have been replaced by turf algae, changing habitat complexity, reducing productivity, and detritus (Layton et al. 2020). Even if Devilweed does not completely replace Kelp, it is expected to continue to invade Kelp forests, and declines in kelp cover may facilitate this invasion (Cruz-Trejo et al. 2015, Marks et al. 2020). Moreover, it has been suggested that although Devilweed in California has a reduced thermal tolerance compared to populations in its native habitat (the Seto Inland Sea of Japan), current and future ocean temperatures are not likely to stop its northward and southward invasion success (Small and Edwards 2021). Subsequently, Devilweed will continue to change wrack species composition on the coast. In addition to encountering Devilweed as detritus, intertidal consumers are increasingly co-occurring with living, benthic Devilweed. For instance, Devilweed has been found in lower intertidal zones in Todos Santos Bay, Baja California, Mexico (Cruz-Trejo et al. 2015) and more recently in high to low intertidal pools in San Clemente and San Nicolas Islands (Pollard et al., in prep). This is of special concern in areas inhabited by recovering Black abalone populations such as San Nicolas Island.

Considerable progress has been made in the study of resource subsidies and consumer interactions; however, the diversity and extraordinary nature of species introductions and climate-mediated range shifts continue to pose a challenge to identifying and understanding general patterns (Yang et al. 2010). Consumer-specific impacts may prevent the identification of a single, unifying theory about how plant invasions influence detritivores and may suggest limited usefulness of HFA and Prey Naiveté. Such specificity could lead to contrasting results within and between studies. For example, two meta-analyses were unable to agree about the impact of invasive plants on detritivores, with one study finding positive and one study finding negative effects. Our results did not find strong evidence to support either side, rather, we highlight the importance of species-specific responses to novel subsidies and potential indirect effects on recipient communities.

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**Conflict of interest statement**

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**Figure 1**

Final dry tissue mass of Red abalone (A) and Black turban snails (B) starved or fed Kelp, Devilweed, or mixed diets for 42 days. The dotted line separates the starved treatment that was not included in the analysis. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier ranges. Lower case letters above boxes denote significance. The black dots are outliers. Illustrations by R. DeSantiago.

**Figure 2**

Initial and final righting times (sec) for Red abalone starved, or fed Kelp, Devilweed or mixed diets. The dotted line separates the starved treatment as it was not included in the analysis. Bars represent the mean righting time for individuals in that treatment and lines represent standard error.

**Figure 3**

Total detrital seaweed biomass consumed by Black abalone (A), Black turban snails (B), Striped shore crabs (C), and Blue banded hermit crabs (D) in choice feeding experiments. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier values. The black dots are outliers, and the asterisks denote statistical significance (p<0.05). Illustrations by R. DeSantiago

**Figure 4**

Total mass of artificial foods made from detritus (either Kelp or Devilweed) and *C. clavulatum, Ulva spp.,* and *S. compressa* consumed by assemblage of consumers in native (gray) and invasive (white) wrack treatments. The lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non outlier values. The black dots are outliers.

Figure 1

A diagram of a butterfly

Description automatically generated

Figure 2

A graph of different sizes of objects

Description automatically generated with medium confidence

Figure 3

A diagram of seaweed consumption

Description automatically generated

Figure 4

A graph showing the different stages of treatment

Description automatically generated with medium confidence