# **Evaluating the Relationship Between Kelp Forest Ecosystems and Water Temperature in the Southern Gulf of Maine**

Jarrett Byrnes University of Massachusetts Boston

### **Definition of the problem**

Warming Waters and Foundation Species in Massachusetts and New England

As waters warm in New England (Balch et al. 2012), many of our temperate cold-water foundation species may suffer negative consequences. Removal of these key species has the potential to cascade to reductions in ecosystem biodiversity (Byrnes et al. 2011) and multiple ecosystem functions (Worm et al. 2006, Lefcheck and Duffy 2014). Major shifts in foundation species abundance are unlikely in the immediate future. We can, however, build predictive models by using observational datasets examining foundation species abundance, physical parameters, and biodiversity. Here I propose to use surveys of New England kelp forests model how shifts in water temperatures may alter rocky reef ecosystem biodiversity and health in Massachusetts and New England.

The Role of Kelps in New England

In New England, kelps like the dominant *Saccharina* and *Laminaria* genera, provide a pivotal role within local communities. New England kelps shape the community around them. They and confamilials across the Atlantic host a wide variety of marine organisms, such as sea urchins (Miller and Mann 1973), lobsters (Bologna and Steneck 1993), or a wide variety of organisms that live directly on kelp blades themselves or within complex kelp holdfasts (Norderhaug et al. 2002). By shading macroalgae, kelps also facilitate curstose corraline algae (Melville and Connell 2008). Their loss via grazing or other disturbances can open up large amounts of space for invasive species or transitions to other ecosystem states (Harris and Tyrrell 2001, reviewed in Steneck et al. 2013).

Beyond regulating communities, the kelps, such as those found in Massachusetts and New England, provide a wide variety of ecosystem services. They are incredibly productive, with productivity from *Laminaria* and *Saccharina* species estimated between 110 - 1780 gC per m² per year (Mann 1973). This high productivity can have profound consequences. They are key to local nutrient recycling (Krumhansl and Scheibling 2012b, 2012a). They are suggested to slow shorelines erosion and change local flow conditions (Asano et al. 1992) (Mork 1996) (Løvås and Tørum 2001). Kelps are beginning to be explored as a potential source of blue carbon storage (Chung et al. 2010, Wilmers et al. 2012) due to their ability to soak up carbon as a part of

photosynthesis and then deposit it for later burial as detritus. While the early reproductive stages of some kelps might be affected by changes in pH (Gaitán-Espitia et al. 2014), their increased growth from increases in future CO<sub>2</sub> for at least some species appears to more than make up for it (Roleda et al. 2011), implying that they could continue to be a major habitat in at high CO<sub>2</sub> future.

### Kelps and Climate Change

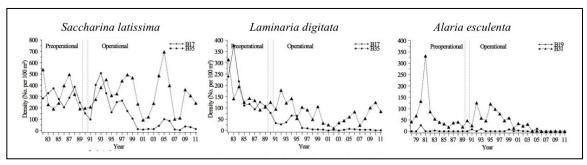
The loss of a dominant habitat forming foundation species (*sensu* Dayton 1971) can set off a cascade of indirect changes within an ecosystem (Dunne et al. 2002a, Novak et al. 2011). Climate change could thus have its strongest effects where temperature has strong effects on foundation species. Temperate marine ecosystems dominated by large structure forming brown macroalgae – kelp forests - present a unique opportunity to understand the effects of climate change via shifts in the ecology of foundation species.

Kelps are particularly susceptible to changes in ocean temperature due to their physiological and ecological dependence on cold water. Kelps equatorward range limits are set by a combination of physiological tolerance of adults (Lüning 1984, Hatcher et al. 1987), limits to reproduction (Bartsch et al. 2008), tolerance of gametophytes (Tom Dieck 1993), failure of recruits (Ladah et al. 2002), and nutrient availability (Dayton 1985a, 1985b) which often correlates with temperature (Deysher and Dean 1986). Changes in temperature threaten to act on any and all of these. In particular, temperature induced decreases in growth and reproduction in kelps suggest that increases in temperature may inhibit kelps ability to recover from strong but local short-term disturbances (Wernberg et al. 2010, 2012). If kelps are not able to recover from a strong short-term disturbance, then the ecosystem may shift into one of several alternate states dominated by sea urchin barrens (Harrold and Reed 1985), algal turfs (Connell et al. 2008), foliose understory algae (Arkema et al. 2009), sessile suspension feeders (Rassweiler et al. 2010) and more. Each of these alternate community states has radical implications for all species in the kelp forest food web.

In systems where climate change has not yet been documented to impact kelp forests, we have witnessed climatic events, such as El Niños, that give us a window into how climate change may alter these systems. For example, while giant kelp (*Macrocystis sp.*) forests have not had any documented climate-change related shifts, we know that increased temperatures after strong storms from ENSO events can suppress their recovery due to shifts in nutrient availability (Ladah et al. 2002, Edwards 2004, Edwards and Hernández-Carmona 2005, Edwards and Estes 2006). While there are hints that similar communities in northern Europe are shifting, with kelps like *Saccharina digitata* migrating northward (Raybaud et al. 2013), less information is available in the Northwestern Atlantic. Current similar generalizations regarding changes in the Gulf of Maine and north into Canada, are not possible due to inadequately standardized data (Merzouk and Johnson 2011).

Filling the Gap: Surveys of New England Kelp Bed Communities & Temperature

There are hints that communities are shifting, potentially due to climate. In New Hampshire, for example, long-term monitoring of the impacts of the Seabrook power plant has shown a decrease in kelp abundances since 1983 in both control and impact sites (Figure 1, Normandeau Associates 2012) . This has correlated with shifts in temperature. While fleshy algae has recovered after urchin grazing in the 1980s and 1990s in many regions (Steneck et al. 2013), often the recovering algae has been invasive red turf algae rather than kelps (Schneider 2010, Savoie and Saunders 2013, Newton et al. 2013).



**Figure 1:** Abundances of three species of kelp at sites in New Hampshire. These measurements have been ongoing since the 1980's as part of a power plant impact assessment project. Controls are the lower number in each plot. All kelps at all sites show decreases in density, save *Saccharina latissima* which is still highly variable at the control site. Figure provided by Normandeau Associates.

To build an understanding of change in kelp bed communities, starting in 2013, I have been surveying the biodiversity and annual temperature profiles of rocky reefs around New England. In Massachusetts, this includes eight sites in Salem Sound and eight sites at the Boston Harbor Islands around Little Brewster and Calf Island. I have also included twelve additional sites at the Shoals Marine lab, further north, with colder water temperatures. These reefs consist of a lush community of kelps and a wide diversity of associated invertebrates and fish. During these surveys, I have observed major differences in community structure in physically similar sites. I have also observed large differences in kelp size distributions in years with different average annual temperatures (Figure 2), leading to my lab beginning to assess not just density but size distributions of kelps in our sampling in the summer of 2014.

With two more years of data (112 data points total from 2013-2017), I will be able to build statistical models that allow me to understand how temperature, kelp size distribution and abundance, and temperate rocky reef food web structure, are interrelated (Figure 3). The results of this effort will fill a key knowledge gap in planning for climate change in Massachusetts waters. Further, I will do so by working with undergraduate students, bringing them into the field of subtidal marine research. Last, I will make the data freely available to any users as it is collected.



Figure 2: Sampled sites in Massachusetts

## **Objectives of the Proposed Work**

To achieve the goal of both building models of how ocean temperature and kelp forest communities are related while making the work accessible to a variety of stakeholders, I have four objectives:

Objective 1) Build a food web for New England rocky reefs in order to estimate the trophic height and breadth of local-scale food webs.

Objective 2) Sample and model the relationship between annual temperature, kelp abundance and size. and species diversity, and trophic height.

Objective 3) Involving UMB Undergraduates in Practical Research Experiences.

Objective 4) Make data on Massachusetts rocky reefs publically available.

Objective 5) Teach our subtidal sampling protocol and species identification guides to other local research groups

## Approach and Methodology

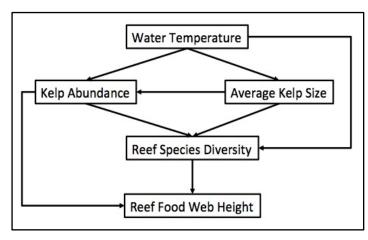
Objective 1) Build a food web for New England rocky reefs in order to estimate the trophic height and breadth of local-scale food webs: In order to understand changes in kelp bed food webs, we need to be able to transform data regarding the presence/absence and abundances of key species into a suite of metrics that summarize the state of a local food web. In fisheries biology, this is often done by simply summarizing trophic height – the number of feeding links between a basal resource species such as algae and the top of the food web. Other useful metrics include species richness, the number of species present; food web connectance, the number of feeding links divided by the square of species richness; average food chain length, and more (Dunne et al. 2002b). In order to assess all of these metrics save richness, however, I will need to build a regional food web for all species found in local kelp beds. Thus far in my sampling of local subtidal food webs, I have identified 120 species that are visible and straightforward to enumerate to divers in situ (i.e., not amphipods) which I will use for this food web.

To build the web, I will employ similar techniques to those I used successfully for kelp forests in Southern California with 256 species (Byrnes et al. 2011). I will review the literature for all 120 species I survey in the Gulf of Maine, using ISI Web of Knowledge, Google Scholar, and physical searches of libraries at the Darling Marine Center, Woods Hole Oceanographic Institute, The Marine Biological Laboratory, Northeastern Marine Science Center, and UMass Boston. Using each, I will search for papers, dissertations, theses, and undergraduate reports that contain information on targeted species as either predator or prey. Results will be recorded in a simple spreadsheet database that is compatible with the Darwin Core data standard (Wieczorek et al. 2012) so that the resulting web can be included in the Encyclopedia of Life's Global Biotic Interactions database (Poelen et al. 2014).

To use the master web to create local webs for single transects in individual years, I can subsample the master web to only include species included in surveys below. I can then use these subwebs to calculate food web metrics.

Objective 2) Sample and model the relationship between annual temperature, kelp abundance and size, and species diversity, and trophic height: In order to understand the links between temperature, kelps, and kelp bed ecosystems in Massachusetts, I will

use an combination of observational surveys and causal modeling techniques. I will take data that summarizes kelp size distribution and abundance, the abundance of all algae, invertebrate, and fish that I can observe along 80m<sup>2</sup> subtidal transects at 16 sites in Massachusetts and 12 in Maine (supported by outside funding), and annual temperature fluctuations at each of these transects. Temperature likely affects kelp abundance and size, size can affect abundance via light competition, and there may be a combination of indirect and direct affects on reef species richness and



**Figure 3:** Conceptual model of temperature and its influence on New England Rocky Reefs. Reef food web height is included as a response variable for purposes of demonstration. Many other food web metrics could be included in its place.

food web trophic height (Figure 3). To tease this apart, I will combine this data with the food web from Objective 1 to assess transect-level food web structure. Data will then be used in a Structural Equation Model (Bollen 1989, Grace and Bollen 2005, Grace et al. 2012) that models a series of indirect effects from temperature to a suite of food web metrics.

To sample transects, I will use established methods from the Kelp Ecosystem Ecology Network for surveying kelp forests in the Gulf of Maine (Byrnes et al. 2014, full handbook and materials available at http://bit.ly/keen-methods-v1). These methods are adapted from the SBC-LTER, the Partnership for Interdisciplinary Study for Coastal Oceans, and the Tasmanian Marine Protected Area program. Four transects are sampled within a single site, defined as an area with common wave exposure and benthic substrate. Transects within sites consist of 40m x 2m areas sampled by divers on SCUBA. Along each transect, abundances of all large fish and large mobile invertebrates are sampled in four 20m x 1m swaths. Individual sessile algae, sessile invertebrates, and small mobile fish and invertebrates are sampled in 6 evenly spaced 1m<sup>2</sup> guadrats. Ten individuals of all kelps spaced evenly along transects are sampled for blade length and width and stipe length so that their abundance can be translated to biomass using standard equations. Last, colonial invertebrates and space-filling algae are sampled using 40 uniform point contacts along the transect (n=80 over both sides). All species under a point are counted, such that total transect cover may be >100% due to layering of species. Last, 15 pieces of kelp are removed from each site taken from random locations along the transect. On the surface they are measured for stipe length, maximum blade length, and either maximum width (for forking kelps such as Saccharina digitata or blade width 10cm above the stipe-blade juncture. This protocol typically takes 3-4 divers one dive per transect, depending on kelp density. Food web metrics, such as connectance or trophic height, can be derived for each transect (by determining the transect-level food web) based on the master food web from Objective 1. At each site, I will maintain two redundant temperature sensors (HoboTemp Pendant Loggers) recording hourly temperature in order to estimate mean annual seawater temperature between sampling intervals.

To tease these relationships apart, I will fit a model matching figure 1 using Structural Equation Modeling (Grace 2006) with data collected from these surveys. I will use equation-level SEM (Grace et al. 2012), as this will give me the flexibility to fit generalized linear mixed model (i.e., models with nonlinear functional forms and nonnormal error terms) where necessary for particular responses (Shipley 2009). This test assesses whether I have missed any causal links in the model, thus giving a strong test of the multivariate hypothesis. While Figure 3 shows trophic height, I will fit a series of models with trophic height, average trophic level, and food web connectance to evaluate the indirect effects of temperature on all three.

Objective 3) Involving UMB Undergraduates in Practical Research Experiences: Kelp beds in Massachusetts are invisible ecosystems. They lie beneath the surface of the water, preventing citizens from building an understanding of the beauty and productivity of these systems. It also hinders people's ability to think about how climate change may

have larger effects than they might anticipate on the sea, mediated by changes to kelps. Beginning at the undergraduate level, I hope to change this by introducing students to thinking critically about the subtidal world with first-hand experience.

This summer, working with my lab, I helped to run the first UMB course in underwater research methods, compliant with the guidelines of the American Academy of Underwater Scientists. To help students to gain experience and environmental literacy with this unappreciated habitat, I will work with these students and have them help us sample transects within Boston Harbor each July. This experience will also give them experience that they can translate to later work for government agencies, consulting firms, or a graduate career in marine science.

Objective 4) Make data on Massachusetts rocky reefs publically available: The data from this research describes fundamental properties of local subtidal ecosystems. It serves no purpose being kept private. Furthermore, while the process of analysis and publication of a manuscript using this data can take additional time, depending on the vagaries of the peer review process, the data is needed now. I therefore plan to make all data collected public as soon as it is quality controlled.

In collaboration with the Australia Ocean Data Network, I am building a database of kelp forest observations around the globe. They currently have my data from 2013-2014, and the data portal is planned to launch this fall. Data will be fully quality controlled during the fall of each year by a student who has come from my subtidal research class. This data will then be uploaded and made immediately available to any stakeholders that wish to use it. For example, I have already contacted Salem Sound CoastWatch to make them aware of the data, as it may provide additional context to their local water quality sampling program. It is my hope that this data can be used by both the scientific and management communities well into the future.

Objective 5) Teach our subtidal sampling protocol and species identification guides to other local research groups: As mentioned above, the subtidal sampling protocol is part of the Kelp Ecosystem Ecology Network (http://kelpecosystems.org). In particular, my lab organizes the New England wing of KEEN. Each July, we run a public workshop on KEEN sampling methods for other labs to join in order to ensure that local research groups doing subtidal benthic monitoring are coordinating our methods. In 2014, we had four lab groups in attendance (Grabowski lab at Northeastern University, Ted Maney from Salem State, my lab, and the Dijkstra lab from University of New Hampshire). In 2014 we plan to add two more (the Grace lab from Southern Connecticut State College and the Freeman lab from Adelphi University), and hope to add more research groups to this spring meeting in the future. I hope to add more lab groups in the future, and will advertise our summer meeting for other attendees at local agencies and universities starting in 2016. At each meeting, we not only go over the entire sampling protocol in detail, but we also review species identification, provide species ID guides, and usable datasheets for any and all interested in working with our sampling protocols. I also facilitate data deposition for any lab group conducting KEEN-compliant sampling with the AODN database.

### **Expected Outcomes and Impacts**

This project will have several different targeted outcomes that match Woods Hole Sea Grant's strategic plan. At its most basic level, it meets the Woods Hole Sea Grant plan target under Healthy Coasts and Ecosystems of "Support research to understand species responses to changes in environmental conditions". This project will enable us to understand how climate shifts – whether via natural cycles or climate change – will affect the future of our coastal ecosystems. It will achieve this via publication of scientific manuscripts and data for use by the scientific and public community. Second, it will provide the Massachusetts marine ecological community with the first ever food web for subtidal ecosystems. Future researchers will be able to use this network to examine features of subtidal food web dynamics. It will allow them to put their results into a larger context. It will also be useful as one of the few high-quality literature based subtidal food webs that can be used by the larger food web network topology community to examine how food webs across the planet are structured.

This project also falls under the Woods Hole Sea Grant Environmental Literacy and Work Force Development target area, satisfying the goal of "Students within Massachusetts will have access to ocean sciences research and information to develop an appreciation for the oceans and an awareness of marine science related career opportunities." It will do so by involving undergraduates at UMass Boston in an ongoing subtidal research project. This will give them a hands-on appreciation for the process of subtidal research and how it might be applied. Furthermore, any students who go on to write honors theses will have full access to the data. Unlike giving a student access to a dataset in the classroom setting, however, these students will have intimate knowledge of what the data can and cannot be used for, as they will have participated in collecting it. It is my hope that by participating in our survey effort, they will also place themselves at an advantage for future agency or consulting jobs.

This project will also address "Support for undergraduate, graduate and postdoctoral students will be provided through research awards to their universities or research institutions" as part of the Woods Hole Sea Grant Environmental Literacy and Work Force Development target via graduate and undergraduate training and "Researchers from the ocean science community will have access to and participate in scientific, educational and outreach opportunities" via the workshops on kelp bed sampling.

### **Project significance**

This project will present an integrated picture of how climate, foundation species, and biodiversity interact on New England rocky reefs. The model will begin to answer basic questions about consequences of potential shifts in climate. It will also provide points of departure for future investigations of rocky reef processes. Last, by the end of this grant, I will have established a five-year time series of reefs around Massachusetts and New England that will serve as a baseline for any future exploration of New England subtidal Ecology. This dataset will be fully open and available to anyone who wishes to use it. It will create a baseline for future local subtidal researchers, agency scientists, or

consultancy firms. Additionally, we will provide training in a set of methods that are compliant with international standards, enabling local researchers to not only be able to easily compare their sites between each other, but to also compare what is going on in Massachusetts and New England to global patterns and trends in temperate subtidal communities.

### **Evaluation of Project Outcomes and Outreach**

The project's success can be judged via several metrics: 1) students trained, both in the UWR class as well as graduate students that participate in the project, 2) number of downloads of the dataset once published, 4) number of times specific food web entries in GLoBI are accessed, 5) number of publications from the project, 6) number of conference presentations and seminars, 7) number of attendees at our July sampling protocol workshops. Each metric can immediately be evaluated, although downloads of data and citations to publications may take more time to accrue.

Woods Hole Sea Grant can further disseminate results of the project by sharing access to our data of Massachusetts subtidal community data, sharing publications, and the content of talks that will be available online via slideshare.net and youtube.com. I would also like to disseminate the announcement for our 2016 and 2017 subtidal sampling methods workshop via Woods Hole Sea Grant to the larger community, broadening the reach of our growing network of local subtidal researchers.

### **Project Management**

The direct project team consists of myself, a graduate student, and an undergraduate data manager. As the project manager, I coordinate sampling schedule, ensure continuity of protocol, species identifications, and plan the summer field logistics for sampling. I will coordinate the incorporation of underwater research students into our sampling program and work out details to ensure they can get academic credit for their efforts. I also run the sampling workshops, aiding in knowledge transfer of our sampling protocol to other research labs. During intensive sampling periods, we also utilize other students in the lab, as this dataset is resource amongst all members of my lab. The graduate student will be responsible for completing the subtidal food web. During the summer, they will coordinate daily operations and preparation for sampling in the summer. They and the undergraduate data manager will coordinate data entry, quality control, and data deposition at the AODN database. In so doing, I will work with them to teach them how to use scripted solutions in R for data quality control before data deposition. The basic scripts have already been written, but each year requires some additional modification, giving students a learning opportunity to use quality code as a jumping off point to learn more about computational approaches to data analysis and management. The graduate student will write-up a manuscript describing the food web utilizing a framework of their choice that falls in line with their own research interests. I will write the data analysis manuscript in collaboration with the graduate student. Where possible we will involve hired undergraduates in reading and discussion of drafts of the manuscript to further introduce them to the process of publishing science.

# **Project Duration & Timeline**

Sampling will take place over the course of two summers with data management in the fall. Food web construction will take place in the fall of year one. Results from each effort will be presented at the spring Benthic Ecology Meetings in years one and two respectively. The food web manuscript will be submitted in the end of year one, and the data analysis manuscript will be submitted in the fall or winter of year two. Meetings to teach the sampling protocols will be conducted in July of both year one and two. Data will be submitted in the fall of year one and two.

### **MULTI-YEAR MILESTONE CHART**

Timetable for initiation, performance, and completion of tasks included in the

program for the two-year funding period

<u> </u>	ogram for the two-year funding perio	u		
Wo	ork Plan Tasks:	2016	2017	Jan. 2018
1.	Food Web Construction	Х		
2.	Sampling Workshop	Х	X	
3.	Kelp Bed Sampling and Temperature Sensor Deployment with Students	х	Х	
4.	Data Upload		Х	Х
5.	Publication	Food Webs		Data Analysis

# **2016 YEARLY MILESTONE CHART**

Wor	k Plan Tasks:	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	ОСТ	NOV	DEC
1.	Construct food web from the literature		х	Х	х								
2.	Prep for Field Season (gear & boat maintenance)					х	х						
3.	Teach sampling workshop							Х					
4.	UMB Underwater Research Class						х						
5.	Sample Sites							Х	Х				
6.	Enter Data									Х	Х	Х	
7.	Data Quality Control												X
8.	Write and submit food web for publication										X	Х	Х
9.													
10.													

# **2016 YEARLY MILESTONE CHART**

Wor	k Plan Tasks:	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	ОСТ	NOV	DEC
1.	Submit data to AODN	Х											
2.	Prep for Field Season (gear & boat maintenance)					X	х						
3.	Teach sampling workshop							X					
4.	UMB Underwater Research Class						Х						
5.	Sample Sites							Х	Х				
6.	Enter Data									х	Х	Х	
7.	Data Quality Control												X
8.	Upload food webs to GLoBI	х											
9.													
10.													

# **2018 YEARLY MILESTONE CHART**

Worl	k Plan Tasks:	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	ОСТ	NOV	DEC
1.	Submit SEM analaysis for publication	Х											
2.	Submit data to AODN	Х											
3.													
4.													
5.													
6.													
7.													
8.													
9.													
10.													

### References

- Arkema, K. K., D. C. Reed, and S. C. Schroeter. 2009. Direct and indirect effects of giant kelp determine benthic community structure and dynamics. Ecology 90:3126–3137.
- Asano, T., H. Deguchi, and N. Kobayashi. 1992. Interaction between water waves and vegetation. Coastal Engineering Proceedings 1.
- Balch, W. M., D. T. Drapeau, B. C. Bowler, and T. G. Huntington. 2012. Step-changes in the physical, chemical and biological characteristics of the Gulf of Maine, as documented by the GNATS time series. Marine Ecology Progress Series 450:11–35.
- Bartsch, I., C. Wiencke, K. Bischof, C. M. Buchholz, B. H. Buck, A. Eggert, P. Feuerpfeil,
  D. Hanelt, S. Jacobsen, R. Karez, U. Karsten, M. Molis, M. Y. Roleda, H. Schubert,
  R. Schumann, K. Valentin, F. Weinberger, and J. Wiese. 2008. The genus
  Laminaria sensu lato: recent insights and developments. European Journal of
  Phycology 43:1–86.
- Bollen, K. A. 1989. Structural Equations with Latent Variables. Wiley, New York.
- Bologna, P. A. X., and R. Steneck. 1993. Kelp beds as habitat for American lobster *Homarus americanus*. Marine Ecology Progress Series 100:127.
- Byrnes, J. E. K., A. J. Haupt, D. C. Reed, T. Wernberg, A. Pérez-Matus, N. T. Shears, B. Konar, and P. Gagnon. 2014. Kelp Ecosystem Ecology Network Monitoring Handbook. Kelp Ecosystem Ecology Network.
- Byrnes, J. E., D. C. Reed, B. J. Cardinale, K. C. Cavanaugh, S. J. Holbrook, and R. J. Schmitt. 2011. Climate driven increases in storm frequency simplify kelp forest food webs. Global Change Biology 17:2513–2524.
- Chung, I. K., J. Beardall, S. Mehta, D. Sahoo, and S. Stojkovic. 2010. Using marine macroalgae for carbon sequestration: a critical appraisal. Journal of Applied Phycology 23:877–886.
- Connell, S. D., B. D. Russell, D. J. Turner, S. A. Shepherd, T. Kildea, D. Miller, L. Airoldi, and A. Cheshire. 2008. Recovering a lost baseline: missing kelp forests from a metropolitan coast. Marine ecology progress series. Oldendorf 360:63.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–389.
- Dayton, P. K. 1985a. Ecology of kelp communities. Annual Review of Ecology and Systematics 16:215–245.
- Dayton, P. K. 1985b. The structure and regulation of some South American kelp communities. Ecological Monographs 55:447–468.
- Deysher, L. E., and T. A. Dean. 1986. In situ recruitment of sporophytes of the giant kelp, *Macrocystis pyrifera* (L.) C.A. Agardh: Effects of physical factors. Journal of Experimental Marine Biology and Ecology 103:41–63.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002a. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology letters 5:558–567.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002b. Food-Web Structure and

- Network Theory: The Role of Connectance and Size. Proceedings of the National Academy of Sciences of the United States of America 99:12917–12922.
- Edwards, M. S. 2004. Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. Oecologia 138:436–447.
- Edwards, M. S., and G. Hernández-Carmona. 2005. Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Niño. Marine Biology 147:273–279.
- Edwards, M. S., and J. A. Estes. 2006. Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective. Marine ecology progress series. Oldendorf 320:79–87.
- Gaitán-Espitia, J. D., J. R. Hancock, J. L. Padilla-Gamiño, E. B. Rivest, C. A. Blanchette, D. C. Reed, and G. E. Hofmann. 2014. Interactive effects of elevated temperature and pCO 2 on early-life-history stages of the giant kelp Macrocystis pyrifera. Journal of Experimental Marine Biology and Ecology 457:51–58.
- Grace, J. B., and K. A. Bollen. 2005. Interpreting the Results from Multiple Regression and Structural Equation Models. Bulletin of the Ecological Society of America 86:283–295.
- Grace, J. B., D. R. Schoolmaster Jr., G. R. Guntenspergen, A. M. Little, B. R. Mitchell, K. M. Miller, and E. W. Schweiger. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere 3:art73.
- Harris, L. G., and M. C. Tyrrell. 2001. Changing community states in the Gulf of Maine: Synergism between invaders, overfishing and climate change. Biological Invasions 3:9.
- Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169.
- Hatcher, B. G., H. Kirkman, and W. F. Wood. 1987. Growth of the kelp *Ecklonia radiata* near the northern limit of its range in Western Australia. Marine Biology 95:63–73.
- Krumhansl, K. A., and R. E. Scheibling. 2012a. Production and fate of kelp detritus. Marine Ecology Progress Series 467:281–302.
- Krumhansl, K., and R. Scheibling. 2012b. Detrital subsidy from subtidal kelp beds is altered by the invasive green alga Codium fragile ssp. fragile. Marine Ecology Progress Series 456:73–85.
- Ladah, L. B., J. A. Zertuche-Gonzalez, and G. Hernandez-Carmona. 2002. Giant kelp (*Macrocystis pyrifera*) recruitment near its southern limit in Baja California after mass dissapearance during ENSO 1997-1998. Journal of Phycology 35:1106–1112.
- Lefcheck, J.S., Byrnes, J.E.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., Hensel, M.J.S., Hector, A., Cardinale, B.J., Duffy, J.E., 2000. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature Communications 6, 6936.
- Lüning, K. 1984. Temperature tolerance and biogeography of seaweeds: the marine algal flora of Helgoland (North Sea) as an example. Helgolander Meeresuntersuchungen 38:305–317.
- Løvås, S. M., and A. Tørum. 2001. Effect of the kelp *Laminaria hyperborea* upon sand dune erosion and water particle velocities. Coastal Engineering 44:37–63.
- Mann, K. H. 1973. Seaweeds: Their Productivity and Strategy for Growth. Science 182:975–981.

- Melville, A. J., and S. D. Connell. 2008. Experimental effects of kelp canopies on subtidal coralline algae. Austral Ecology 26:102–108.
- Merzouk, A., and L. E. Johnson. 2011. Kelp distribution in the northwest Atlantic Ocean under a changing climate. Journal of Experimental Marine Biology and Ecology 400:90–98.
- Miller, R. J., and K. H. Mann. 1973. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. Marine Biology 18:99–114.
- Mork, M. 1996. The effect of kelp in wave damping. Sarsia 80:323-327.
- Newton, C., M. E. S. Bracken, M. McConville, K. Rodrigue, and C. S. Thornber. 2013. Invasion of the Red Seaweed *Heterosiphonia japonica* Spans Biogeographic Provinces in the Western North Atlantic Ocean. PloS One 8:e62261.
- Norderhaug, K. M., H. Christie, and E. Rinde. 2002. Colonisation of kelp imitations by epiphyte and holdfast fauna; a study of mobility patterns. Marine Biology (Berlin) 141:965–973.
- Novak, M., J. T. Wootton, D. F. Doak, M. Emmerson, J. A. Estes, and M. T. Tinker. 2011. Predicting community responses to perturbations in the face of imperfect knowledge and network complexity. Ecology 92:836–846.
- Poelen, J. H., J. D. Simons, and C. J. Mungall. 2014. Global Biotic Interactions: An open infrastructure to share and analyze species-interaction datasets. Ecological Informatics.
- Rassweiler, A., R. Schmitt, and S. Holbrook. 2010. Triggers and maintenance of multiple shifts in the state of a natural community. Oecologia 164:489–498.
- Raybaud, V., G. Beaugrand, E. Goberville, G. Delebecq, C. Destombe, M. Valero, D. Davoult, P. Morin, and F. Gevaert. 2013. Decline in Kelp in West Europe and Climate. PloS one 8:e66044.
- Roleda, M. Y., J. N. Morris, C. M. McGraw, and C. L. Hurd. 2011. Ocean acidification and seaweed reproduction: increased CO2 ameliorates the negative effect of lowered pH on meiospore germination in the giant kelp *Macrocystis pyrifera* (Laminariales, Phaeophyceae). Global Change Biology 18:854–864.
- Savoie, A. M., and G. W. Saunders. 2013. First record of the invasive red alga *Heterosiphonia japonica* (Ceramiales, Rhodophyta) in Canada. BioInvasions Record 2.
- Schneider, C. W. 2010. Report of the new invasive alga in the Atlantic United States: "*Heterosiphonia*" *japinoca* in Rhode Island. Journal of Phycology 46:653–657.
- Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.
- Steneck, R. S., A. Leland, D. C. McNaught, and J. Vavrinec. 2013. Ecosystem Flips, Locks, and Feedbacks: the Lasting Effects of Fisheries on Maine's Kelp Forest Ecosystem. Bulletin of Marine Science 89:31–55.
- Tom Dieck, I. 1993. Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. Marine ecology progress series. Oldendorf 100:253–253.
- Wernberg, T., D. A. Smale, F. Tuya, M. S. Thomsen, T. J. Langlois, T. de Bettignies, S. Bennett, and C. S. Rousseaux. 2012. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Climate Change.

- Wernberg, T., M. S. Thomsen, F. Tuya, G. A. Kendrick, P. A. Staehr, and B. D. Toohey. 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecology letters 13:685–694.
- Wieczorek, J., D. Bloom, R. Guralnick, S. Blum, M. Döring, R. Giovanni, T. Robertson, and D. Vieglais. 2012. Darwin Core: An Evolving Community-Developed Biodiversity Data Standard. PloS one 7:e29715.
- Wilmers, C. C., J. A. Estes, M. Edwards, K. L. Laidre, and B. Konar. 2012. Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. Frontiers in Ecology and the Environment 10:409–415.
- Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson. 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science 314:787–790.