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 resilience 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. For example, the home-field advantage and the prey naiveté hypotheses predict differing impacts of novel detrital subsidies on consumers (e.g. predicting that novel detritus will be under- or overutilized by consumers, respectively). Further, two recent meta-analyses disagree about the impacts of invasive plants on detritivore populations. Here, we examined the impact of a human-mediated shift in detrital subsidy (native kelp to invasive Devilweed, *Sargassum horneri*) to recipient rocky shores, with an emphasis on exploring species-specific impacts. We assessed consumer performance on these 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 detritus with invasive Devilweed had consumer-specific performance impacts – 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. Replacing native kelp with invasive devilweed increased grazing of native benthic seaweeds by a realistic detritivore assemblage, but only on the brown seaweed, *Silvetia*. 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 detritral pathways.

*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 in donor habitats arising from species introductions and climate-mediated range shifts may lead to changes in detrital subsidies that could destabilize recipient ecosystems. 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. Identifying a general theory about how species invasions affect recipient detritivores and their communities would improve our ability to predict future environmental change. 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.

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 detrital subsidies and the habitats that rely on them (Zhang et al. 2019).

Such impacts are likely to be seen and mediated by primary consumers in recipient ecosystems (e.g. detritivores) because they are the first responders to these novel subsidies. These detrital shifts could impact such consumers in at least two ways. First, compositional shifts in donor systems could modify consumer performance. The direction of these impacts will at least depend on 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. For example, 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.

Unfortunately, we lack a clear understanding about how novel subsidies will impact detritivores. For example, two important ecological hypotheses make opposing predictions about the response of recipient consumers to novel resources. The Home-Field Advantage Hypothesis predicts that consumers will underutilize novel resources, primarily because of a lack of evolutionary history. In contrast, the Prey Naiveté Hypothesis predicts that consumers will prefer novel resources because this lack of evolutionary history limits the ability of prey to defend against novel consumers.

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 soil detritivore abundance in recipient habitats (Zhang et al. 2019).

The uncertainty about invasion impacts on detritivores extends to seaweeds and the consumers that use them. 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 arthropods, but not mollusks, had reduced preference for non-native red seaweeds (Swantje et al. 2017).

We tested the impacts of a seaweed invasion (Devilweed) on growth and preference of rocky intertidal detritivores. To test how shifts towards devilweed impact consumer performance, we fed snails kelp, Devilweed, or a mixture of both, and measured soft tissue growth and righting times. To test if devilweed changed feeding, 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**

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.

*Study organisms*

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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 (i.e. they can be classified, at least in part, as 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 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 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).

*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 the entire pile, we the WAITING TO INSERT CALCULATION TEXT UNTIL WE AGREE ON THE APPROACH. For each devilweed individual encountered on the surface of the pile, we also measured its longest length and width. These measurements were used to calculate the area of each devilweed individual on the pile surface 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 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. Using this method, the relative contribution of devilweed to wrack for a large pile could be estimated in minutes as opposed to hours.

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

*Performance Assays*

To understand how shifting wrack populations could affect the performance of rocky shore primary consumers, we measured the growth of two consumer species [turban snails and juvenile Red abalone (*Haliotis rufescens*)] fed kelp, devilweed, or an equal mixture of the two. For Red abalone, we also recorded the behavioral measurement of righting times. 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 representative of the current state of the invasion 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, and would thus not reveal growth effects. We justify using a congener as a proxy species further because both abalone species 1) consume brown seaweeds (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 on April 17, 2020 (i.e. six weeks after the start). 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*. 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 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 growth, we assessed how diet impacted abalone righting times. can informal (e.g. diet)on predator-prey e.g. slow righting times suggests an increased vulnerability to predators, During r, abalone were placed-15seawater. We measured the time dorsal side of thefaced up passed 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 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). 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, 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 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 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: 7.5 ± 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 ~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 consumers known to eat seaweed and wrack, 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 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 recognize this approach creates an assemblage with relatively more abundant shore crabs and therefore might overestimate the role of shore crabs.

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 (*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. 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 formula.

**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, . Thus,To test the effect of all diet treatments including seaweeds (i.e., all but “starved” treatment) on final dry tissue mass, 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 with 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. For the native benthic seaweed assay, 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 (*Ulva spp., Silvetia compressa,* or *Centroceras clavulatum*) as fixed factors, and their interaction. We also included a random intercept for replicate number to account for non-independence because seaweed choice was not independent within replicates.

**Results**

*Performance*

After controlling for estimated initial dry tissue mass, wrack diet influenced Red abalone and Turban snail growth (Fig. 1: F2,54= 3.88, p<0.005, F2,54=3.939, p=0.02; respectively), but in opposing directions. 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 a reduction in the availability 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, athis effect was not statistically significant

*Preference*

Animals 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 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 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=0.00239). 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). 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**

Replacing kelp detritus with invasive Devilweed had detritivore-specific performance impacts – suppressing growth of Red abalone but enhancing growth of Black turban snails. The effect of mixed diets on consumer growth also displayed consumer-specificity (abalone displayed intermediate growth on mixed diets whereas turban snail growth on mixed diets was high and indistinguishable from Devilweed). Replacing native kelp with invasive devilweed increased grazing of native benthic seaweeds by a realistic detritivore assemblage, but only on the brown seaweed, *Silvetia*. Thus, invasion mediated changes in wrack composition had consumer- and seaweed-specific impacts.

Detritivore-specific performance impacts of an invasive seaweed on different intertidal snails are consistent with detritivore-specific population-level impacts of invasive plants (see references in Zhang et al. and McCary et al.). Such specificity has been observed across several taxonomic levels. For example, stands with the invasive giant knotweed had reduced densities of detritivorous isopods but similar densities of detritivorous amphipods relative to uninvaded plots (i.e. Subclass variation, Kappes et al. 2007). Similarly, leaf litter detritus from plots invaded by an annual invasive *Impatiens* had higher densities of leaf litter dwelling Acari but did not show differences in springtail densities relative to leaf litter from uninvaded plots (Subphylum variation, Rusterholz et al. 2015). When these impacts are specific to detritivores, invasions may shift competition between recipient detritivores and may modify predator-prey interactions.

Invasive plants could have detritivore-specific impacts (e.g. adding invasive devilweed to a kelp diet suppressed abalone growth but enhanced turban snail growth) via several pathways. First, detritivores may differ in their attraction to or preference for detritus from these plants. However, because both 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 detritus. Second, detritivores may be differentially impacted by how detritus from invasive plants modifies abiotic conditions. For example, invasive seaweeds may release allelopathic chemicals into seawater or may modify abiotic factors like pH or oxygen. However, this shouldn’t lead to detritivore specificity as they would likely have a general impact on all snails. Finally, detritivores may differ in post-ingestive processes that influence their ability to assimilate or detoxify detritus from invasive plants. CAN WE PROVIDE REFS MORE GENERALLY, AND THEN CAN WE SAY ANYTHING ABOUT TURBANS VS ABALONE DIFFS? This appears likely in our system because devilweed-only diets suppressed abalone but enhanced turban snail growth. Interestingly, because both snails preferred kelp, this apparent post-ingestion impact was associated with a relatively small amount of devilweed. That suggests that a) devilweed provided a key limiting nutrient for turban snails, b) devilweed had a toxic effect on abalone, or both.

In addition to direct effects on detritivore performance, shifts in detrital subsidies may shape recipient primary producer communities indirectly. 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). 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 (e.g. arthropods feeding on red seaweeds display a preference for native species but molluscs 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 review).

Although a complete replacement of giant kelp is unlikely, devilweed is expected to continue to invade kelp forests, and subsequently, change wrack composition. In addition to encountering devilweed as detritus, intertidal consumers are increasingly co-occurring with living, benthic devilweed. For example, 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.

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 naivete. 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

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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.

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.

**Acknowledgements**

Thanks to the Navy Marine Ecology Consortium for access to San Nicolas Island and San Clemente Island field sites. Matthew Sato, Mackenna Denton, Samantha Folger, Summer Wheeler, Bria Gorman, Sydney Height, Jacob Dioli, and Rania Abualjis provided field and lab assistance. This project was supported by funding from ….

R. DeSantiago was supported by a NSF Graduate Research Fellowship

**\*\*author contributions here\*\***

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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 right themselves after being flipped upsdie-down in 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 mass of artificial foods made from detritus (either 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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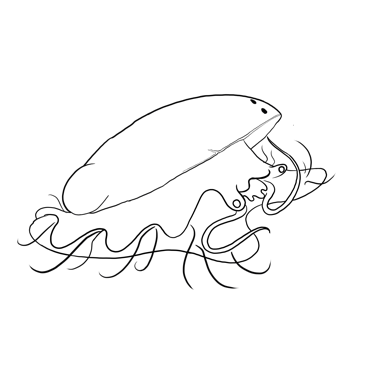
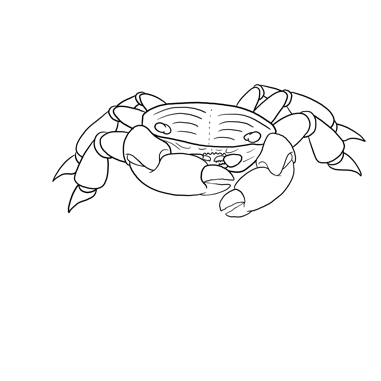
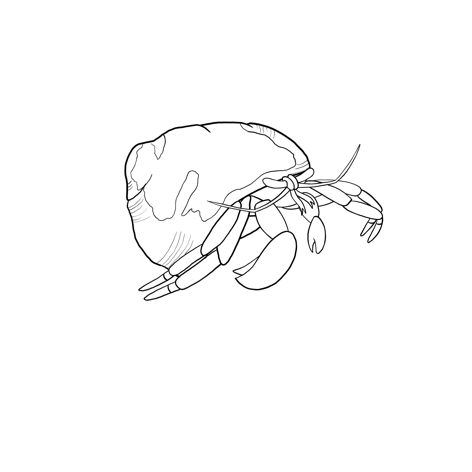
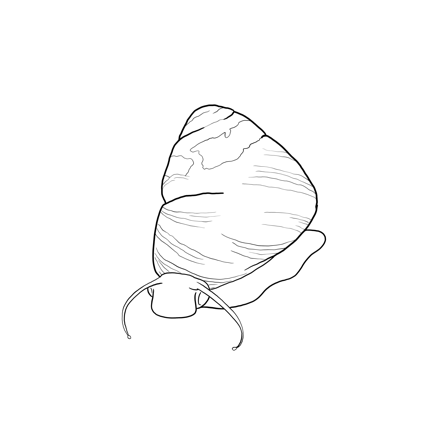


Figure 4

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