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, *Macrocystis pyrifera,* 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 compressa.* Thus, invasion mediated changes in detrital wrack composition had consumer- and seaweed-specific impacts. Such species-specificity could underlie disagreements about the impact of species invasions on detritivore populations and could impede our ability to identify a general theory about how species invasions will impact recipient communities via detrital pathways.

*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, Moore et al. 2004). 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 (Collins and Baxter 2014). For example, species shifts in donor systems may change the quantity and quality of detrital supply leading to consequences on populations of recipient primary consumers (i.e., detritivores), and the species they interact with. 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 organisms, energy, materials, and information from donor systems that can alter species abundances and interactions in recipient food webs (Polis and Hurd 1996, Nakano et al. 1999, Talley et al. 2006, Gratton et al. 2008, Greig et al. 2012). For example, detrital subsidies can modify key ecological processes (e.g. competition and predation; Yang 2006, Piovia-Scott et al. 2011, Kenny et al. 2017), generate trophic cascades (Polis and Hurd 1996, Polis et al. 1997, Nakano et al. 1999, Jefferies 2000), and stabilize food webs (Takimoto et al. 2002). Changes to these donor communities via species introductions and range shifts are likely to change detrital subsidies and the habitats that rely on them (Zhang et al. 2019).

Such impacts are likely to be seen and mediated by primary consumers in recipient ecosystems (e.g. detritivores) because they are ubiquitous in every ecosystem (Yang 2006) and early responders to these novel subsidies (Moore et al. 2004, Levin et al. 2006). 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 (Duggins et al. 1989, Bustamante et al. 1995, Parker and Hay 2005). 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 (Polis and Strong 1996).

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 on growth and preference of rocky intertidal detritivores. To test how shifts towards Devilweed impact consumer performance, we fed snails *Macrocystis pyrifera, Sargassum horneri* (Hereafter, “Kelp” and “Devilweed,” respectively) or a mixture of both, and measured soft tissue growth and self-righting times. To test if Devilweed changed feeding, we offered several rocky intertidal wrack consumers a choice between native Kelp and invasive Devilweed. Lastly, we offered an assemblage of wrack consumers foods made from native benthic seaweeds and either Kelp or Devilweed to determine if replacement of Kelp with Devilweed shifts grazing onto native seaweeds.

**Methods**

*Study organisms*

The naiveté of these ecosystems to introduced Devilweed 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 several 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 (Neuman et al. 2010, Raimondi et al. 2015, VanBlaricom and Kenner 2020). Many rocky shore consumers, including abalone at these sites consume 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) that often dominates the wrack (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 20 m2 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 how this novel wrack subsidy will impact recipient detritivores and their communities.

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 et al. 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.

*Devilweed prevalence surveys*

To confirm that Devilweed is present and to determine the relative contribution of Devilweed to wrack, we surveyed large wrack piles deposited on 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 measured the longest length and width of the pile. 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 one half 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.

*Performance Assays*

To understand how shifting wrack composition could affect the performance of rocky shore consumers, we measured the growth of two wrack 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 self-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 openings) covers. The performance assay began March 5, 2020. At this time, all containers were completely submerged in tanks with 14°C recirculating, aerated water with a pH of 7.75. Due to facility closures 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. Because the relationship between maximum shell length and dry tissue mass was strong and linear for both Turban snails (R2 = 0.89, F(1,18)=148.20, p<0.001)and Red abalone(R2 = 0.89, F(1,18)=160.71, p<0.001)*,* we used this regression to estimate starting soft tissue biomass, non-lethally.

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 (e.g. diet) on predator-prey interactions (e.g. slow righting times suggests an increased vulnerability to predators, Baldwin et al. 2007, Lachambre et al. 2017). During 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. 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 (32.71972° N, -117.25725° W), 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 Science 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 mesh (2 mm openings) to improve water exchange. Black abalone were housed individually in 280 x 230 x 180 mm mesh-lined (5 mm openings), PVC-framed cages with a Plexiglas® floor. We offered animals an equivalent biomass of Kelpand Devilweed, 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 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 openings) 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**

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 compared overall grazing using a paired t-test and tested for interactions using ANOVA. We used a LMEM to investigate the effects of wrack species and native benthic seaweeds on consumption. The model included wrack type (native or invasive) and seaweed species (*Ulva spp., Silvetia compressa,* or *Centroceras clavulatum*) 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= 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, after controlling for differences in initial righting time, this effect was not statistically significant (F2,57=2.091, p=0.133).

*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) did not influence overall grazing rates (native: 5.97 ± 0.22 g, invasive: 5.22 ± 0.20g; t-test, t = -1.261 p = 0.215), however, there was a significant interaction between wrack and native benthic seaweed grazing (ANOVA, F=17.116, p<0.001). This decrease in grazing on wrack increased grazing on *S. compressa* (M=0.75, SE=0.28, p=0.0265), but did not affect feeding on the two other benthic native seaweed (p>0.05; Figure 4).

**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 (Red 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 compressa*. 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 McCary et al. 2016 and Zhang et al. 2019). 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. 2014). When these impacts are specific to detritivores, invasions may shift competition between recipient detritivores and may modify predator-prey interactions (Heleno et al. 2009).

Invasive plants could have detritivore-specific impacts (e.g. adding invasive Devilweed to a Kelp diet suppressed Red 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 (Mews et al. 2006). However, because both Red 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 (Rodil et al. 2008). 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 (Frost et al. 2005). This appears likely in our system because Devilweed-only diets suppressed Red abalone but enhanced turban snail growth. Interestingly, because both 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 Red abalone, or both.

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

Such impacts may be particularly common for rocky shore consumers that directly and indirectly affect community dynamics and structure by influencing seaweed abundance, diversity, and productivity (Sousa 1984, Aquilino and Stachowicz 2012, Rhoades et al. 2018). Therefore, changing wrack that shifts consumption onto habitat-forming species like *S. compressa* (Sapper and Murray 2003, Whitaker et al. 2010, Graham et al. 2018), may have additional community level impacts. For example, *S. compressa* understories inhabited by diverse algae, sessile and mobile invertebrate communities that are protected from desiccation during tidal emersion will suffer from *Silvetia* reductions (Sapper and Murray 2003, Truong et al. in 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 Naiveté. Such specificity could lead to contrasting results within and between studies. For example, two meta-analyses were unable to agree about the impact of invasive plants on detritivores, with one study finding positive and one study finding negative effects.

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**References**

Abbott, D. P., and E. C. Haderlie. 1981. Intertidal invertebrates of California. Systematic Zoology 30:218.

Altstatt, J., R. Ambrose, J. Engle, P. Haaker, K. Lafferty, and P. Raimondi. 1996. Recent declines of black abalone Haliotis cracherodii on the mainland coast of central California. Marine Ecology Progress Series 142:185–192.

Aquilino, K., M. Coulbourne, and J. Stachowicz. 2012. Mixed species diets enhance the growth of two rocky intertidal herbivores. Marine Ecology Progress Series 468:179–189.

Aquilino, K. M., and J. J. Stachowicz. 2012. Seaweed richness and herbivory increase rate of community recovery from disturbance. Ecology 93:879–890.

Ault, J. S. 2009. Some quantitative aspects of reproduction and growth of Red abalone, Haliotis rufescens (Swainson). Journal of the World Mariculture Society 16:398–425.

Baldwin, J., J. P. Elias, R. M. G. Wells, and D. A. Donovan. 2007. Energy metabolism in the tropical abalone, Haliotis asinina Linné: Comparisons with temperate abalone species. Journal of Experimental Marine Biology and Ecology 342:213–225.

Barry, J. P., and M. J. Ehret. 1993. Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California. Environmental Biology of Fishes 37:75–95.

Ben-Horin, T., H. S. Lenihan, and K. D. Lafferty. 2013. Variable intertidal temperature explains why disease endangers black abalone. Ecology 94:161–168.

Bolser, R. C., and M. E. Hay. 1996. Are tropical plants better defended? Palatability and defenses of temperate vs. tropical seaweeds. Ecology 77:2269–2286.

Bustamante, R. H., G. M. Branch, S. Eekhout, B. Robertson, P. Zoutendyk, M. Schleyer, A. Dye, N. Hanekom, D. Keats, M. Jurd, and C. McQuaid. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102:189–201.

Collins, S. F., and C. V. Baxter. 2014. Heterogeneity of riparian habitats mediates responses of terrestrial arthropods to a subsidy of Pacific salmon carcasses. Ecosphere 5:art146.

Cruz-Trejo, G. I., S. E. Ibarra-Obando, L. E. Aguilar-Rosas, M. Poumian-Tapia, and E. Solana-Arellano. 2015. Presence of Sargassum horneri at Todos Santos Bay, Baja California, Mexico: Its effects on the local macroalgae community. American Journal of Plant Sciences 06:2693–2707.

David, P., E. Thébault, O. Anneville, P.-F. Duyck, E. Chapuis, and N. Loeuille. 2017. Impacts of invasive species on food webs: A review of empirical data. Advances in Ecological Research. 56:1-60.

Dolecal, R. E., and J. D. Long. 2013. Ephemeral macroalgae display spatial variation in relative palatability. Journal of Experimental Marine Biology and Ecology 440:233–237.

Dugan, J. E., D. M. Hubbard, M. D. McCrary, and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science 58:25–40.

Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173.

Frost, P. C., M. A. Evans‐White, Z. V. Finkel, T. C. Jensen, and V. Matzek. 2005. Are you what you eat? Physiological constraints on organismal stoichiometry in an elementally imbalanced world. Oikos 109:18–28.

Graham, S., B. Hong, S. Mutschler, B. Saunders, and J. Bredvik. 2018. Changes in abundance of Silvetia compressa at San Clemente Island before and during the 2015–2016 El Niño. Western North American Naturalist 78:605.

Gratton, C., J. Donaldson, and M. J. V. Zanden. 2008. Ecosystem linkages between lakes and the surrounding terrestrial landscape in northeast Iceland. Ecosystems 11:764–774.

Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. Global Change Biology 18:504–514.

Hayes, W. B. 1974. Sand-beach energetics: Importance of the isopod Tylos Punctatus. Ecology 55:838–847.

Heleno, R. H., R. S. Ceia, J. A. Ramos, and J. Memmott. 2009. Effects of alien plants on insect abundance and biomass: a food‐web approach. Conservation Biology 23:410–419.

Jefferies, R. L. 2000. Allochthonous inputs: integrating population changes and food-web dynamics. TREE 15:19-22.

Kappes, H., R. Lay, and W. Topp. 2007. Changes in different trophic levels of litter-dwelling macrofauna associated with giant knotweed invasion. Ecosystems 10:734–744.

Kenner, M. C., and J. A. Tomoleni. 2020. Kelp forest monitoring at Naval Base Ventura County, San Nicolas Island, California: Fall 2018 and Spring 2019, fifth annual report. Open-File Report.

Kenny, H. V., A. N. Wright, J. Piovia-Scott, L. H. Yang, D. A. Spiller, and T. W. Schoener. 2017. Marine subsidies change short-term foraging activity and habitat utilization of terrestrial lizards. Ecology and Evolution 7:10701–10709.

Lachambre, S., S. Huchette, R. Day, P. Boudry, A. Rio-Cabello, T. Fustec, and S. Roussel. 2017. Relationships between growth, survival, physiology and behaviour — A multi-criteria approach to Haliotis tuberculata phenotypic traits. Aquaculture 467:190–197.

Leighton, D., and R. A. Boolootian. 1963. Diet and growth in the Black abalone, Haliotis cracherodii. Ecology 44:228-238.

Levin, L. A., C. Neira, and E. D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. Ecology 87:419–432.

Maggi, E., L. Benedetti‐Cecchi, A. Castelli, E. Chatzinikolaou, T. P. Crowe, G. Ghedini, J. Kotta, D. A. Lyons, C. Ravaglioli, G. Rilov, L. Rindi, and F. Bulleri. 2015. Ecological impacts of invading seaweeds: a meta‐analysis of their effects at different trophic levels. Diversity and Distributions 21:1–12.

Marks, L., P. Salinas-Ruiz, D. Reed, S. Holbrook, C. Culver, J. Engle, D. Kushner, J. Caselle, J. Freiwald, J. Williams, J. Smith, L. Aguilar-Rosas, and N. Kaplanis. 2015. Range expansion of a non-native, invasive macroalga Sargassum horneri (Turner) C. Agardh, 1820 in the eastern Pacific. BioInvasions Records 4:243–248.

McCary, M. A., R. Mores, M. A. Farfan, and D. H. Wise. 2016. Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis. Ecology Letters 19:328–335.

Mews, M., M. Zimmer, and D. Jelinski. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. Marine Ecology Progress Series 328:155–160.

Miner, C. M., J. M. Altstatt, P. T. Raimondi, and T. E. Minchinton. 2006. Recruitment failure and shifts in community structure following mass mortality limit recovery prospects of black abalone. Marine Ecology Progress Series 32:107–117.

Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. de Ruiter, Q. Dong, A. Hastings, N. C. Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni, and D. H. Wall. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7:584–600.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in stream food web. Ecology 80:2435–2441.

Nelson, M. M., D. L. Leighton, C. F. Phleger, and P. D. Nichols. 2002. Comparison of growth and lipid composition in the green abalone, Haliotis fulgens, provided specific macroalgal diets. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology 131:695–712.

Neutel, A. M., J. B. T. M. Roerdink, and P. C. de Ruiter. 1994. Global Stability of Two-level Detritus Decomposer Food Chains. Journal of Theoretical Biology 171:351-353.

Neuman, M., B. Tissot, and G. VanBlaricom. 2010. Overall status and threats assessment of Black abalone (Haliotis cracherodii Leach,1814) populations in California. Journal of Shellfish Research 29:577-586.

Odum. 1969. The Strategy of Ecosystem Development. Science 164:262-270.

Parker, J. D., and M. E. Hay. 2005. Biotic resistance to plant invasions? Native herbivores prefer non‐native plants. Ecology Letters 8:959–967.

Piovia-Scott, J., D. A. Spiller, and T. W. Schoener. 2011. Effects of experimental seaweed deposition on lizard and ant predation in an island food web. Science 331:461–463.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. The American Naturalist 147:396–423.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. The American Naturalist 147:813–846.

Raimondi, P., L. J. Jurgens, and M. T. Tinker. 2015. Evaluating potential conservation conflicts between two listed species: sea otters and black abalone. Ecology 96:3102–3108.

Raimondi, P., C. Wilson, R. Ambrose, J. Engle, and T. Minchinton. 2002. Continued declines of black abalone along the coast of California: are mass mortalities related to El Niño events? Marine Ecology Progress Series 242:143–152.

Rhoades, O. K., R. J. Best, and J. J. Stachowicz. 2018. Assessing feeding preferences of a consumer guild: Partitioning variation among versus within species. The American Naturalist 192:287–300.

Rodil, I. F., C. Olabarria, M. Lastra, and J. López. 2008. Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. Journal of Experimental Marine Biology and Ecology:13.

Rusterholz, H.-P., J.-A. Salamon, R. Ruckli, and B. Baur. 2014. Effects of the annual invasive plant Impatiens glandulifera on the Collembola and Acari communities in a deciduous forest. Pedobiologia 57:285–291.

Sapper, S. A., and S. N. Murray. 2003. Variation in structure of the subcanopy assemblage associated with southern California populations of the intertidal rockweed Silvetia compressa (Fucales). Pacific Science 57:433–462.

Sotka, E. E., and M. E. Hay. 2002. Geographic variation among herbivore populations in tolerance for a chemically rich seaweed. Ecology 83:2721-2735.

Sousa, W. P. 1984. Intertidal mosaics: Patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918–1935.

Stierhoff, K. L., M. Neuman, and J. L. Butler. 2012. On the road to extinction? Population declines of the endangered white abalone, Haliotis sorenseni. Biological Conservation 152:46–52.

Swantje, E., S. Josefin, S. A. WikströM, and P. Henrik. 2017. A Review of Herbivore Effects on Seaweed Invasions. Pages 421–440 *in* S. J. Hawkins, A. J. Evans, A. C. Dale, L. B. Firth, D. J. Hughes, and I. P. Smith, editors. Oceanography and Marine Biology. First edition. CRC Press.

Takimoto, G., T. Iwata, and M. Murakami. 2002. Seasonal subsidy stabilizes food web dynamics: Balance in a heterogeneous landscape: Seasonal subsidy and food web stability. Ecological Research 17:433–439.

Talley, D. M., G. R. Huxel, and M. Holyoak. 2006. Connectivity at the land–water interface. Pages 97–129 *in* K. R. Crooks and M. Sanjayan, editors. Connectivity Conservation. First edition. Cambridge University Press.

Thornber, C., E. Jones, and J. Stachowicz. 2008. Differences in herbivore feeding preferences across a vertical rocky intertidal gradient. Marine Ecology Progress Series 363:51–62.

VanBlaricom, G. R. 1993. Dynamics and distribution of Black Abalone Populations at San Nicolas Island, California. Proceedings of the Third California Channel Islands Symposium.

VanBlaricom, G. R., and M. C. Kenner. 2020. Dietary patterns in Black abalone Haliotis cracherodii Leach, 1814 as indicated by observation of drift algal and seagrass capture on San Nicolas Island, California, USA, 1982 - 2019. Journal of Shellfish Research 39:1-12.

Whitaker, S. G., J. R. Smith, and S. N. Murray. 2010. Reestablishment of the southern California rocky intertidal brown Alga, Silvetia compressa: An experimental investigation of techniques and abiotic and biotic factors that affect restoration success. Restoration Ecology 18:18–26.

Winter, F. C., and J. A. Estes. 1992. Experimental evidence for the effects of polyphenolic compounds from Dictyoneurum californicum Ruprecht (Phaeophyta: Laminariales) on feeding rate and growth in the red abalone Haliotis rufescens Swainson. Journal of Experimental Marine Biology and Ecology 155:263–277.

Yang, L. H. 2006. Interactions between a detrital resource pulse and a detritivore community. Oecologia 147:522–532.

Zhang, P., B. Li, J. Wu, and S. Hu. 2019. Invasive plants differentially affect soil biota through litter and rhizosphere pathways: a meta‐analysis. Ecology Letters 22:200–210.

**Figure Legend**

Figure 1

Final dry tissue mass of Red abalone (A) and Black turban snails (B) starved or fed Kelp, Devilweed, or mixed 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 ranges. Lower case letters above boxes denote significance. The black dots are outliers.

Figure 2

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

Figure 3

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

Figure 4

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

**Figures**

Figure 1

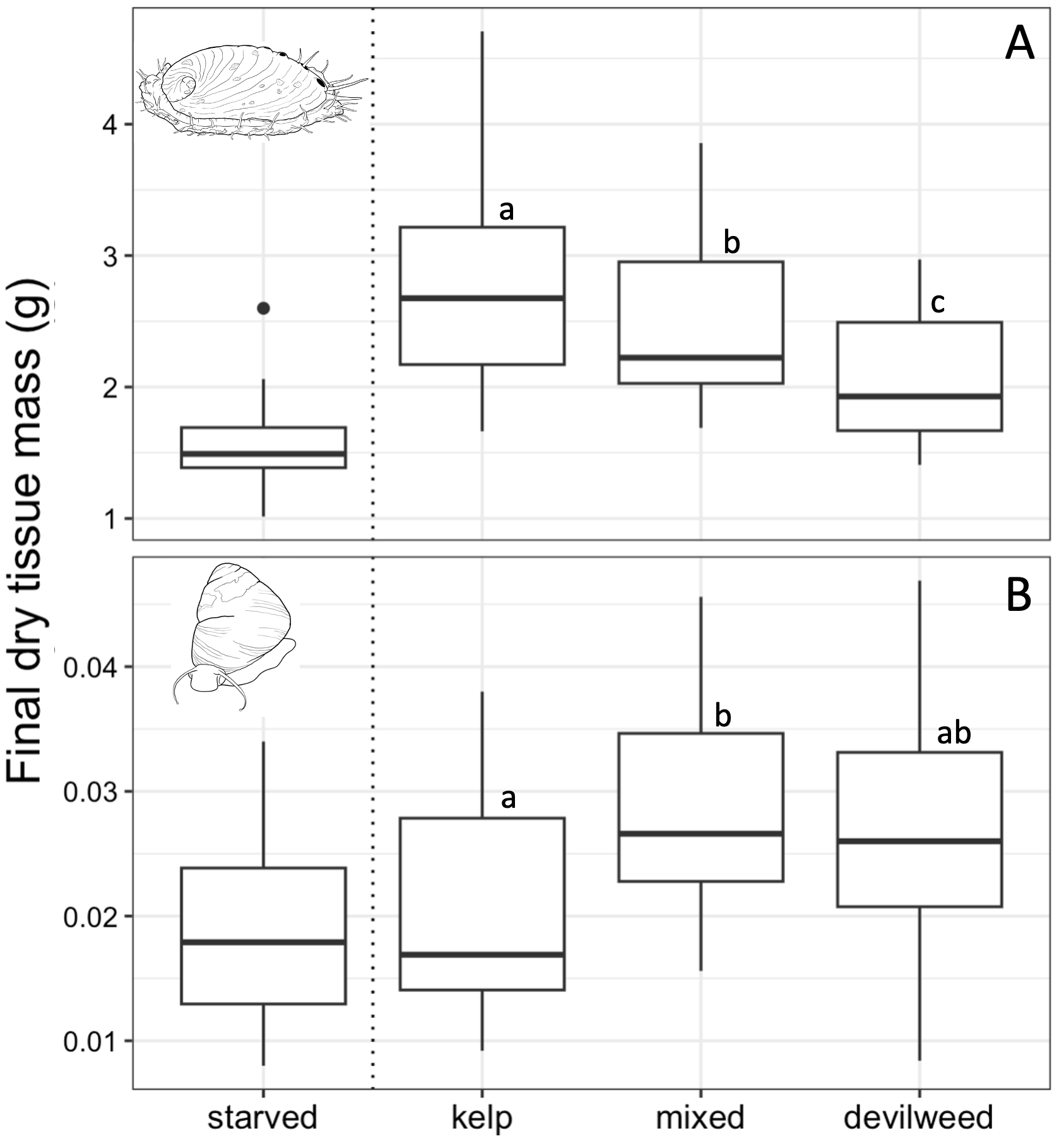
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Figure 2

A graph of different sizes and colors

Description automatically generated with medium confidence

Figure 3

A diagram of seaweed consumption

Description automatically generated

Figure 4

A graph showing different types of treatment

Description automatically generated with medium confidence