Direct and indirect trophic effects of predator depletion on basal trophic levels

Honors Thesis

Steve Hagerty
Sc.B. Candidate
Environmental Science

Brown University
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**Thesis Abstract**

**Date:** 5/1/15  
**Student Name:** Steven Hagerty  
**Practicum Advisor:** Mark Bertness  
**Project Title/Subject:** Direct and Indirect Impacts of Predator Depletion on Basal Trophic Levels

**Purpose of Research:** Human growth and development have heavily degraded coastal ecosystems through cascading impacts across multiple trophic levels. Understanding both the direct and indirect trophic effects of human activities has important implications for coastal conservation. In New England, recreational overfishing has triggered a regional trophic cascade. Depletion of predators releases the herbivorous purple marsh crab from consumer control, leading to overgrazing of marsh cordgrass and salt marsh die-off. The direct and indirect trophic effects of predator depletion on basal trophic levels, however, are not well understood.

**Methods:** Using observational and experimental data, we examined the hypotheses that: 1) direct trophic effects of predator depletion decrease meiofaunal abundance by releasing deposit feeding fiddler crabs from consumer control, and/or 2) indirect trophic effects of predator depletion increase meiofaunal abundance through ecosystem engineering - increasing borrowing releases blue carbon via the erosion of accreted marsh peat.

**Results, Conclusions, and Recommendations:** Experimental deposit feeder removal led to 23% higher meiofaunal density at die-off than at healthy sites, while reciprocal transplant of sediment from die-off and healthy sites revealed that carbon-rich die-off sediment increased meiofauna density by over 164%. This suggests that consequences of the trophic downgrading of coastal habitats can be driven by both direct and indirect trophic mechanisms that may vary in direction and magnitude, making elucidation of their effects dependent on experimental manipulations.
INTRODUCTION

Human impacts on coastal ecosystems

Human impacts on ecosystems and the services they provide is one of the most pressing problems for conservation biology and ecology (Vitousek et al. 1997a, Kareiva et al. 2007). Understanding these impacts sufficiently to predict and/or mitigate them requires elucidating their mechanistic nature, interactions and cumulative effects.

All ecosystems have been impacted by human activity, whether on local scales by human development and point source pollution (Vitousek et al. 1997a, Goudie 2013) or on global scales by climate change and shifts in the global nitrogen supply (Hulme at al. 1999, Vitousek et al. 1997b, Galloway et al. 2008). Accelerated by unchecked human population (Luck 2007, Goudie 2013) and economic growth (He et al. 2014), these impacts have led to the unprecedented collapses or major degradation of critical marine ecosystems, including coral reefs (Mora et al. 2008, Hughes et al. 2015), seagrasses (Lotze et al. 2006), mangroves (Kathiresan and Bingham 2001, Alongi 2002), benthic continental shelves (Jackson et al. 2001, Hall 2002), pelagic communities (Game et al. 2009) and salt marshes (Gedan et al. 2009, Bertness et al. 2002). A recent compilation of available data predicts that human impacts on marine ecosystems has globally pushed most marine ecosystems to tipping points of ecological collapse (McCauley et al. 2015). This makes elucidating the causes and effects of human impacts on ecosystems an ecological problem of large concern (Barbier et al. 2008, Barbier 2012).

Some critical questions remain regarding human influence, such as whether impacts are additive, synergistic, or counteractive (Vitousek et al. 1997a, Crain et al. 2008), whether effects are largely direct or indirect (Wootton 1994, Werner and McPeek 1994, Schmitz and Suttle 2001, Vetter et al. 2001).
2005) and the cumulative impact of direct and indirect effects (Vitousek et al. 1997, Engelhardt and Ritchie 2001, Vetter et al. 2005). Here we examine the combination of effects of human-driven predator depletion in New England salt marshes. We test whether predator depletion is strengthening lower trophic level consumer control on meiofauna, and/or leading to salt marsh die-off conditions that promote meiofauna abundance, by increasing carbon substrate supply through ecosystem engineering.

Predator depletion and New England salt marshes

Salt marsh die-off was first reported in New England in 2004 (Smith 2005), but was later shown by historical reconstruction to have started in the early 1980s (Coverdale et al. 2013a). Comparative and experimental studies have shown that predator depletion leads to increased densities of the herbivorous, burrowing purple marsh crab, *Sesarma reticulatum*. At high densities, *Sesarma* denude the low marsh of *Spartina alterniflora* (hereafter *Spartina* or cordgrass), both above and belowground (Holdredge et al. 2010, Altieri et al. 2012). Along steep creek banks, barren, heavily burrowed peat calves off and gradually erodes away. On less steep marsh banks, heavily burrowed peat erodes in situ, expanding abandoned burrows and releasing dead plant debris and sediment no longer bound together by live plant roots. This release of carbon-based peat sediment initiates a microbial food chain and meiofauna production links (Lopez and Levinton 1987). On Cape Cod (Altieri et al. 2012), Narragansett Bay (Bertness et al. 2014) and Long Island Sound (Coverdale et al. 2013b), this has led to the conversion of hundreds of acres of marsh habitat, which represents the legacy of over 200 years of peat accretion (Coverdale et al. 2014), to carbon rich peat sediment.

New England salt marsh die-off is not impacting all salt marshes. While still spreading (Bertness et
al. 2014), die-off almost exclusively occurs on marshes near or affected by heavy recreational fishing pressure (Altieri et al. 2012). Even on Cape Cod where die-off has been ongoing for 35 years, marshes protected from recreational fishing (e.g. in reserves, embedded within communities or inaccessible by boat or car) are largely free from die-off (Altieri et al. 2012, Bertness et al. 2014). Recreational fisheries landings exceed 10 million tons globally (Cooke and Cowx 2004), and can rival or exceed commercial fishing in coastal habitats (Beal et al. 1998, Schroeder and Love 2002).

**Consequences on meiofauna**

To date, mechanisms of the salt marsh recovery have been explored (Altieri et al. 2013, Bertness and Coverdale 2014), but the consequences of salt marsh die-off on other trophic levels have yet to be examined. Lower or basal trophic groups, like meiofauna, have received little attention. Meiofauna are small benthic invertebrates in both marine and freshwater habitats that are operationally defined as organisms that pass through a 1000 µm sieve, but are retained by a 63µm sieve. They are important in benthic habitats due to their high abundance, diversity, productivity and essential role in benthic food webs, particularly in processing detritus via the microbial food web (Coull, 1999). A limited number of studies have examined the response of benthic meiofauna to direct deposit feeder addition or removal (Hoffman et al. 1984, Schratzberger and Warwick 1999, Fleeger et al. 2008), most providing evidence for the meiofauna regulatory capacity of deposit feeders.

However, the underlying mechanisms of higher trophic level effects on meiofauna are not fully understood, especially for the indirect pathways such as altering habitat structure or nutrient cycling through ecological engineering effects. In fact, a recent research from freshwater realm (Majdi et al. 2013) has posited that the meiofauna colonization was indirectly improved by predator-flatworm through enhancing the deposition and retention of fine sediments. In New England salt marshes, *Sesarma* and *Uca* crabs engineer their environment in numerous ways (Holdredge et al. 2010, Coverdale et al. 2012), most notably through burrowing activity which increase rates of biological
and chemical exchange, and transport of detritus, which enhances microhabitat heterogeneity and decomposition rates. At die-off sites, with more consumer activity from fewer top predators, the effects of engineering should be more pronounced. The direct and indirect impacts of this anthropogenic trophic cascade collapse on meiofauna are unknown.

QUESTION AND HYPOTHESES

In this paper we examine the consequences of predator depletion in New England salt marshes on meiofauna. What are the mechanisms and direction of impact of predator depletion on meiofauna? Specifically, we experimentally test competing hypotheses (Fig. 1):

1) predator depletion directly decreases meiofaunal abundance and control by increasing deposit feeder densities and consumer control of meiofauna

and/or

2) predator depletion indirectly increases meiofaunal abundance by driving salt marsh die-off, leading to more favorable conditions for meiofauna

- with fewer predators, Sesarma burrow and engineer their environment more, releasing accumulated peat and sequestered carbon, more favorably supporting microbial and detritus food sources for meiofauna.

Since the direct trophic consequences of human-generated trophic cascades are relatively predictable and well-studied, our work is focused on the less studied indirect consequences of trophic cascades.
This work can help assess the relative importance of these indirect effects in trophic interactions, as these effects are often characterized as system specific and difficult to predict or generalize (Menge 1995).

MATERIALS AND METHODS

Study Sites
Our research was carried out on Cape Cod, MA and Narragansett Bay, RI at eleven previously studied sites (Fig. 2; Coverdale et al. 2013c, Bertness et al. 2014). Five of these sites had never experienced catastrophic creek bank die-off (> 50% of marsh edge entirely vegetated) and were operationally designated as “healthy” marshes (Common Fence Point, Herring River, Red River, Sippiwissett, and Waquoit Bay), three were operationally defined as “recovery” sites (Parker River, Smith Cove, and Wing’s Neck) that had experienced severe die-off, but more than 50% of the marsh creek bank edges had recovered, and three were operationally defined as “die-off” marshes (Colt State Park, Hundred Acre Cove and Saquatucket Harbor) that had active die-off with >50% of their creek banks currently affected. Detailed information and the location of these sites can be found elsewhere (Coverdale et al. 2013c, Bertness et al. 2014).

Correlative sampling
At each of these sites we quantified predation pressure on fiddler crabs (*Uca pugnax*, hereafter *Uca*), *Uca* burrow densities, meiofaunal densities, and substrate characteristics (% nitrogen and carbon).

Predation pressure on *Uca* was quantified in early August 2014 at each site by tethering 45 adult male crabs, 15 in open controls, 15 protected from predation in hardware cloth cages, and 15 exposed to predation in cage control treatments. Crabs were tied and glued to 15cm tethers (see Altieri et al. 2012 for methods) and pinned to the low marsh substrate at low tide with access to a shallow burrow
and scored for survivorship after two tidal cycles. Predation was easily assessed since crab predation events left broken carapaces attached to the tethers or no remnants.

*Uca* burrow density counts were made in the low marsh at each site in late August 2014, by randomly throwing a 1 × 1m quadrat >3m apart along creek banks and counting the *Uca* burrows (*N* = 10/site). *Uca* burrows are easily distinguished from the burrows of the herbivorous crab *Sesarma reticulatum*, since *Sesarma* burrows are larger, have multiple surface openings and never associated with deposit feeding pellets. *Uca* burrows have a single surface opening, are typically in softer substrate and are usually associated with feeding pellets.

Nitrogen and carbon content by weight was determined by taking 8 independent replicate samples from each site. Each sample was obtained with a 2.5 cm diameter corer to a depth of 3cm from sampling plots (0.25 × 0.25 m) randomly established at each site 50-100cm below the cordgrass border. After drying to constant weight at 60 °C, sediment samples were ground and analyzed for percent carbon and nitrogen with an elemental autoanalyzer (Model NC2100; ThermoQueat CE Instruments, San Jose, CA, USA). Sediment carbon content was used as a proxy for organic content or the contribution of eroded peat to the substrate (Coverdale et al. 2014).

Meiofaunal densities were evaluated by taking sediment from sampling plots (0.25 × 0.25 m) at three healthy (Common Fence Point, Herring River and Waquoit Bay), recovery (Wing’s Neck, Smith Cove and Parker River) and die-off (Saquatucket Harbor, Hundred Acre Cove and Colt State Park) sites in August 2014. Six sampling plots (0.25 × 0.25 m) were randomly established at each site 50-100cm below the cordgrass border. Three sediment cores were taken with a 2.5 cm diameter corer to a depth of 3cm from each plot and combined into a single composite sample to reduce spatial variance. These samples were immediately fixed with 10 % formalin for > 7 days, after which time meiofauna were extracted by flotation with Ludox TM and counted under a dissecting microscope.
Uca and meiofauna density were analyzed with nested ANOVA (sample sites nested within site types) to determine differences among habitat types (die-off, recovery and healthy). Tukey’s HSD test was used for post-hoc analysis. Since homogeneity of variances could not be achieved for predation pressure and substrate characteristics, non-parametric Kruskal-Wallis tests followed by a Dunn’s post-hoc test were performed with site type as the main factor. We performed linear regression to examine the relationship between Uca density, substrate carbon content and predation rate.

Consumer removal experiment

To test the hypothesis that predator depletion at salt marsh die-off sites leads to increased Uca densities and concomitant reduction in meiofauna densities, we ran a total consumer removal caging experiment at two die-off (Colt State Park and Saquatucket Harbor) and two healthy sites (Common Fence Point and Herring River). We predicted that if direct trophic interactions dictated meiofaunal densities, experimentally excluding consumers would have a greater effect at die-off than control sites. At each site we randomly marked 18 plots (25 × 25 cm) in sediment 50-100cm below the cordgrass border as: control plots (N = 6/site), consumer removal cages (20 × 20 × 5cm (L × W × H) 4 cm mesh stainless steel hardware cloth; N = 6/site), and cage controls (identical to consumer removal cages but with their sides removed to allow access to crawling benthic organisms like Uca; N = 6/site).

These treatment replicates and ambient sediment samples were taken adjacent to each replicate the first week of June 2014. Plots were maintained weekly for 8 weeks after which time plot sediment was sampled for meiofaunal analysis with a 2.5 cm diameter corer to a depth of 3cm. Three cores from each plot were sampled and bulked into a composite sample. Total meiofauna density was analyzed with a split-plot ANOVA, with habitat (die-off and healthy) as the between-plot factor, site nested within habitat types, and caging treatment (cage, cage control, control) as a with-plot factor.
Data were log-transformed to meet the ANOVA assumptions. Tukey’s HSD test was used for post-hoc analysis.

**Sediment-type experiment**

To examine the hypothesis that carbon rich sediment at die-off sites leads to increased meiofaunal densities in comparison with healthy sites that have not been enriched with eroding carbon rich peat, we ran a sediment type manipulation experiment between a die-off (Squatuket Harbor: % carbon = 18.6 ± 0.3; % nitrogen = 1.1 ± 0.02; C to N ratio = 16.8 ± 0.07) and a healthy (Herring River: % carbon = 0.2 ± 0.01; % nitrogen = 0.02 ± 0.001; C to N ratio = 8.3 ± 0.2) site. At both sites, we collected ~ 2L of surface (top 5cm) sediment and returned it to the laboratory. Sediments from each site were filled into 18 containers each (PVC tubes, 50mm in length and 2.6 mm in diameter) and retained with fishing net end caps (1 mm mesh nylon). The meiofauna in 12 containers of each sediment type were eliminated by freezing at -20 °C for 48hr, then incubating at 30 °C for 72hr, and freezing for another 48hr (Ronn et al. 1988; Blouin et al. 2005). The remaining 6 tubes of each type were not frozen and returned to the original site as a procedural control to test the tube effect on meiofauna communities. Sediment type was labeled with color-coded cable ties and fishing line. Sediment tubes were deployed at each site (6 die-off meiofauna-eliminated sediment, 6 healthy meiofauna-eliminated, and 6 procedure control) 50cm below the intertidal cordgrass border at a depth of 3cm. Tubes were buried horizontally and separated by > 25cm. Plots were checked and maintained weekly. After 8 weeks, sediment tubes were collected, and 6 control sediment samples of the same volume were taken near the tubes. Meiofauna in each replicate was washed and quantified. Meiofauna densities were transformed as necessary and analyzed with a 2-way ANOVA, with treatment (die-off sediment, healthy sediment, procedural control and control) and site (Herring River, Squatuket Harbor) as factors.
RESULTS

Correlative sampling
Predation intensity varied across habitat types ($H_{2.11} = 6.69, p = 0.035$; Fig. 3A). The predation rate on tethered *Uca* at healthy sites ($80 \pm 11\%$) was four times higher than at die-off sites ($20 \pm 7\%$). Predation at recovery sites ($58 \pm 5\%$) was also greater than at die-off sites, but the difference was not significant. *Uca* abundance varied among marsh types in reflecting differences in predator control ($F_{2.99} = 128.6, p < 0.001$; Fig 2B). *Uca* density at die-off sites was twice that of healthy sites, and intermediate at recovered marshes. Substrate carbon content (Fig. 3C) and nitrogen content (Fig. 3D) also varied among marsh types with a similar pattern ($H_{2.88} = 66.5, p < 0.001$; $H_{2.88} = 64.4, p < 0.001$, respectively). Healthy sites had the lowest carbon and nitrogen content, recovery sites intermediate, and die-off sites the highest. Regressions between *Uca* densities, sediment carbon content and predation rate revealed that inter-site variation in predation depletion explained 82% of the inter-site variation in *Uca* density ($p < 0.001$; Fig. 4A) and 67% of the inter-site variation in sediment carbon content ($p = 0.002$; Fig. 4B). Recovery sites had higher meiofaunal density than healthy and die-off sites ($F_{2.45} = 10.49, p < 0.001$; Fig. 3E), but no difference in meiofaunal density was detected between healthy and die-off sites (Tukey’s HSD post hoc, $p > 0.05$).

Consumer removal
After eight-weeks of consumer removal, meiofaunal density in cages was significantly higher than in controls and cage controls at both die-off and healthy sites, suggesting that the consumer control by *Uca* on meiofauna is significant ($F_{2.64} = 42.0, p < 0.001$; Fig. 5). Excluding *Uca* led to a 75% increase in meiofaunal density at die-off marshes, but only a 52% increase in healthy marshes, reflecting differences in *Uca* densities between marsh types.

Sediment-type experiment
The sediment type manipulation experiment revealed differences in meiofaunal density across
treatments ($F_{3,40} = 9.73, p < 0.001$; Fig. 6). Meiofaunal density increased by 164% more in die-off sediment than in healthy sediment. Open control meiofaunal density was similar to die-off sediment but was higher than healthy sediment. There was no significant difference between procedural controls and other treatments. Site effect on meiofauna density in this experiment was not significant ($F_{1,40} = 2.71, p = 0.11$).

DISCUSSION

Predator depletion on New England salt marshes has led to increased *Uca* densities (Fig 3B, 4A) and deposit feeding, directly decreasing meiofaunal abundance (Fig. 5) through a trophic cascade. Released from predator control, however, burrowing and herbivory by *Sesarma* has led to salt marsh die-off and the release of organic carbon substrate (Fig. 4B) that supports microbial and meiofauna populations (Fig. 6). This process indirectly increases meiofaunal abundance by increasing the erosion and availability of sequestered carbon from centuries of accreted peat (Coverdale et al. 2014). Thus, both direct and indirect trophic effects may play important regulatory functions on marsh basal trophic levels through counteractive mechanisms.

Predator depletion impacts on lower trophic levels

Our previous work in this system revealed that fishing pressure near recreational fishing access areas leads to increased abundance of the nocturnal burrowing herbivorous crab, *Sesarma reticulatum* (Holdredge et al. 2008, Altieri et al. 2010). This in turn leads to consumer-driven salt marsh die-off on a regional scale and the loss of hundreds of acres and over 200 years of accreted salt marsh peat on Cape Cod (Coverdale et al. 2013b).

In this paper, we examined how predator depletion influences lower trophic levels directly and indirectly. Inter-site surveys and *Uca* tethering predation pressure assays reveal that elevated *Uca* densities do occur at predator depleted die-off sites (Fig. 3A) decreasing meiofaunal abundance.
through direct trophic interactions (Fig. 5). Our data also show that die-off site sediment is carbon rich (Fig. 3C) due to peat erosion and that carbon rich sediment supports higher meiofauna densities as an indirect effect of predator depletion (Fig. 6). Thus, our data show that the direct and indirect trophic effects of predator depletion on meiofauna interact antagonistically, canceling out the magnitude of each effect, and making them cryptic without explicit experimentation to separate and isolate them.

**Direct vs. indirect trophic effects**

Our results suggest that human impacts may be difficult to generalize among communities because of the idiosyncratic nature of indirect trophic effects. In communities where human impacts, like predator depletion, result in direct trophic effects, human impacts may be predictable and deterministic. Specifically, if disturbance affects an autogenic engineer (foundation species) that provides refuge for consumers, foundation species effects can impact consumers and direct effects can predictably extend to lower trophic levels. If, on the other hand, disturbance indirectly affects allogenic ecosystem engineers that convert a resource from one state to another, like *Sesarma* converting peat to carbon rich sediment, food web structure and trophic impacts will be indirect, unpredictable and lead to ecosystem-specific responses. Trophic cascades have been identified in many ecosystems (Pace et al. 1999). Significant work elucidated the direct causal links of these cascades - for instance, sea otter populations control herbivorous sea urchins through consumptive effects. Sea otter removal leads to overgrazing and loss of kelp forest communities (Estes and Palmisano 1974). However, less experimental and conceptual work has emphasized the indirect effects in these cascades or systems (Estes et al. 2004).

**Indirect Habitat Modification Effects**

How common are human impacts that lead to trophic structure shifts mediated by indirect trophic
effects? Indirect effects are ubiquitous in natural ecosystems (Menge 1995), suggesting that most human impacts have both significant direct and indirect consequences.

More recently, indirect trophic effects of predator depletion in marine systems have been studied (Duggins et al 1989, Reisewitz 2002, Vicknair 1996, Irons et al 1986, Dayton 1975, Dulvy et al. 2004), showing large impact across functional groups and changing community structure (Estes et al 2004). Other examples of coupled direct and indirect trophic effects have been observed in overfishing of Caribbean coral reefs, which led to coral loss and algal dominated food webs (Hughes 1994) and the extermination of wolves from North America which led to overgrazing, the loss of foundation species and the emergence of novel food webs (Ripple and Beschta 2004). Like our results, these are all examples of the direct and indirect effects of predator depletion impacting community organization and require experimental studies to understand.

Indirect trophic mechanisms are also ubiquitous structuring forces by themselves, in the absence of direct trophic mechanisms. Invasive species, like the European herbivorous snail *Littorina littorea* clearing North American Atlantic estuarine shorelines of sediment and algal cover (Bertness 1984) and invasive zebra mussels filtering North American lakes of planktonic biomass and shifting whole lake trophic structure (Strayer 2009), are examples of allogenic ecosystem engineers indirectly changing community composition and structure. These indirect effects also require experimental studies to quantify.

Nutrient pollution is an additional human impact that can shift estuarine pelagic and benthic food webs from seaweed, seagrass and coral-based ecosystems to rapidly growing phytoplankton and ephemeral algal-based ecosystems that increase sedimentation effects via indirect effects (e.g. Schramm and Nienhuis 1996, Burkholder et al. 2007, McCook 1999). Nutrient loading in New England salt marshes facilitates the invasion of non-native to invasive *Phragmites* genotypes and the
displacement of the native nitrogen fixing *Phragmites* (Holdredge et al. 2010b) and the entire native vascular plant assemblage (Bertness et al. 2002). These are all examples of human impacts on autogenic ecosystem engineers that led to shifts in trophic structure through ecosystem-specific indirect effects, and these mechanisms are only shown through experimentation.

**CONCLUSION**

Human-driven predator depletion has significant cascading effects, through direct consumptive interactions and indirect habitat engineering effects. Here, we examined the effects of predator depletion on New England salt marshes on an ecologically important basal trophic group, meiofauna. We tested the mechanisms of this impact - direct deposit feeder increase, or indirect sediment modification - to predict the direction of community change on meiofauna.

Overall, we found correlative evidence that meiofauna densities did not vary significantly between marsh types. Through experimentation, we found that both deposit feeder densities and sediment type are important in regulating meiofauna density, and work in differing directions. Thus, the balance between direct and indirect effects of human impacts among community types may rarely be generalizable. Scientists will need to utilize experimentation to predict the mechanistic basis and cumulative outcome of human impacts in communities.

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LITERATURE CITED


Blouin, M., Y. Zuily


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FIGURE LEGENDS

FIG. 1. Conceptual model

FIG. 2. Creekbank characteristics and site designation. Site was defined according to the dominant marsh bank characteristic (> 50%) of each marsh.

FIG. 3. Results of surveys that link predation depletion with meiofaunal density: (A) predation intensity, (B) Uca density, (C) carbon content, (D) nitrogen content, and (D) meiofaunal density. Data are mean ± 1SE.

FIG. 4. Relationship between Uca density, carbon content and predation pressure. As predation pressure decreases, Uca density (A) and carbon content (B) increase. Data are mean ± 1SE.

FIG. 5. Consumer removal experiment. Data are mean ± 1SE for 6 replicates per treatment. Different letters denote significant difference at $P < 0.05$ (Tukey HSD post hoc test).

FIG. 6. Sediment transplant experiment. Data are mean ± 1SE for 6 replicates per treatment. Different letters denote significant difference at $P < 0.05$ (Tukey HSD post hoc test).
FIG. 2
FIG. 3.
FIG. 4.
FIG. 5.
FIG. 6.
Thank you to the Bertness lab!

(From left): Matt Bevil, Elena Suglia, Sinead Crotty, Steven Hagerty, Huili Chen. Photo taken by Mark Bertness.