Title: Invasion-mediated changes to detrital subsidies impact recipient intertidal invertebrate growth and feeding preferences

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**Abstract**

Habitat subsidies, such as nutrients and organic materials, play a crucial role in shaping recipient ecosystems. Human activities, including species introductions and climate-driven range shifts, are altering the quantity and quality of these subsidies. For instance, changes in the composition of donor communities driven by biological invasions can affect detrital subsidies across ecotones. However, there is no clear consensus about the impact of novel subsidies on primary producers and consumers in recipient communities. Here, we conducted lab feeding assays to assess the preference and performance of rocky shore wrack consumers when fed a diet that includes the invasive devilweed (*Sargassum horneri*). Additionally, we examined the potential impacts this invasive may have on native benthic seaweeds. We fed two species of gastropods a diet that included kelp (*Macrocystis pyrifera*), devilweed, or a mix of both, and their growth and behavior were measured after 42 days. We found that Red abalone (*Haliotis rufescens*) exhibited reduced growth on diets that included devilweed, while Black turban snails (*Tegula funebralis*) exhibited improved growth on devilweed and mixed diets. Further, we found that diet generally increased the righting times of abalone, although statistical significance between treatments was not detected. To determine preference between native and invasive seaweeds, we offered Black abalone (*Haliotis cracherodii*), Black turban snails, Striped shore crabs (*Pachygrapsus crassipes*), and Blue banded hermit crabs (*Pagurus samuelis*) a choice between native kelp and invasive devilweed tissue. Food preference was species-specific. Some consumers favored kelp (abalone and turban snails), one consumer favored devilweed (hermit crabs), and one consumer displaying no preference (shore crabs). Finally, we conducted a cafeteria-style choice assay where an assemblage of these consumers was given agar-based foods made from Sea lettuce (*Ulva spp.*)*,* brown rockweed (*Silvetia compressa*)*,* and a red seaweed (*Centroceras clavulatum*) with either kelp or devilweed (i.e., native and invasive, respectively). Although total consumption did not differ between treatments, grazing shifted onto familiar native benthic seaweeds, specifically brown rockweed, when offered with invasive devilweed. Overall, our findings suggest that changes in wrack composition, including the presence of devilweed, may disproportionally affect certain consumers and native seaweeds. In our study, black abalone and brown rockweed, two organisms that have suffered precipitous declines and low recovery, were particularly impacted.

*Keywords: Habitat subsidies, detritivores, donor-controlled system*

**Introduction**

Detrital food webs may better resist perturbations because of donor control and trophic diversity in recipient habitats (Odum 1969), Neutel et al. 1994). Compositional changes to donor ecosystems arising from species introductions and climate-mediated range shifts may lead to changes in detrital subsidies, and therefore destabilize recipient ecosystems. For example, changes in the species composition of donor systems may change the quantity and quality of detrital supply leading to consequences on recipient primary consumers (i.e., detritivores) and the species they interact with. Unfortunately, meta-analyses focused on the consequence of invasive plants disagree about the direction of these impacts – with one study reporting negative to neutral effects on detritivores (McCary et al. 2016) and another reporting positive effects on detritivores (Zhang et al. 2019). Furthermore, ecological theory (e.g., Home Field Advantage Hypothesis; Gholz et al. 2000) predicts that decomposers are specialized in decomposing organic matter that they frequently encounter, suggesting a neutral or negative response to novel subsidies. Clearly, there is a need to better understand how human-mediated changes to donor ecosystems influence recipient detritivores and their communities.

Ecosystems are connected through fluxes of material and energy from donor systems that can alter species abundances and interactions in recipient food webs (Polis and Hurd 1996, Nakano et al. 1999, Gratton et al. 2008, Greig et al. 2012). For example, detrital subsidies can modify key ecological processes (e.g. competition and predation; (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 (Ruiz et al. 1997, Rilov and Crooks 2009) are likely to change the quantity and quality of detrital subsidies (Zhang et al. 2019). Thus, changes in donor systems are likely to have direct impacts on subsidy-dependent communities.

Such impacts are likely to be seen and mediated by primary consumers (e.g., detritivores) in recipient ecosystems because they are the first responders to these novel subsidies. These detrital shifts could impact consumers in at least two ways. First, compositional shifts in donor systems lead to shifts in detritus that modify consumer performance. The direction of these impacts will at least depend on the relative quality of the donor system species before and after these changes occur. Second, compositional shifts in donor systems could behaviorally shift feeding to/from recipient resources. For example, if novel subsidies are less preferred by recipient consumers, the arrival of novel subsidies may shift consumption onto recipient system resources/species. Both altered consumer performance and preference could change the strength of interactions between recipient consumers and the species they interact with.

Unfortunately, we lack a clear understanding about how novel subsidies will impact detritivores despite two important meta-analyses related to this topic. 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 soil detritivore abundance in various ecosystems including the aforementioned (Zhang et al. 2019). The impact of novel subsidies is likely context-dependent, although some generalities may apply throughout various ecosystems. For example, fast colonization, with rapid growth, and little investment in permanent structures, are traits attributed the most successful invaders, thus, the higher litter production is a predictable consequent (Prescott and Zukswert 2016). Moreover, detritivores can switch between litter and intact plants to obtain nutrients (Farmer and Dubugnon 2009, Endlweber et al. 2009, Prescott and Zukswert 2016), thus, can choose to consume local plants over novel subsidies. However, there is no clear consensus about detritivore preference, performance, or diet shifts as a result of invasion-mediated changes to subsidies.

In this study, we used a donor-controlled system to elucidate how invasion-mediated changes in donor systems impact subsidy-recipient communities, using rocky intertidal decomposers of beached seaweeds (hereafter referred to as “wrack”) as a model system. Wrack subsidies provide important resources to nearshore and shore habitats (Duggins et al. 1989, Bustamante et al. 1995, Orr et al. 2005). For example, wrack on Bahamian Island coastlines temporarily shift predator behavior, increase predator densities, and ultimately result in a herbivore-mediated trophic cascade on some plants (Spiller et al. 2010, Wright et al. 2013, Piovia-Scott et al. 2017, Kenny et al. 2017, Piovia‐Scott et al. 2019). Thus, quantity and quality of subsidies can affect consumers at an individual level by changing grazing behavior of consumers, numerical response at a population level if consumers utilize the resource, and at the community level by shifting competitive balance (Piovia‐Scott et al. 2019). Human-mediated changes to the abundance and composition of seagrasses and seaweeds before they wash ashore could have profound implications on their use by recipient shoreline ecosystems, but these impacts are largely unknown.

The naiveté of these ecosystems to these subsidies suggests their use may be different than familiar subsidies. This is especially important when recipient communities include sensitive and endangered species that rely on wrack. The recent invasion by Devilweed*,* in southern California kelp forests, may pose consequences for recovery of the endangered Black abalone*.* Although black abalone are federally protected, their recovery has been slow since various species of abalone suffered precipitous declines due to overharvesting and disease (Altstatt et al. 1996, Raimondi et al. 2002, Miner et al. 2006, Stierhoff et al. 2012, Ben-Horin et al. 2013). Although not comparable to historical densities, the California Channel Islands support some populations of black abalone within rocky intertidal habitats (Newman et al. 2010, Raimondi et al. 2015, VanBlaricom and Kenner 2020). Many rocky shore consumers, including abalone at these sites consume various benthic seaweeds and are subsidized by drift kelp (VanBlaricom and Kenner 2020). California Giant kelp is a relatively high preference food for abalone (Leighton and Boolootian 1963) often dominates the wrack composition (Hayes 1974, Dugan et al. 2003, VanBlaricom and Kenner 2020). Many of these donor kelp forests have experienced increases in abundance of devilweed since it was first detected in 2003 (Marks et al. 2015). A report by Kenner and Tomoleoni (2020) estimated that devilweed density has increased from <1 individual per 20m2 in 2015 to 23.1 in 2019. As such, we expect that wrack composition will increasingly include devilweed as donor kelp forests are invaded. Thus, it is important to understand if native primary consumers in the naïve community will consume the novel wrack subsidy.

There are few examples of the impact of seaweed invasions on detritivores and contrasting results make clear predictions difficult. For example, one meta-analysis found no overall effect of seaweed invasions on density or biomass of consumer communities, or density, biomass, and growth of consumer species (Maggi et al. 2015). Another meta-analysis found that non-native red seaweeds had no effect on palatability to mollusks but were less palatable to arthropods while non-native brown seaweeds had no effect (Swantje et al. 2017). Alternately, an invasive seaweed may have a positive influence on performance if it has a high nutritional value and is preferred by consumers in the invaded habitat, however, to our knowledge, there are no examples to support this alternative hypothesis.

We tested the impacts of invasive devilweed on growth and preference of rocky intertidal wrack and benthic seaweed consumers to assess whether invasion-mediated changes to subsidies have positive or negative impacts on recipient communities. To test how a diet including devilweed impacts the performance of consumers, we fed snails diets that include devilweed and measured soft tissue growth and righting times. To test if devilweed changed the feeding preference, we offered several rocky intertidal primary consumers a choice between native kelp and invasive devilweed. Lastly, we offered an assemblage of 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*), and Black turban snails (*Tegula funebralis*)are abundant seaweed consumers and wrack detritivores along rocky shores of southern California and the Channel Islands (Abbott and Haderlie 1981, Barry and Ehret 1993, Aquilino and Stachowicz 2012). 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 in the study as they represent a typical assemblage of rocky intertidal primary consumers in areas experiencing the invasion of devilweed.

*Surveys*

To determine the relative contribution of devilweed to wrack in this region, we surveyed large wrack piles deposited on beaches at two sites on San Nicolas Island (33.27335° N, 119.57629° W, 33.28310° N, 119.53557° W). We started by haphazardly selecting a pile of wrack longer than 1 m, and we measured the dimensions of each devilweed at the surface of the pile and the entire pile. Then, we walked along the beach and recorded these same measurements for at 10-15 wrack piles, along a 50 m transect. For each pile, we measured the longest visible lengths and widths of each devilweed individual found on the pile surface. These measurements were used to calculate the area of each devilweed using the equation for an ellipse (*A=πab*), where “a” and “b” are the length and width of the devilweed individual. For a single pile, we then added the area of all devilweed individuals. We also measured the longest length and longest width of the entire pile. These dimensions were used to calculate the pile surface area (i.e., the area visible without moving the piles). We divided total devilweed area by visible pile area to estimate the proportion of wrack that consisted of devilweed.

I THINK WE INCLUDED HEIGHT TO GET SURFACE AREA OF AN ELLIPSOID????

We surveyed rocky intertidal primary consumer densities ed at Sunset Cliffs Natural Park (32.71972° N, -117.25725° W) 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 that avoided quadrats. But because shore crabs were present throughout the site, we used only one shore crab per replicate. We acknowledge that this may overestimate the abundance of shore crabs relative to hermit crabs and turban snails in the field. To determine the number of animals to add to our experiments so that we would have ecologically realistic densities, we multiplied field densities by the floor area of the plastic containers used in the assay.

*Performance Assays*

To understand how shifting wrack populations affect the performance of rocky shore primary consumers, we measured the growth and behavior of two consumer species [turban snails and juvenile red abalone (*Haliotis rufescens*)] fed 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, including that the limited number of captive individuals that we have access to are mature adults that might grow extremely slowly. This approach is further justified because both abalone species include brown seaweeds as important components oftheirdiets (Leighton and Boolootian 1963, Winter and Estes 1992, Nelson et al. 2002), and both abalone have similar growth rates (Ault 2009).

We collected turban snails from Sunset Cliffs Natural Park (shell length = 6-10 mm). We used lab-reared, juvenile Red abalone from a single cohort (May 2017) provided by NOAA Southwest Fisheries. Because juvenile abalone have a greater capacity to grow than adults, we selected individuals 45-60 mm in length. All organisms were transported to the 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) 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 because of the COVID-19 pandemic, we transported all organisms to LongLab GarageLab (a temporary recirculating seawater system setup in J. Long’s home garage) on March 19, 2020. The experiment was continued at this location until the termination of the experiment (April 17, 2020). At the GarageLab, 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 the GarageLab portion and used these data to determine dates of partial water replacements (conducted on March 28 and April 1, 2020; 30% and 80%, respectively).

Animals were offered one of four diets (kelp*,* devilweed*,* a ~1:1 mixture of kelp: devilweed, or starvation, n=20). Although seaweed biomass was not quantified, we added enough seaweed to prevent animals from becoming food-limited and we tried to add similar amounts of kelp and devilweed in the mixture treatment. We included the entire thallus (i.e., stipes, blades, and pneumatocysts) to account for tissue-specificity in animal choices. 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 this 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. This regression was then used to estimate starting soft tissue biomass, non-lethally, based on initial shell lengths.

In addition to impacts on growth, we assessed how diet impacted defensive behaviors of the abalone. We measured righting times at the start and end of the experiment. Specifically, we measured the amount of time abalone needed to right themselves. Because abalone are extremely vulnerable to predators when their ventral tissues are exposed, such assays have been used to understand how environment might influence interactions with predators (Baldwin et al. 2007, Lachambre et al. 2017). Righting tests involved placing abalone, dorsal side down, in a 14°C water tank without flowing seawater, and timing how long it took abalone to flip over so that their shell was facing up. These tests were conducted until abalone corrected their orientation or timed out at 4 minutes.

*Preference Assays*

To understand how shifting wrack composition affects feeding preferences of rocky intertidal consumers, we offered them 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). We transported seaweeds to CMIL. Separate feeding choice assays were conducted with each of the four primary consumer species (Shore crabs, Hermit crabs, Turban snails, and Black abalone). Non-abalone animals were collected from Sunset Cliffs Natural Park and transported to CMIL. Animals were held in flow-through seawater. Black abalone (collected and held under ESA Permit #19571-2R) were held in chilled, recirculating seawater at NOAA Southwest Fisheries Center (La Jolla, California). Prior to the assay, all animals were fed *Ulva spp.* for three days before starving for two days. This pre-assay period attempted to standardize hunger level and to motivate our animals to feed. 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 window screen (2 mm openings) to improve water exchange. Black abalone were housed individually in 280 x 230 x 180 mm mesh-lined (5 mm), PVC-framed cages with a Plexiglas® floor. We offered animals an equivalent biomass of kelpand devilweed, and we anchoredthese with binder clips (mean ± SE: 7.48 ± 0.40 g for hermit crabs, 7.48 ± 0.33 g for shore crabs, 6.51 ± 0.32 g for turban snails, 20.66 ± 0.35 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 ~3/4 of either seaweed was consumed or after 6 days. 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 (e.g., from kelp to devilweed) cause intertidal consumers to change consumption of native benthic seaweeds, we offered an assemblage of intertidal seaweed and wrack consumers a choice of native benthic seaweeds in the presence of either kelp or devilweed. This could occur given that shifts in the wrack composition might change the relative palatability of the wrack and the native benthic seaweeds. We collected all animals and seaweed from Sunset Cliffs Natural Park and transported them to CMIL. Animal densities in this assay were determined based on the survey described above (turban snails n=3, hermit crabs n=6, shore crabs n=1). We offered animals a choice between foods made from green benthic seaweed (*Ulva spp.*)*,* brown rockweed (*Silvetia compressa*)*,* and red benthic seaweed (*Centroceras clavulatum*),and 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 our lab, we fed animals 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 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. Once ready, the agar-foods were blotted dry and weighed before being offered to consumers.

Based on previous experiments showing negligible autogenic growth in agar-based foods and due to tank space limitations, we reduced the number of controls to one control for every two experimental replicates. We used thermoplastic adhesive to secure the petri dishes containing agar-based foods in random order along the length of 330 x 190 x 108 mm containers with mesh (2 mm) covered tops (n=20, and n=10 controls). The animals were placed on the opposite side of the container and allowed to feed. These assays began simultaneously on November 11, 2019. After ~36 hours, all petri dishes were removed from the replicate, blotted dry, and reweighed. We calculated changes in mass using the autogenic growth formula with the average correction factor from controls.

**Statistical Analyses**

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. We tested significance of fixed effects and interactions with type III sums of squares using the *Anova* function in the carpackage. Necessary assumptions were met for statistical analyses and post-hoc tests were conducted as needed.

For the performance assays, we estimated initial dry soft tissue masses using linear regression models. To test the effect of all diet treatments including seaweeds (i.e., all but “starved” treatment) on final dry tissue growth, we analyzed consumer species independently with Analysis of Covariance (ANCOVA). Starvation treatments were included for reference. Initial soft tissue dry mass estimates were included as a covariate. We also used ANCOVA to examine the effects of diet on final abalone righting times. This model used initial righting time as a covariate. The model included the interaction between both factors as well as a residual term to account for variability unrelated to the two predictors.

For preference assays, we compared changes in seaweed mass, corrected for autogenic growth, using Paired t-tests for each consumer species. We used a Linear Mixed-Effects model to investigate the effects of wrack species and native benthic seaweeds on consumption. The model included wrack type (native vs. invasive; i.e. kelp vs. devilweed, respectively) and seaweed species as fixed factors, and their interaction. We also included a random intercept for replicate number to account for non-independence (seaweed choice was not independent within replicates).

**Results**

*Performance*

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 estimated initial dry tissue mass from initial maximum shell length and included this estimate as a covariate in our growth analysis. After controlling for initial dry tissue mass, wrack diet influenced Red abalone and turban snail growth, but in opposing directions (F2,54= 3.88, p<0.005, F2,54=3.939, p=0.02; respectively). For Red abalone, replacing kelp wrack with devilweed wrack reduced final dry tissue mass by 25% (Fig. 1a). Further, partially replacing kelp wrack with devilweed also reduced final dry tissue mass, but this effect was weaker than the complete replacement (11%). For turban snails, however, partially replacing kelp wrack with devilweed increased final dry tissue mass by 35% and completely replacing kelp with devilweed increased final dry tissue mass by 31% (Fig. 1b). After controlling for differences in initial righting time, diet did not influence abalone righting time although there was a trend for devilweed diets to increase righting time (Fig. 2, F(2,54)=1.219, p=0.305).

*Preference*

Animals displayed species-specific feeding preferences for the two types of wrack. Both Black abalone and turban snails preferred kelp, with 111% and 158% more kelp being consumed than devilweed, respectively (Fig. 3a and 3b, t=4.5053, p<0.001 and t= 5.7152, p<0.001, respectively). Although these consumers preferred kelp, both animals did consume 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 consumed only consumed devilweed (Fig. 3d, t=-3.7593, p=0.00239). Interestingly, hermit crabs seemed to avoid consuming kelp entirely (One sample t-test, t=0.147, p=0.89).

*Native Benthic Seaweed Assay*

Replacing native wrack with invasive wrack (i.e., kelp with devilweed) led to a reduction in grazing by the assemblage on wrack (t-test, t=-7.5289, p<0.001). This reduction in grazing was related to an increase of grazing in *S. compressa* (M = 3.2304, SE = 0.2272, p < 0.001)*.* No differences in grazing were found in the other native benthic seaweeds (p > 0.05; Figure 4).The replacement of kelp wrack with devilweed did not influence overall grazing rates ( native: 5.22 ± 0.20g, invasive: 5.97 ± 0.22 g, M= -0.0878; SE = 0.2272, p = 0.6990).

**Discussion**

Invasive species have become increasingly abundant around the world and their effects on native communities are generally unclear as some decimate ecosystems while others assume similar roles to native counterparts (Williams and Smith 2007, Kaplanis et al. 2016, Chapman 2016). Species introductions have resulted in positive and negative impacts on invaded communities, but few studies have investigated how they impact subsidies between ecosystems and the communities that depend on such subsidies (MacMillan et al. 2016, Suárez-Jiménez et al. 2017). Here, we showed through feeding assays that invasive devilweed in the wrack will likely have species-specific impacts on performance and preference of consumers, and indirect effects on native benthic seaweeds.

Unlike previous studies, we did not see strong benefits of a mixed diet. Studies suggest that mixed diets generally result in higher performance than a monospecific diet (e.g., growth or reproductive output; (Worm et al. 2006, Aquilino et al. 2012). Benefits of a mixed diet are often attributed to 1) higher overall quality of diet due to nutrient balance and complementarity or 2) dilution of toxins and secondary compounds of any one species in the diet (Bernays et al. 1994, Hägele and Rowell-Rahier 1999). A meta-analysis of 493 experimental manipulations in 161 studies, revealed that mixed diets did not significantly enhance fitness components beyond the *best* single-species diet and reduced fitness when one of the diet components was a toxic species (Lefcheck et al. 2013). At this time, it is unknown to us if devilweed is chemically defended, however, our experiments found that although it is a lower preference food for turban snails, there are benefits to consuming it with or instead of kelp.

Nutritional values of seaweeds vary spatially and temporally but some studies suggest that Giant kelp generally has lower protein and lipid content and higher carbohydrate content than devilweed (14% protein, <1% lipids, 75% carbohydrates for kelp, 21.96-22.94% protein, 1.38-1.96% glycolipids, 19.93-20.81% carbohydrates (Hossain et al. 2003, Biancacci et al. 2022). Although we did not measure nutrient quality of the seaweeds in these experiments, higher nutritional values of devilweed may only explain increased performance for black turban snails since abalone growth decreased when devilweed was included in their diet. It should also be noted that although abalone righting times increased in all treatments, righting times for abalone that were fed only devilweed were generally more similar to starved individuals. While that pattern may not be statistically significant, there may be ecological implications in slower righting times when it comes to predator avoidance or resistance to turbulence and other disturbances. Evidently, abalone avoided food that results in lower performance but for some species (i.e., turban snails), performance is not necessarily related to food preference.

When given a choice between devilweed and kelp, turban snails preferred kelp and generally avoided devilweed. This is consistent with previous studies comparing the palatability of devilweed to native and naturalized non-native congeners (*S. agardhianum* and *S. muticum*, respectively), which resulted in lowest consumption of devilweed by black turban snails and purple urchin, (*Strongylocentrotus purpuratus*) (Kaplanis 2020). However, palatability of novel seaweeds is species-specific and predictions about the palatability of invasive seaweeds likely require experiments using the species of interest. For example, rocky shore consumers (*Lottorina littorea* and *Psammechinus miliaris*) in the North Sea preferred to eat *Sargassum muticum* from a sympatric population over *S. muticum* from an allopatric Japanese population (Schwartz et al. 2016). Similarly, two rocky shore consumers (*Littorina littorea* and *Aplysia punctata*) in Galicia, Spain, preferred native *Ulva sp.* and *Fucus vesiculosus* over invasive *S. muticum,* (Cacabelos et al. 2010). Conversely, *Dexamine spinosa* amphipods in North Ireland preferred invasive *M. muticum* over native seaweeds (Strong et al. 2009). As such, assessing the impacts of an invasive seaweed in donor and subsidy-dependent communities, likely requires direct experimentation with ecologically important species.

Rocky shore consumers 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, a shift in wrack palatability that shifts consumption onto habitat-forming species like *S. compressa* (Sapper and Murray 2003, Whitaker et al. 2010, Graham et al. 2018), may have community level impacts beyond reduction in biomass from consumption. For example, *S. compressa* understories are inhabited by diverse algae, sessile and mobile invertebrate communities that are protected from desiccation during tidal emersion (Sapper and Murray 2003). Moreover, it is anticipated that future climatic events will lead to changes in abundance and distribution of brown seaweeds that may be replaced with turf-forming red algae (Graham et al. 2018), likely leading to further declines of *S. compressa* and species that rely on it.

While various examples exist of nonnative species contributing to biodiversity (Chapman 2016), there are very few examples of invasive species positively changing subsidies (MacMillan et al. 2016, Quijón et al. 2017). In examples where invasive species become part of a subsidy, like *Undaria pinnatifida* in the wrack in southern New Zealand, palatability of the novel species tends to be lower than native species (Suárez-Jiménez et al. 2017). This study revealed that *U. pinnatifida* was a low preference food for important semi-terrestrial detritivores, talitrid amphipods (*Bellorchestia quoyana*), but in a no-choice and agar-based food assays, they consumed the invasive at the same rate or more than native seaweeds (Suárez-Jiménez et al. 2017). In such case, the complex interaction between the consumer and food sources was not explained by chemical (i.e., organic and caloric content, %N, C:N) and biomechanical (toughness and elasticity) properties that were measured. The authors argue that higher consumption rates may be due to the intricate structure of *U. pinnatifida* giving amphipods better grip to facilitate consumption over the flat, smooth, structure of native *M. pyrifera* (Suárez-Jiménez et al. 2017)*.* Similarly, in our experiments, the structural complexity (thin and narrow branching blades) of devilweed compared to kelp may have influenced choice of consumers. Smooth, flat, kelp blades may be easier for snail radulae to scrape, small branching stipes of devilweed may be easier for relatively small hermit crabs to process, while larger striped shore crabs can easily process either seaweed.

Although a complete replacement of giant kelp is unlikely, devilweed will continue to invade kelp forests, and subsequently, change wrack composition. Consumers will not only continue to encounter devilweed in wrack but may also encounter it growing intertidally. 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). Devilweed thrives in disturbed habitats and its invasion in southern California is partially attributed to reduction of biomass of native seaweeds during its peak growth and reproduction period (Cruz-Trejo et al. 2015, Marks et al. 2020, Sullaway and Edwards 2020). This is of special concern in areas inhabited by recovering Black abalone populations such as San Nicolas Island.

Our results indicate that while human activity will continue to impact ecosystems by altering subsidies across ecotones, understanding how donor-controlled systems are affected by changes in subsidies is context-dependent. While terrestrial herbivores tend to prefer invasive plants and marine herbivores tend to prefer native seaweeds, an extra level of complexity when herbivores also assume the role of detritivores in a system. The Home Field Advantage Hypothesis predicts that primary consumers in our system would be perform best and prefer native kelp, but our results showed that hermit crabs prefer devilweed and shore crabs were not selective. Additionally, since performance is not necessarily correlated with preferred food for some primary consumers, potential benefits of novel subsidies could be lost if consumers do not utilize them. Because performance and choice were species-dependent, our results did not find strong evidence to support either of the opposing meta-analyses. Ultimately, it is important to assess the all the potential impacts of species invasions beyond invaded habitats, including native primary producers and consumers in subsidy-dependent communities.

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**Figure Legend**

Fig. 1

Final dry tissue mass of Red abalone (A) and Black turban snails (B) in starved, kelp, mixed, and devilweed diets. The dotted line separates the starved treatment as it was not included in the analysis. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier values. Lower case letters above boxes denote significance. Black dots represent outliers.

Fig. 2

Time (sec) elapsed for Red abalone to correct their orientation by starved, kelp, mixed, and devilweed diet treatments, before (Initial) and at the end of the experiment (Final). 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.

Fig. 3

Total seaweed biomass consumed by Black abalone (A), Black turban snails (B), Striped shore crabs (C), and Blue banded hermit crabs (D) in kelp and devilweed treatments. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier values. Black dots represent outliers.

Fig.4

Total biomass of kelp or devilweed and red seaweed, sea lettuce, and brown rockweed consumed by assemblage of consumers in native and invasive wrack treatments. The dotted line separates the starved treatment as it was not included in the analysis. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non outlier values. Black dots represent outliers.

**Figures**

Figure 1

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Figure 2

A picture containing screenshot, diagram, text, design

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Figure 3 1

A picture containing text, receipt, diagram, parallel

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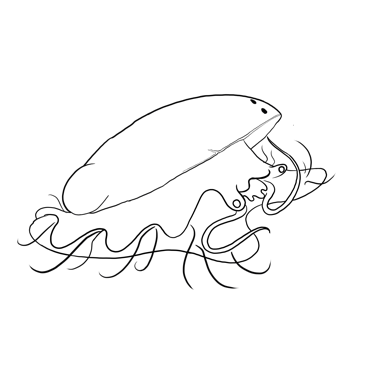
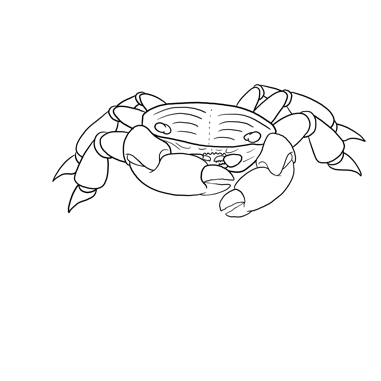
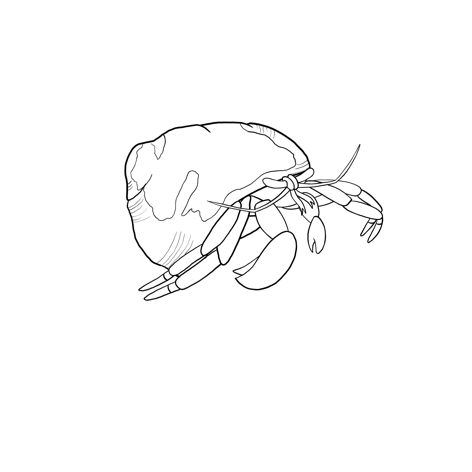
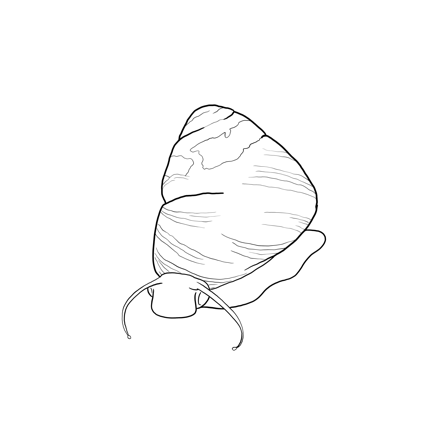


Figure 4

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