Anthropogenic impacts on an intertidal seaweed: population density predicts decline in size of *Mazzaella splendens* over a 150-year period

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Abstract

It is well established that ecosystems exhibit “threshold effects” whereby a small change in the intensity of a human disturbance produces large responses in the ecosystem. In a dataset spanning over 150 years of size data of the intertidal macroalga *Mazzaella splendens* obtained from herbarium specimens, we show that a statistically significant decrease in size occurred among specimens collected from two urban areas with the highest human population densities (San Francisco, Puget Sound) but not among specimens collected from areas with lower human population densities (San Juan, Monterey, San Luis Obispo, and Marin Counties). These results run counter to earlier work which suggested that small amounts of human disturbance were sufficient to produce substantial decreases in intertidal macroalgal size and that initial disturbances produced larger decreases in macroalgal size than subsequent disturbances.

Introduction

Changes in community structure and species morphology due to anthropogenic impacts are notoriously difficult to detect in marine systems due to high levels of intrinsic variability (Dayton et al. 1998). Detecting any kind of change in ecosystems requires a well-defined baseline, but due to so-called shifting baseline syndrome (Pauly 1995), such baselines are often difficult to define. Both experimental and even long-term field studies used to detect change are often severely limited in their spatial scales, often restricted to particular biomes located near major universities, and are limited in length by funding cycles and the life histories of academics (Meinke et al. 2018). Biological collections, such as herbaria, include specimens that span a much greater spatial and temporal extent and have been used to illuminate changes in species characteristics such as morphology, physiology, and phenology that were not apparent in studies with more limited spatial and temporal extents (Pyke and Ehrlich 2010). While herbaria contain systematic biases - larger, healthier, more aesthetically pleasing specimens are generally chosen - assuming that these systematic biases remain fairly consistent over time - that collectors consistently chose larger, better looking specimens - biological collections are particularly useful for correlating change in morphology with change in anthropogenic impacts (Pyke and Ehrlich 2010).

While little long-term data exist about the effects of anthropogenic impacts on intertidal macroalgal size, there is substantial evidence which demonstrates the effects which anthropogenic impacts have had on intertidal communities. Barry et al. (1995) documented substantial change in the invertebrate fauna in rocky intertidal communities in Central California consistent with changes predicted by studies of thermal physiology. Murray and Bray (1994) also documented substantial reductions in biodiversity of rocky intertidal systems in heavily visited Southern California marine reserves. Intertidal species are affected by global change drivers (GCDs) which affect all marine species, such as the warming of sea surface temperatures (including marine heat waves), ocean acidification, and nutrient runoff, but are also subject to additional pressures including trampling and human collection (Murray et al. 1999). While there have been many studies on the effects of each of these GCDs on seaweed growth, the precise effects of each GCD on the growth and performance of intertidal seaweeds is not always clear. For instance, while decreases in physiological performance and growth due to increased temperatures and lower pH have been documented across a wide variety of seaweed taxa, higher nitrate levels can often ameliorate the effects of temperature and pH (Schmid et al. 2019). Moreover, the effects of temperature on seaweed growth and physiological performance often depends intimately on both the region in the intertidal zone which the species inhabits (Roman et al. 2020) and the life history of the species (Hansen 1977). While trampling has been shown to have marked effects on the biomass of intertidal macroalgae including *Fucus gardneri* (Irvine 2005) and *Hormosira banksii* (Povey and Keough 1991), one would expect that the effect of trampling would depend intimately on both the species which is being trampled and the substrate which the trampling occurs upon. Furthermore, global change drivers often interact to impact ecosystems and organisms in unpredictable and nonadditive ways (Komatsu et al. 2019, Crain et al. 2008). Therefore, it is critical to explicitly test whether change in morphology for a given seaweed species has occurred in its natural environment, instead of making inferences from models of global change or from physiological experiments.

In this study, I tracked the change in size of 601 *Mazzaella splendens* (Setchell et N.L. Gardner) from sites along the Pacific Coast of both California and Washington state which were collected over a 150 year period (1851-2007). I was interested in determining: (i) whether a change in size had occurred; (ii) whether this change was dependent on the degree of human development at the site where the specimens were collected; and (iii) if change had occurred, whether there were possible mechanisms to account for that change. I chose *M. splendens* because it is a common species and thus a common herbarium specimen. Also, its maximum size is smaller than most herbarium sheets so I could be confident that the size data which I collected were reflective of the size of actual specimens. It also has a very long collection history. Most herbarium specimens do not have sufficient spatial and temporal extent to indicate whether long term change has occurred (Thom, personal communication).

This study has the potential to demonstrate that, despite high levels of intrinsic variability, change in morphology due to anthropogenic disturbances can be detectable in marine species over long time horizons and that the effects of anthropogenic disturbances on the morphology of seaweeds could exhibit threshold effects whereby sufficiently high levels of disturbance are needed in order to produce a change in morphology. If these threshold effects exist in a wide variety of seaweed taxa, it is possible that many intertidal species which have not yet experienced a change in morphology are at or near a tipping point where even a small change in levels of disturbance could result in substantial morphological change, and possibly, as a result, the structure and function of the intertidal ecosystems which these species inhabit.

Methods

I collected data from 601 *Mazzaella splendens* (Setchell et N.L. Gardner) herbarium specimens. All specimens originated from sites in the intertidal zone along the Pacific Coast of Washington and California. *M. splendens* is a common lower intertidal alga on the open rocky coast headlands from southern Oregon to California - with its full range extending from Honsu, Japan to northern Mexico (Abbott 1972). The collection spanned over 150 years with the earliest specimen collected in 1851 and the most recent set of specimens collected in 2007. The specimens were collected from the following locations in Washington: San Juan County (n=128), the Puget Sound proper (n=18), the Outer Coast and Bellingham (n=11). The collection sites from California were the following: Marin County (n=136), San Luis Obispo County (n=119), San Francisco County (n=70), and Monterey County (n=119). The majority of digital herbarium specimens (n=474) came from the UC Berkeley's Jepson Herbarium and the remaining set of digital specimens came from the UW Burke Herbarium Image Collection (n=47). All physical specimens were from the herbarium at Friday Harbor labs (n=80).

I measured the length and width of all digital *M. splendens* specimens using ImageJ. Length was calculated by taking the length from the end of the stipe to the apex of the blade along the central axis of the plant (Figure 1). For digital specimens, length was measured using the segmented line tool, and for physical specimens I used a string and a yardstick. Width was measured at the widest point along the specimen. The area of any curved leaflike shape is proportional to the length along its central axis rather than to its total length. In fact, any two leaves with identical sets of widths and central axis lengths will be equal in area (Ueda and Al-Sheikh, personal communication). Consequently, I measured the length along the central axis of all *M. splendens* specimens, because I felt that this measurement was more reflective of total thallus size. For specimens with multiple blades, length and width measurements were recorded only from the longest blade. I did not measure thallus size itself, because while those measurements would have been easy to perform initially, I wanted to use a measurement technique that would be easy to replicate in field studies.

For the pooled data across all sites, I performed a simple linear regression between length of *M. splendens* specimens, latitude and collection year. I also performed a simple linear regression between *M. splendens* width and collection year. Because length was more reflective of the area of *M. splendens* and the relationship between length and collection year in the pooled data was more robust than the relationship between width and collection year, I performed a simple linear regression between length of *M. splendens* specimens for specimens at each collection site. I excluded Bellingham and Outer Coast specimens from my analysis, because I felt that the small number of specimens (n=11) in that cohort weakened the statistical power of those data.

In order to estimate the anthropogenic impacts present at each site I used census data to calculate change in population density in the counties where collections were made. I initially planned on using percent change in population density, but population densities were close to zero at many sites, so I reasoned that current population density in 2010 (the census closest to when specimen collection ended) would better capture intensification of human impacts. For Puget Sound, I used census data from Seattle to calculate population density.

I was interested in comparing the functions describing the relationship between level of human impact and change in algal size between my study system and earlier studies. I used data from Povey and Keough (1991) to show how initial experimental tramples produced larger decreases in macroalgal size than subsequent tramples. I applied a log-scale to the number of tramples and then performed a simple linear regression to show that the relationship between number of tramples and loss of biomass followed a logarithmic function.

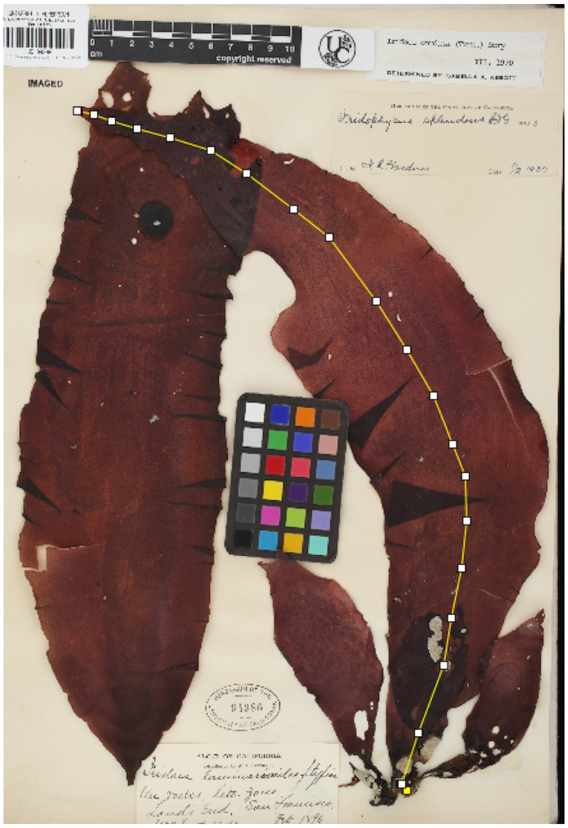

Figure 1. Measuring length along the central axis of a specimen in ImageJ. Yellow segments were made using the segmented line tool.

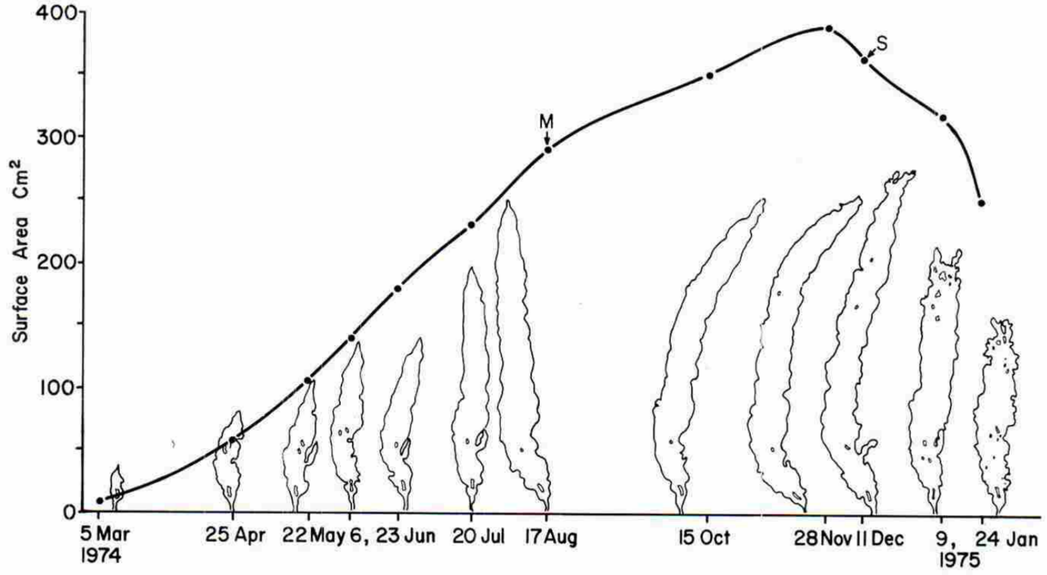

FIG. 1. In situ ontogenetic progression of tagged *Iridaea cordata* (032): M = date tetrasporangial sori first observed (165 days from tagging); S = onset of blade senescence (281 days from tagging).

Figure 2. Seasonal growth of *M. splendens* (formerly Iridaea cordata). Taken from Hanson (1977).

Results

There was a statistically significant relationship between year of collection and length of *M. splendens* specimens for the dataset consisting of specimens from all sites (p=2.62E-09) (Figure 3). In this dataset, year of collection accounted for 5.7% of the variation in the length of *M. splendens*. There was also a statistically significant relationship between latitude and length in the set of all *M. splendens* specimens (p=0.00368) (Figure 4). However, only 1.4% of the variation in length of *M. splendens* specimens could be attributed to the latitude of the collection site. There was no statistically significant relationship between year of collection and the width of *M. splendens* specimens in the set including all sites (p=0.254) (Figure 5).

For Monterey, Marin, San Luis Obispo, and San Juan counties, there was not a significant relationship between year of collection and length of *M. splendens* specimens (p=0.536, 0.558, 0.118, 0.346) (Figures 6-9).

In specimens from the Puget Sound, there was a significant negative relationship between year of collection and *M. splendens* specimen length (p=0.0199) (Figure 10). Year of collection explained 29.7% of the variation in *M. splendens* length. Length of *M. splendens* declined substantially over the course of collection period: the average length of specimens during the last year of collection was only 37.4% of the average length of specimens collected during the first year of collection. The slope of the regression line was -1.40 ± 0.540, further underlining the negative relationship between year of collection and *M. splendens* specimen length.

There was also a significant negative relationship between year of collection and *M. splendens* length in San Francisco County (p=1.01E-5) (Figure 11). Year of collection explained 25.1% of the variation in *M. splendens* length. Length of *M. splendens* declined substantially over the course of collection period: the average length of specimens during the last year of collection was only 35.2% of the average length of specimens collected during the first year of collection! The slope of the regression line was -1.43 ± 0.301, further underlining the negative relationship between year of collection and *M. splendens* specimen length.

Notably, there was a statistically significant negative relationship between year of collection in the two counties with the highest population densities: San Francisco and the Puget Sound. Moreover, San Francisco County, which has the highest population density (17,179 people/square mile) had a more robust relationship between size and collection year.

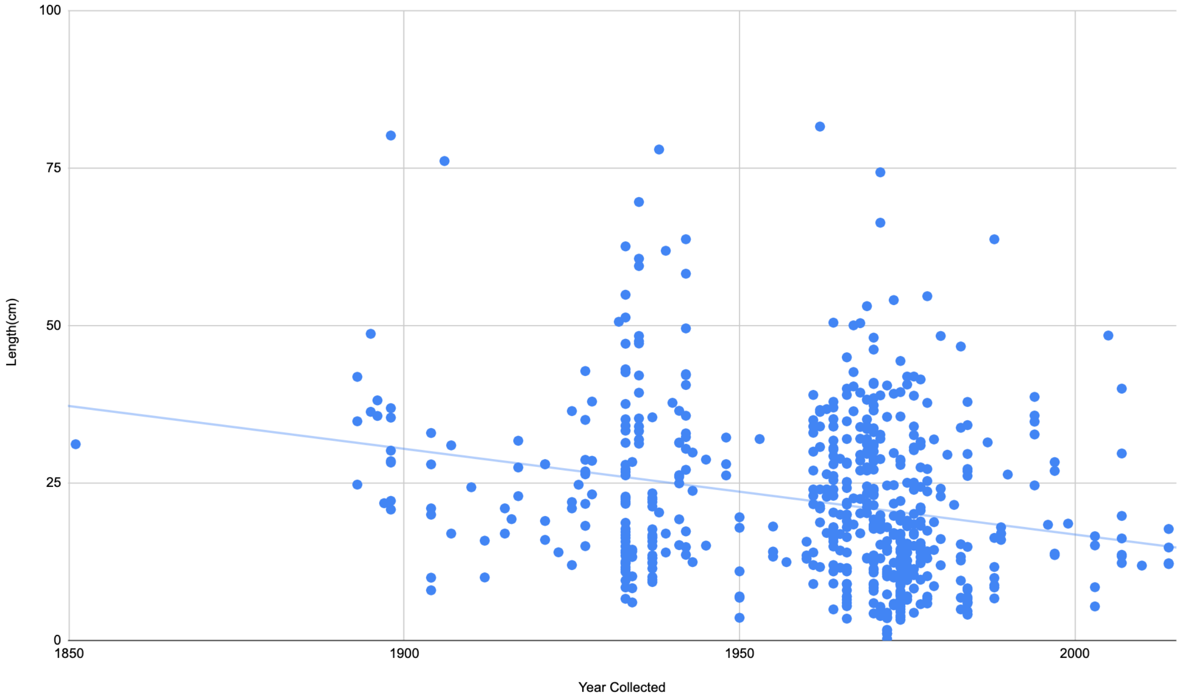

Figure 3. Length of *Mazzaella splendens* vs. year collected (n=601).

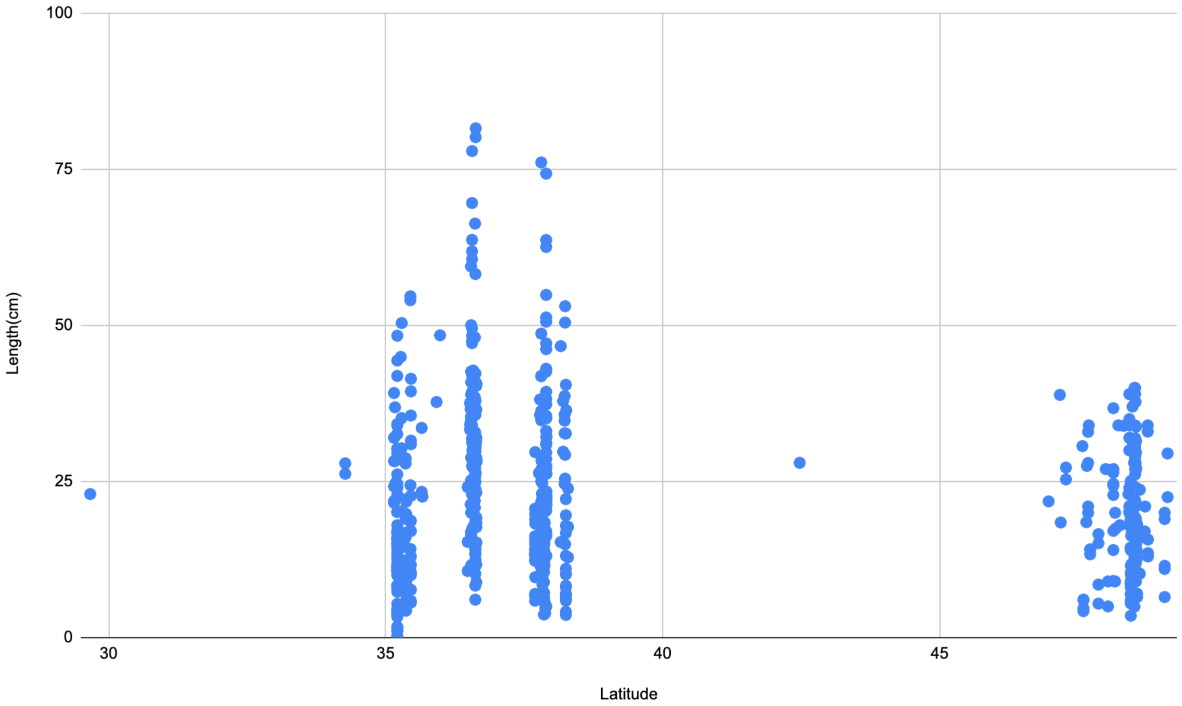

Figure 4. Length of *Mazzaella splendens* vs. latitude of collection site (n=601).

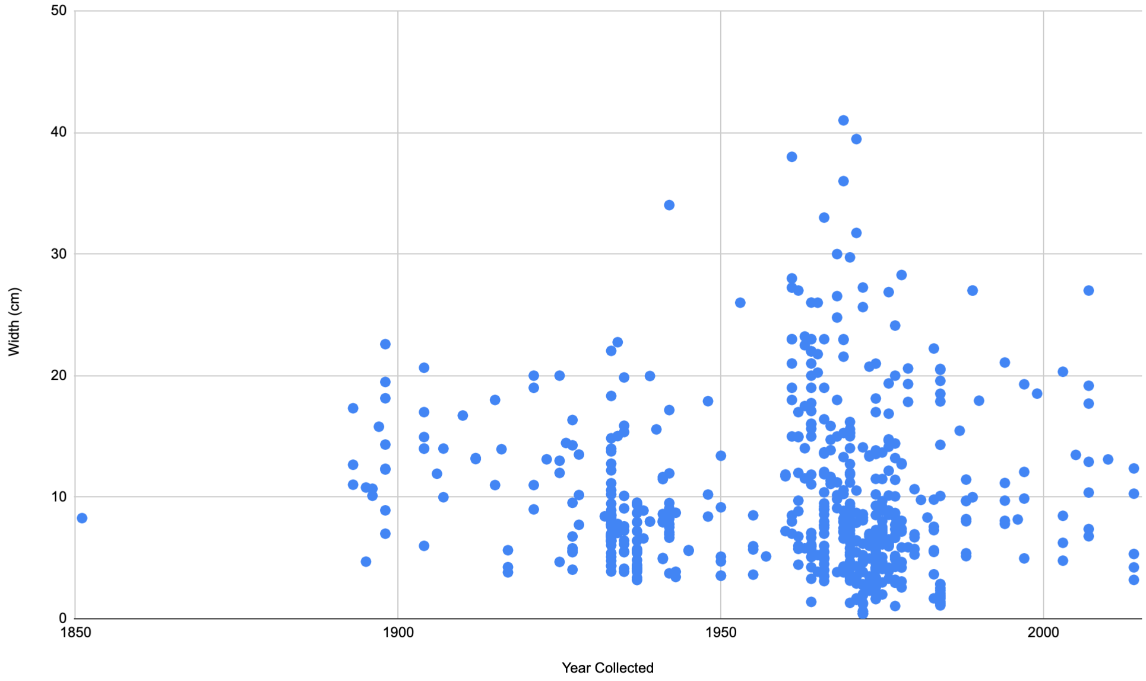

Figure 5. Width of *Mazzaella splendens* vs. year collected (n=601).

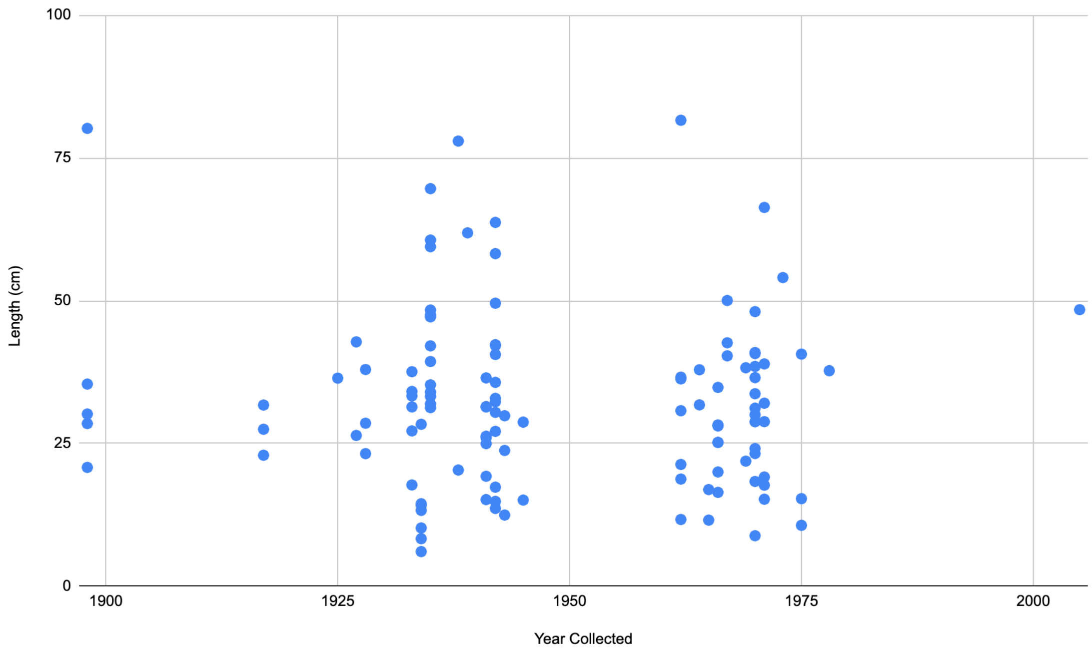

Figure 6. Length of *Mazzaella splendens* vs. year collected in Monterey County

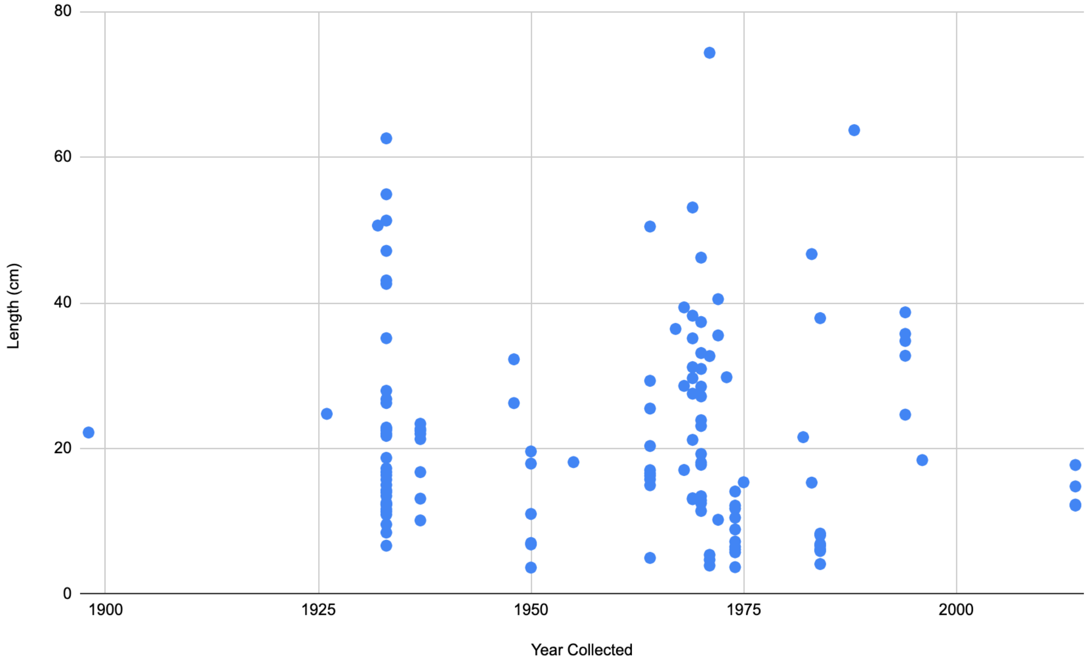

Figure 7. Length of *Mazzaella splendens* vs. year collected in Marin County

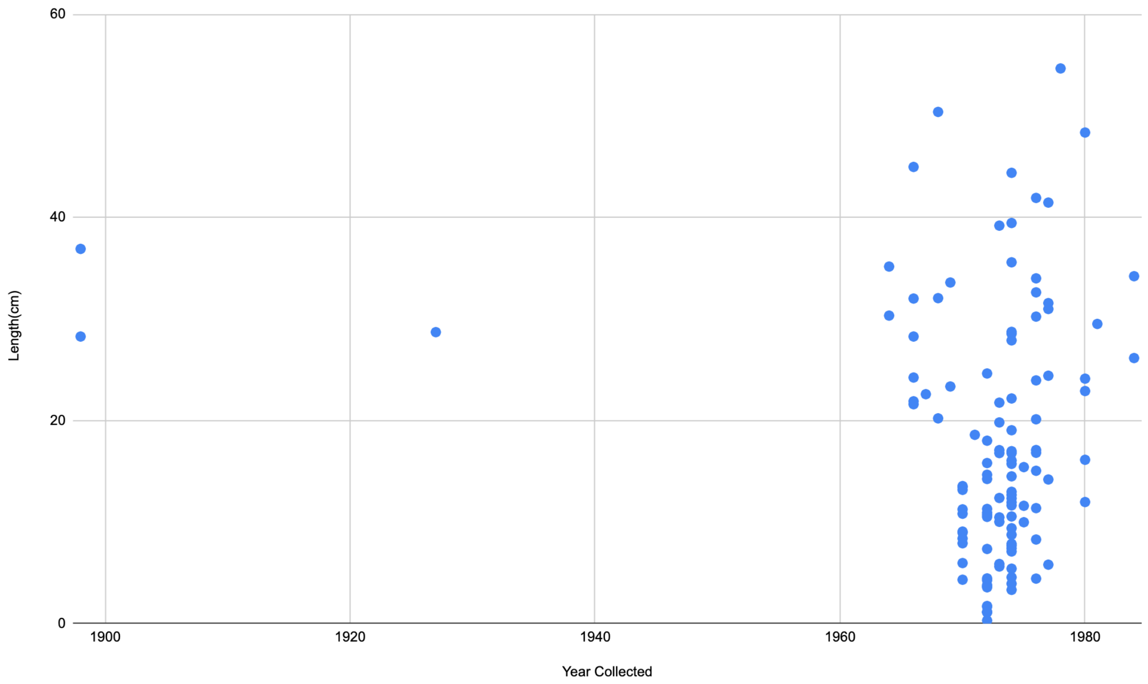

Figure 8. Length of *Mazzaella splendens* vs. year collected in San Luis Obispo County

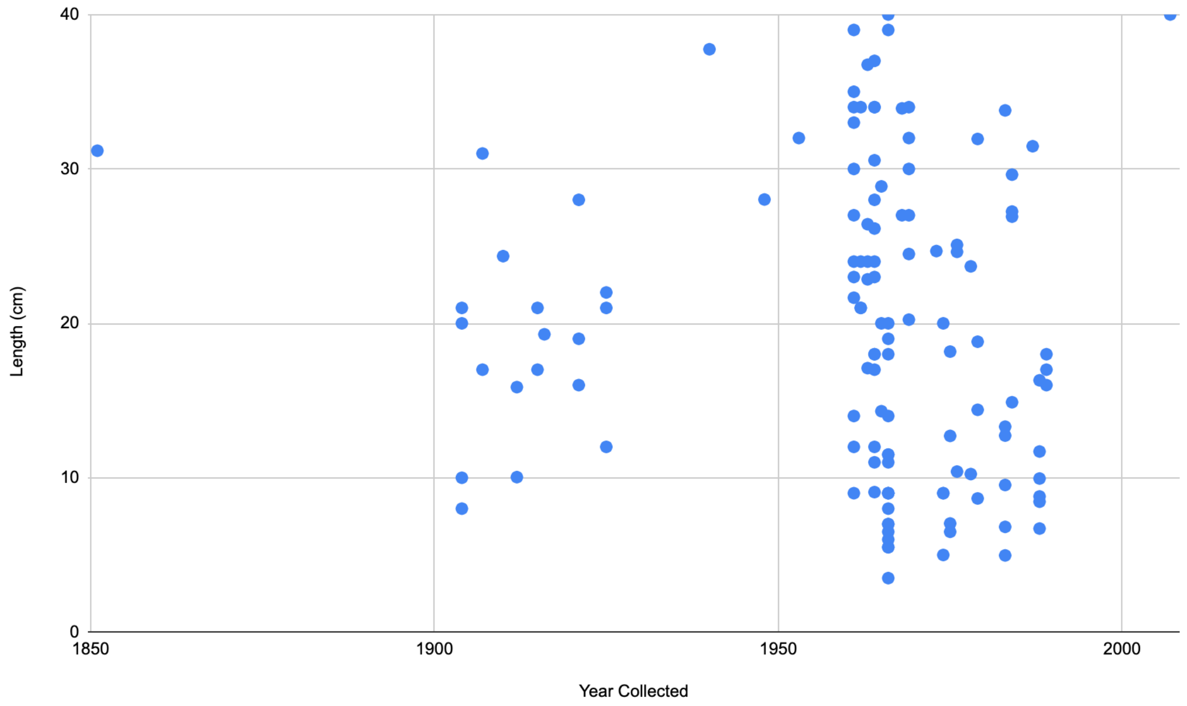

Figure 9. Length of *Mazzaella splendens* vs. year collected in San Juan County

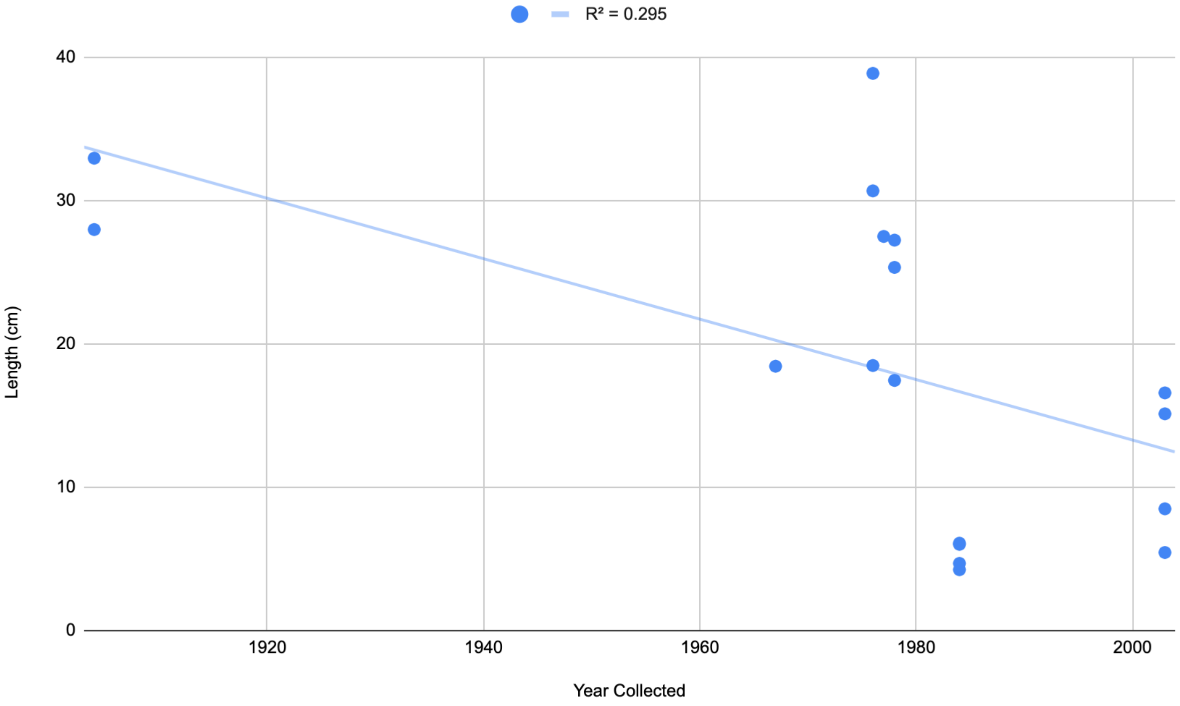

Figure 10. Length of *Mazzaella splendens* vs. year collected in Puget Sound proper.

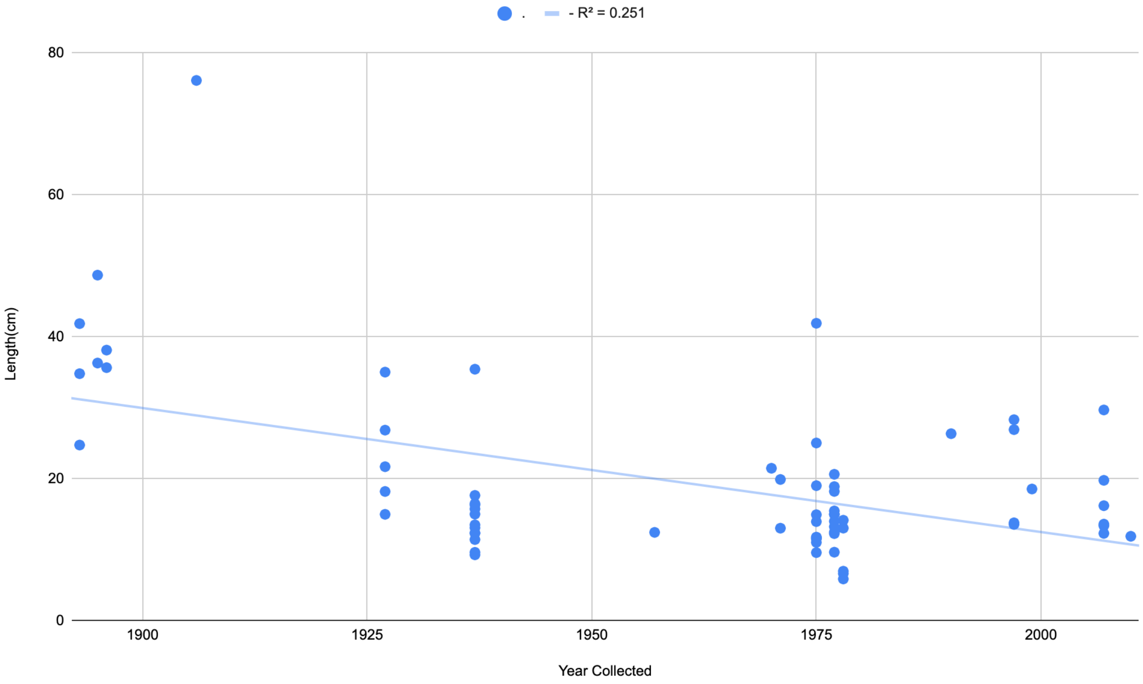

Figure 11. Length of *Mazzaella splendens* vs. year collected in San Francisco County.

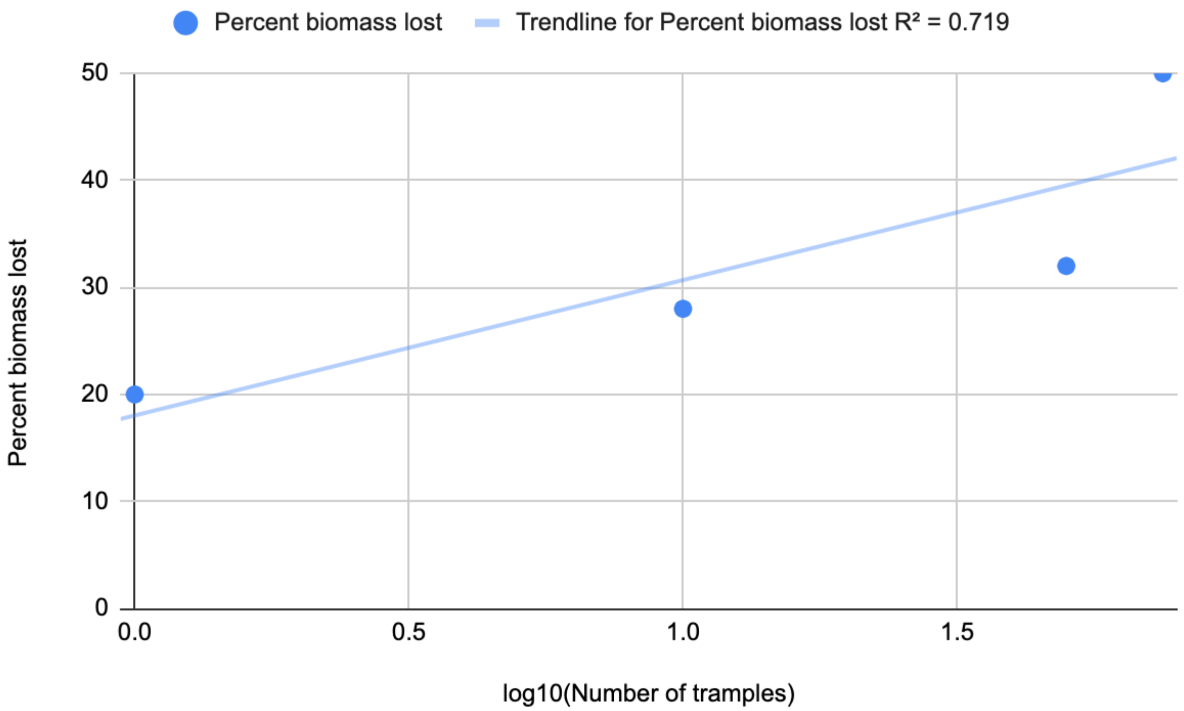

Figure 12. Relationship between # of tramples and percent biomass lost in *Hormosira banksii*. Data from Povey and Kough (1991).

Discussion

The key result from this study is that there was a significant change in size over time among *M. splendens* specimens from the Puget Sound proper and San Francisco County but there was not a significant change in *M. splendens* size from specimens at other sites. The Puget Sound proper and San Francisco have substantially higher population densities (17,179 people/square mile and 7,251/square mile, respectively) than the county with the next highest population density - Marin County (485 people/square mile). Data from experiments by Povey and Kough (1991) on the effects of trampling on the biomass of the intertidal fucoid alga *Hormosira banksii* demonstrate that the percent biomass lost (a close correlate to size) was related to the $\log_{10}$ of trampling intensity (Figure 12). Even a single trample was enough to produce a 20 percent decrease in biomass. Given these results, if trampling had a similar effect on *M. splendens,* one would expect that there would be substantial reductions in size across *M. splendens* across all sites. Assuming that trampling intensity scales with population density, and that size decreases scale with the $\log_{10}$ of trampling intensity, one would expect that *M. splendens* in Marin County would have experienced 63 percent of the total decrease of size seen in specimens from San Francisco county. The fact that a change in size only occurred in the highest population density regions led me to conclude that *M. splendens* exhibits threshold effects with respect to change in morphology which results from anthropogenic disturbance. In this section, I explore why threshold effects may exist and explore the possible mechanism behind the observed change in size of specimens from San Francisco and the Puget Sound. Two likely mechanisms which may have impacted the size of *M. splendens* are trampling and change in temperature. Because an explicit test of the mechanism behind the observed change in the size of *M. splendens* was not performed, all of these proposed mechanisms are purely speculative.

The effects of trampling on a given seaweed obviously depends intimately on the structure and morphology of the seaweed being trampled. *Hormosira* is particularly vulnerable to the effects of trampling - its thallus is composed of a string of delicate water-filled spherical pneumatocysts. One would expect that *M. splendens* might resist trampling more than *Hormosira*. However, the fact that *M. splendens* may resist trampling to a greater degree than *Hormosira* still fails to explain why threshold effects were seen across sites. Schiel and Taylor (1998) demonstrated that season and substrate type all had an effect on the amount of *Hormosira* lost through trampling. While there are likely substantial differences between collection sites in all counties, all specimens were collected in the rocky intertidal and during the summer, so it is unlikely that differences in the substrate types and season are sufficient to account for differences in change of size. Schiel and Taylor (1998) found that loss of biomass was higher at sites with softer substrate. Surfaces with low permeability found in highly populated areas, like concrete, could have increased levels of sediment runoff, which might have effectively increased the "softness" of the substrates found in urban areas. While the effects of sedimentary runoff are a possible effect that could have accounted for the differences in changes of size *M. splendens* specimens, Marin and San Luis Obispo counties still have high levels of concrete cover, so sedimentary runoff is unlikely to have been the sole driver of differences in *M. splendens* size between counties. The effects of trampling also depend on the other species present (Brosnan and Crumrine 1994) and the trophic structure of that community (Menge 1991). I contend that sites in adjoining regions, like San Francisco and Marin country are likely similar enough in their species composition and trophic structure so that differences in these factors would not be sufficient to account for the fact that significant change in size occurred among specimens only in regions with the highest population density.

One possibility is that trampling in areas of lower human density were sufficient to produce changes in morphology of *M. splendens*, but that these changes were sufficiently small that *M. splendens* specimens were able to recover. With higher human populations, one would expect that there would not only be greater intensity of trampling in any individual trampling event, but that there would be greater frequency of (and thus less time between) trampling events. Macroalgae are not only sensitive to the intensity of trampling events but the duration between them (Schiel and Taylor 1998). In a study by Povey and Kough (1991), sites with 2 tramples fully recovered to control levels of density within 300 days, but sites with 25 tramples per day had not recovered to control levels within 500 days. It is also possible that there are density dependent effects on the growth and performance of *M. splendens* and that by reducing density to a sufficient degree, intense trampling would decrease growth and performance. Density dependent effects on growth have been documented in other lower intertidal seaweeds such as *Pterygophora californica* (Reed 1990).

There are also possible edge effects with respect to trampling, and increases in trampling intensity may increase the intensity of these edge effects. Povey and Kough (1991) documented that trampled edges of *Hormosira* mats recovered more slowly, because they were more susceptible to grazing by snails from nearby rocks. One further possibility is that intense trampling compromises the ability of *M. splendens* specimens to reproduce. Thalli of *M. splendens* are either tetrasporophytes, female gametophytes, or male gametophytes. If any of these three thalli types are damaged the ability of a *M. splendens* to reproduce and complete a full life cycle is compromised. While compromising reproductive ability would likely have more effect on abundance than morphology, consistent trampling that affects reproduction could alter population genetics of *M. splendens* in such a way that would alter their physiological performance and therefore growth. Free floating spores of *M. splendens* are only viable for a few days which led Dyck and DeWreede (1995) to propose that the frequency of spores traveling long distances is quite low. Therefore, it is reasonable to infer that any genetic change that occurred in a local population would persist for long periods of time.

As noted earlier, increased temperatures have been associated with declines in physiological performance, growth, and size across many marine and terrestrial organisms (Sheridan and Bickford 2011). These shifts are often driven by the effects of temperature on metabolic processes - raising temperature raises metabolic rates- and sometimes by more complex feedbacks driven by biogeochemical cycles (Sheridan and Bickford 2011). In the case of macroalgae, raising temperature lowers the availability of nitrate by altering patterns of biogeochemical cycling,(Tegner 1996) which ultimately lowers growth. However, high nitrate levels due to runoff may ameliorate the effects of increased temperature on growth of *M. splendens*. Roman et al. (2020) also demonstrated that heat waves – periods of particularly high temperatures - were key in lowering the survivorship and physiological performance of intertidal seaweeds. However, elevated seawater temperatures during immersion had little effect on performance and survivorship relative to air temperature during periods of emmersion in the study. For a lower intertidal seaweed like *M. splendens*, which experiences relatively little emmersion, higher air temperatures may have little effect on physiological performance. In fact, earlier physiological studies demonstrated that growth of *M. splendens* is not correlated with temperature (Hansen 1977). However, it is hard to know whether current (higher) thermal regimes may affect growth in a way that was not apparent in this study. Given that *M. splendens* exhibits strong seasonality in its pattern of growth (Figure 2) it is also possible that a change in SST could influence factors that relate to the timing of growth events. The onset of die-back of *M. splendens* blades is determined by the highest temperature in a season (Hansen 1976). Because one aspect of climate change is higher variability in temperature, it is possible that more extreme temperatures would cause die-offs and size decreases of *M. splendens.* These die-offs are unlikely to be detectable through herbarium collections, however, because collectors are unlikely to collects stub-like specimens. Furthermore, there were not substantial differences in maximum SST in the historical records between Marin and San Francisco counties. One would expect there to be substantial differences in maximum SST between regions if it were driving a change in morphology.

In both marine and terrestrial systems, global change drivers (changes in temperature, ocean acidification, etc.) often interact to impact ecosystems and organisms in unpredictable ways (Komatsu et al. 2019, Crain et al. 2008). Moreover, no single anthropogenic impact clearly drove a change in the size of *M. splendens.* Given that the change in size of *M. splendens* due to anthropogenic impacts may exhibit threshold effects it is particularly useful to think of the effects of human disturbances and global change factors "epidemiologically" (Lewontin and Levins 1985, Paine et al. 1998) whereby the effect of any individual factor is not sufficient to produce a change in morphology, but each factor increases the susceptibility to a change. In the case of the effects of trampling, increases in SST may weaken the algae and make them more susceptible to the effects of trampling. However, assuming that differences in *M. splendens* size are driven by some combination of trampling and more general anthropogenic change, it is unclear whether the underlying driver of a change in morphology is trampling or other global change factors.

Determining the exact mechanism behind the change in size seen in *M. splendens* in San Francisco and the Puget Sound is clearly a direction for further research. It would also be wise to measure samples from other highly populated urban areas along the Pacific Coast (e.g., Los

Angeles) to determine whether a change in size occurred in specimens in those locales. That would strengthen the hypothesis that a threshold effect is occurring. Despite the lack of a mechanism, it is powerful to have demonstrated an observed change in the size of a species in a system with high intrinsic variability. This project underscores the importance of both biological collections and education in natural history. Despite general increases in funding for science, government support for taxonomic and systematic research has declined substantially in the last 40 years. Fewer and fewer students receive any training in natural history (Futuyma 1998, Travis 2020) and can go through a whole undergraduate major in ecology/evolutionary biology without ever going outside or knowing the name of organisms. Hopefully more researchers will realize the important role which natural history plays in detection (and combatting) global change.

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