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 gene rally increased the self-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 (*H. cracherodii*) and brown rockweed (*S. compressa*), 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 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 self-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 invertebrates that often eat kelp wrack (Braje and Erlandson 2009, Beheshti et al. 2021), and thus, can be classified, at least in part, as detritivores. These common along the rocky shores of southern California and the Channel Islands (Abbott and Haderlie 1981, Barry and Ehret 1993, Aquilino and Stachowicz 2012). Additionally, abalone historically filled similar ecological roles along these shores prior to declines related to disease and overharvesting (VanBlaricom 1993, Altstatt et al. 1996, Raimondi et al. 2002). Although 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).

*Devilweed prevalence surveys*

To confirm that devilweed is present in wrack and to determine the relative contribution of devilweed to wrack, 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) and measured the proportion of the wrack pile surface area devilweed represented. We adopted this qualitative metric of devilweed prevalence 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 10-15 large wrack piles encountered along a haphazardly placed 50 m transect. We defined “large” wrack piles as those at least 1 m long. To determine the surface area of each pile, we measured the longest length and width to calculate the area of an ellipse (*A=πab*), where “a” and “b” are the length and width. For each devilweed individual encountered on the surface of the pile, we also measured its longest length and width. For a single pile, we calculated the sum area of all devilweed individuals. We divided total devilweed area by visible pile area to estimate the proportion of wrack that consisted of devilweed. We understand that this formula does not fully capture the three-dimensional shape of wrack deposits and may inflate the proportion of piles made up of devilweed; However, the original intended purpose of these surveys was to catalog the presence of devilweed in wrack and with 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 populations could affect the performance of rocky shore detritivores, we measured the growth and self-righting behaviors of two consumer species [turban snails and juvenile abalone (*H. rufescens*)] fed kelp, devilweed, or an equal mixture of the two. Because devilweed reduces kelp abundance in subtidal habitats but does not make it go locally extinct across short time scales (Sullaway and Edwards 2020), the mixture treatment is more ecologically realistic than the devilweed-only treatment. We used Red abalone as a proxy for Black abalone because of logistical challenges of conducting research with endangered species (i.e. Black abalone). These challenges include the limitation that the few captive individuals that we have access to are mature adults that might grow extremely slowly. Because both abalone species 1) include brown seaweeds as important components oftheirdiets (Leighton and Boolootian 1963, Winter and Estes 1992, Nelson et al. 2002) and 2) 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 (shell length = 45-60 mm). 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 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 and devilweed, or starvation, n=20). Seaweed was offered *ad libitum* 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 feeding preferences. 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 to estimate starting soft tissue biomass, non-lethally, based on initial shell lengths. 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). Thus,we estimated initial dry tissue mass from initial maximum shell length and included this estimate in the model.

In addition to growth, we assessed how diet impacted abalone self-righting times. Because abalone are extremely vulnerable to predators when their ventral tissues are exposed, such assays can inform environmental influence on predator-prey interactions (Ahmed et al. 2005, Baldwin et al. 2007, Lachambre et al. 2017). During self-righting tests, abalone were placed, dorsal side down, in 14-15°C seawater. We measured the time it took 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. Individuals that were unable to correct their orientation within the time limit were not included in the analysis. We conducted these assays at the start and end of the experiment.

*Preference Assays*

To understand how shifting wrack composition affects feeding preferences, we offered rocky intertidal detritivores 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 detritivores species (shore crabs, hermit crabs, turban snails, and abalone). Non-abalone animals were collected from Sunset Cliffs Natural Park, transported to CMIL, and held in flow-through seawater. Adult Black abalone (collected and held under ESA Permit #19571-2R) were held in chilled, recirculating seawater at NOAA Southwest Fisheries Center (La Jolla, California). To standardize hunger level and to motivate our animals to feed, all animals were fedsea lettuce 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 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. 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: 7.5 ± 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 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 detritivores to change consumption of native benthic seaweeds, we offered an assemblage of intertidal seaweed and wrack detritivores a choice of native benthic seaweeds in the presence of either kelp or devilweed. To create realistic assemblages of wrack detritivores, we surveyed the abundance of rocky intertidal detritivores 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. 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. Because we did not have density data for shore crabs, we added a single individual to each replicate.

We collected all animals and seaweed from Sunset Cliffs Natural Park and transported them to CMIL. We offered animals a choice between artificial foods made from three native benthic seaweeds (sea lettuce, brown rockweed, and red seaweed),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 our 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. Once the food was solidified, the agar-foods were blotted dry, weighed, and then offered to consumers.

We secured 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). 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. 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 previous autogenic growth 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 analyzed final dry tissue mass using a Linear Mixed Effects Model (LMEM) with detritivore species and diet as main effects and their interaction. We included estimated initial dry masses as random effect in the model 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. For the native benthic seaweed assay, we used a LMEM 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 (sea lettuce, brown rockweed, and red seaweed) as fixed factors, and their interaction. We also included a random factor for replicate number to account for non-independence 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**

*Performance*

Both diet and detritivore species influenced growth of detritivore soft tissue (F= 15.573, p<0.005, F=1078, p<0.005; respectively), but in opposing directions. There was a significant interaction between diet and detritivore species (F=15.243, p<0.005), thus, we analyzed them separately to understand how each diet impacted the growth of abalone and turban snails separately. After controlling for estimated initial dry tissue mass, wrack diet influenced Red abalone and Turban snail growth (Fig. 1: F2,54=8.162, p<0.005, F2,54=3.939, p=0.02; respectively) Replacing kelp wrack with devilweed suppressed Red abalone tissue mass by 25% but increased turban snail tissue mass by 31% (Fig. 1). The effect on turban snails was not statistically significant. 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, the mixed diet had an intermediate effect on tissue mass compared to animals in the no-choice treatments (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. Because no choice was ever fully consumed, any mixed-diet effect could not be attributed simply to the availability of a higher quality food.

Consistent with devilweed suppressing abalone growth, devilweed increased the amount of time it took abalone to right themselves. Abalone righting times generally increased after the 42 day experiment (7.95 ± 6.22 sec. kelp, 15 ± 6 sec. mixed, and 26 ± 6 sec. devilweed diets), however, after controlling for within subject variability this effect was not statistically significant (F2,57=2.091, p=0.133).

*Preference*

Animals displayed species-specific feeding preferences for wrack seaweeds. 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 they 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 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=0.00239). 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*

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), however, there was a significant interaction between wrack and native benthic seaweed grazing (F=21.208, 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)*.* Replacing kelp with devilweed did not affect feeding on the two other benthic native seaweed (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 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 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) starved, or fed kelp, devilweed or mixed diets for 42 days. 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 range. Lower case letters above boxes denote significance. The black dot is an outlier.

Fig. 2

Initial and final self-righting times for Red abalone starved or fed kelp, devilweed or mixed diets for 42 days. 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 choice feeding experiments. 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 artificial foods made from several seaweed species consumed in choice feeding assay by a realistic detritivore assemblage. The dotted line separates the wrack treatment (kelp or devilweed) offered to the detritivore assemblage along with native benthic seaweeds. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier range. Black dots represent outliers.

**Tables**

Table 1

Median Self-Righting times of Red abalone

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Starved** | **Kelp** | **Mixed** | **Devilweed** |
| **Start (sec)** | 13 | 16 | 12 | 13 |
| **Final (sec)** | 27 | 29 | 28 | 37 |

**Figures**

Figure 1

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Figure 2

A picture containing screenshot, diagram, text, design

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Figure 3 1

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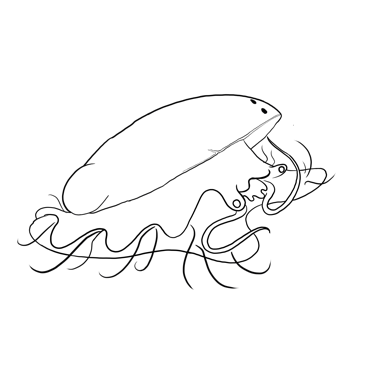
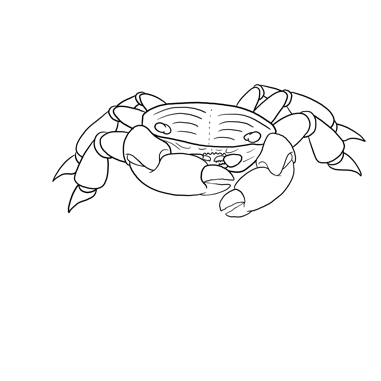
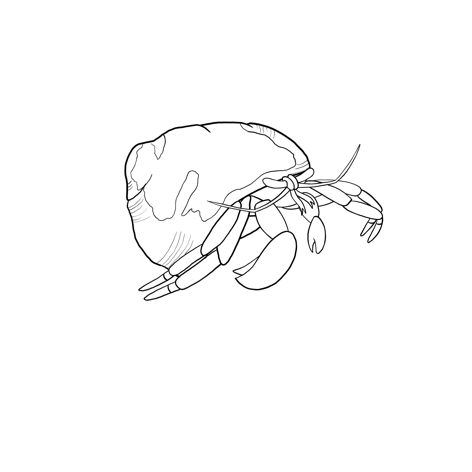
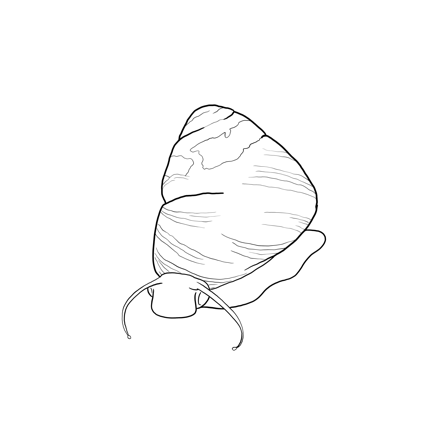


Figure 4

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