



ELSEVIER

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Marine Policy

journal homepage: www.elsevier.com/locate/marpol

Short Communication

Managing for a resilient ocean

R. Fujita^{a,*}, J.H. Moxley^{a,1}, H. DeBey^{b,2}, T. Van Leuvan^{a,3}, A. Leumer^{a,4}, K. Honey^{c,5}, S. Aguilera^{d,6}, M. Foley^{e,7}

^a Environmental Defense Fund, Oceans Program, 123 Mission Street, 28th Floor, San Francisco, CA 94105, United States

^b Yale School of Forestry and Environmental Science, 195 Prospect Street, New Haven, CT 06511, United States

^c Stanford University, Emmett Interdisciplinary Program in Environment and Resources (E-IPER), School of Earth Sciences and Hopkins Marine Station, 120 Oceanview Blvd, Pacific Grove, CA 93950, United States

^d Stanford University, Department of Biology, Gilbert Hall, Stanford, CA 94305-5020, United States

^e Center for Ocean Solutions, 99 Pacific Street, Suite 155a, Monterey, CA 93940, United States

ARTICLE INFO

Article history:

Received 14 February 2012

Received in revised form

16 May 2012

Accepted 16 May 2012

Available online 30 June 2012

Keywords:

Resilience

Ecosystem services

State change

Thresholds

Indicators

ABSTRACT

Ocean policies around the world increasingly emphasize the importance of maintaining resilient ocean ecosystems, communities, and economies. To maintain and restore the resilience of healthy marine ecosystems in practice, specific management objectives with metrics and a policy framework for how to apply them will be needed. Here we present a concept for doing this, based on evidence that marine ecosystems transition from desirable to less desirable states in response to a number of physical, chemical, and biological drivers. More empirical and synthesis research will be necessary to develop quantitative metrics of resilience and thresholds between ecosystem states for specific ecosystems; however, suggestions are provided here for how to manage for resilience when insufficient data and knowledge are available for quantification. A summary of thresholds for biotic and abiotic drivers of ecosystem state drawn from the literature is also provided as a guide to management.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Increasingly, ocean policy in many countries emphasize ecosystem based management, coastal and marine spatial planning, and the maintenance of resilient ecosystems, human communities, and economies. Implementation will require the application of the best available science to the articulation of workable goals, objectives, and management guidance.

Goals and priorities should be responsive to changes in context. Climate change is now underway, new uses of the ocean are being developed, and several biogeochemical cycles are now dominated by human activities [1–6]. Ecosystem resilience – defined here as the capacity of ecosystems to persist in a given state by resisting change or recovering from impacts [7,8] – is an explicitly stated goal of the new U.S. ocean policy (Executive

Order 13547—Stewardship of the Ocean, Our Coasts, and the Great Lakes issued 19 July 2010). It is a goal that is embraced by ocean resource managers in many other countries as well. Managing for resilient, desirable ecosystem states (i.e., states that produce high levels of diverse ecosystem services) seems prudent given the high degree of uncertainty surrounding the impacts of climate change, new ocean uses, and how these will interact with existing threats to marine ecosystems and the goods and services they generate. However, it has been difficult to articulate specific and practical management goals, objectives, and approaches that result in resilience. In this paper, a framework for managing marine ecosystems for resilience is developed based on the evidence that ecosystems transition from desirable states to less desirable states in response to biotic (biological) and abiotic (physical and chemical) drivers, and that certain ecosystem attributes contribute to the resilience of each of these states.

2. Resilience management principles

The first step toward managing for a resilient ocean is to acknowledge that marine ecosystems can exist in many different states, characterized by different species, community structures, and ecosystem processes that can either be resilient or susceptible to change. Some states deliver high levels of many ecosystem services (defined here as desirable states), while other

* Corresponding author. Tel.: +1 415 293 6050; fax: +1 415 293 6051.

E-mail address: rfujita@edf.org (R. Fujita).

¹ Present Address: Duke University, Durham, NC, United States. jerry.moxley@duke.edu. Tel.: +1 415 293 6050.

² Tel.: +1 203 432 5100. henry.debey@yale.edu.

³ Tel.: +1 415 293 6050.

⁴ Tel.: +1 415 293 6050.

⁵ Tel.: +1 831 359 8848. khoney@stanford.edu.

⁶ Tel.: +1 650 723 2413. stacya@stanford.edu.

⁷ Tel.: +1 831 333 2079. mmfoley@stanford.edu.

Table 1
Biotic and abiotic resilience attributes and driver thresholds for coral reefs (coral order: *Scleratinia*).

Drivers	Zone/process	Qualitative resilience attributes	Quantitative resilience attributes (i.e. thresholds)		
			Minimum	Optimal/normal	Maximum
Substrate		Hard substrate with microhabitats, crustose corraline algae [33]. Suboptimal: soft sediment; sand, turf algae; fleshy macroalgae [34,35]			
Light (energy)	All coral reef zones	High light conditions, clear water	10% subsurface irradiance [36]	30–40% of subsurface irradiance (irradiance immediately below the surface) [36]	0.45–45 E m ⁻² day ⁻¹ [37]
	Shallow water		320–600 μmol m ⁻² s ⁻¹ [38]	400 μmol m ⁻² s ⁻¹ [39]	1600–1800 μmol m ⁻² s ⁻¹ [40]
	Deep water/ crevices		8.6–43 μmol m ⁻² s ⁻¹ [38]	385 μmol m ⁻² s ⁻¹ [41]; 456 μmol m ⁻² s ⁻¹ [42]	650 μmol m ⁻² s ⁻¹ [40]; > 1000 μmol m ⁻² s ⁻¹ (supra-optimal irradiance) [40] ~ 1 °C above mean summer maximum Sea Surface Temperature (SST) for several weeks or 3–4 °C above mean summer maximum SST for 1–2 day exposures [18,47]
Temperature	General	Warm, relatively stable	18 °C may be the minimum average temperature for reefs to develop [36,43]	~25 °C [44–46]	
	Overall nutrient concentrations	Low nutrient concentrations and loadings	~1 μM DIN and ~0.1–0.2 μM dissolved inorganic phosphorus [48–50]		
Nutrients	Fore-reef nitrogen and phosphorous concentrations		< 0.04 μM of DIN (from groundwater inputs in Okinawa) [51] 0.025 μM of DIP (in Bermuda) [52]	In Jamaica: 0.59 μM of DIN concentrations and 0.20 μM of phosphorus (most from groundwater inputs) [53,54] In the U.S. Virgin Islands: ≥ 0.283 μM of nitrate and nitrite and 0.025 μmol L ⁻¹ of phosphorus [55]	3.8 μM of DIN concentrations in upwelling areas of the Phoenix Islands [56] 0.56 μM of DIP in upwelling areas of the Phoenix Islands [56]
	Back-reef nitrogen and phosphorous concentrations		< 0.45 μM of DIN in Guam [57] 0.07 μM of DIP in the Great Barrier Reef during summer [52]	In Jamaica: 3.6 μM of DIN concentrations (most from groundwater inputs) and 0.20 μmol L ⁻¹ of phosphorus [53,54] In U.S. > Virgin Islands: ≥ 0.512 μM nitrate and nitrite in the U.S. Virgin Islands [55]	3.6 μM of DIN concentrations (in upwelling areas in Jamaica) [53,54] < 0.9 μM of DIP (from groundwater inputs in Okinawa) [58]
Salinity		Moderate salinity	24‰ (lethal for corals if maintained for longer than 24 h) [13,47]	35‰ (typical for tropical seawater) [59] > 0.05 m sec ⁻¹ : DIN can be supplied from water column; < 0.05 m/s: DIN supplied by benthic sources and water column; > 0.01 m/s: phosphate supplied from water column; < 0.01 m/s: phosphate supplied from benthic sources [60–62]	40‰ [47]
Wave surge					occasional severe hurricane damage has a diversifying effect on Australian reefs [63]
Sedimentation		Little sedimentation (that can smother corals or cloud the water column, thus inhibiting photosynthesis and reducing available substrate) [64]			150 g m ⁻² day ⁻¹ (coral cover and diversity were reduced in an area that received this amount of alluvial sediment in comparison to an area which received only 30 g m ⁻² day ⁻¹ , in Puerto Rico)
pH (acidity)		pH (acidity) or calcium carbonate saturation state	520% saturated with respect to the common CaCO ₃ mineral calcite [44–46]	8.2 (normal pH) [65] 350 μatm (current pCO ₂) [44–46]	480 ppm (carbonate threshold for calcifying organisms like corals) [10] pH of 7.8 [66]
Biological Drivers					
Herbivory		Diverse, abundant, with complementary grazing functions (i.e. scrapers, excavators, etc.)	Incipient macroalgal overgrowth at 850 kg/ha total fishable biomass; sharp decline in herbivory at 650 kg/ha fishable biomass [26]	Estimated multispecies maximum sustainable yield = 300–600 kg/ha fishable biomass [26]	

Table 1 (continued)

Drivers	Zone/process	Qualitative resilience attributes	Quantitative resilience attributes (i.e. thresholds)		
			Minimum	Optimal/normal	Maximum
Predation		Diverse, abundant, large bodied, with different life histories and behavior (i.e. resident, transient, etc.)			

E=1 Einstein=1 mol of photon= 6.02×10^{23} photons.

$\mu\text{M}=\mu\text{mol L}^{-1}$.

mM=millimoles (10^{-3} mol).

nM: nanometers for light wavelength units and nano moles (10^{-9} mol) for dissolved oxygen units.

DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorous.

Light levels for kelp forest data were converted by Foster and Schiel [67] from foot-candles and assuming a 12-h day with constant light; Light levels for coral reef data were converted by the authors from $\mu\text{mol m}^{-2} \text{s}^{-1}$ to $\text{E m}^{-2} \text{day}^{-1}$ assuming a 12-h day with constant light.

ecosystem states are associated with lower levels of fewer services (undesirable states). Ecosystem services include the provision of goods such as seafood and minerals, as well as regulatory services such as flood prevention, cultural services including recreational opportunities, and supporting services such as nutrient cycling and photosynthesis [9]. The point at which the system transitions from more desirable to undesirable states, known as the threshold or tipping point, often occurs relatively rapidly and is often unidirectional [10].

Kelp forests are relatively well understood marine ecosystems that illustrate how changes in biotic and abiotic drivers can result in state changes. Kelp forests can support productive fisheries, kelp harvesting, recreational opportunities, and shoreline protection through wave dampening among other services (desirable state). However, if predators such as sea otters, urchin-eating fish, or lobsters (predators that are known to structure kelp forest communities and contribute to its resilience) are reduced to low levels, the resilience of this desirable state can decrease and the system can “tip” into a less desirable state characterized by a high abundance of urchins and overgrazed kelp, which produces fewer ecosystem services [11].

Similarly, coral reefs can support fisheries, recreational opportunities, shoreline protection and other services. If herbivorous fish are reduced to low levels, resilience can decrease and the system can tip into a less desirable state characterized by low coral cover and a high abundance of fleshy algae [12–18].

Abiotic factors, such as light, temperature, and nutrient levels, can also drive transitions to alternative ecosystem states in both coral reefs and kelp forests. Potential thresholds for biotic and abiotic factors for coral reefs and kelp forests (two particularly well studied marine ecosystems) based on a review of the literature are summarized in Tables 1 and 2, respectively. Typically, the effects and thresholds of these abiotic factors are better characterized than biotic factors. In addition, many biotic and abiotic factors no doubt interact in both systems. For example, high nutrient loadings and lack of grazing by herbivorous fish may interact synergistically to accelerate a transition from coral to algal dominated communities on coral reefs [19,20]. Sewage input or high temperature levels can result in some loss of kelp, which could be accelerated by the overharvest of urchin predators [21,22].

Transitions from desirable to less desirable states can, of course, be hastened by storms, anomalous temperatures, or other shocks (“fast drivers” or “pulse events”). Such transitions can be inhibited by conserving and restoring the attributes of marine ecosystems that are associated with resilience. These include [8]:

1. *ecological redundancy* may buffer ecosystems from perturbations due to the overlap of multiple species that perform a similar ecosystem function, which often helps ecosystems

resist disturbance, recover more quickly, rebound following change;

2. *species complementarity* provides an adaptive capacity within the ecosystem to buffer uncontrollable changes in the environmental drivers due to the diverse response to drivers among multiple species;
3. *intra-species complementarity* provides similar adaptive capacity and may also contribute to increased resistance and accelerated recovery due to high genetic variation within species; and
4. *higher productivity and recruitment rates* may help increase recovery rates or resistance to major shifts in ecosystem state (productivity may be related to biodiversity, but there are cases in which nutrients, by upwelling for example, and other physical factors may play more important roles).

Restoration to historical desirable states is rare, but recovery to more desirable states can be facilitated by reducing stressors. In some cases, active recovery efforts such as re-stocking depleted species may be required [23]. Disproportionately large changes (e.g., large reductions in herbivores or large increases in predators) may also be required for recovery [24,25].

For some marine ecosystems, the factors (drivers) that influence these states are well understood, and some key attributes of marine ecosystems that seem to contribute to resilience have been identified [8]. Moreover, the levels of certain drivers that define thresholds between desirable and undesirable states have been determined in some cases [26]. Taken together, information on states, drivers, and thresholds can be used to articulate practical management objectives and metrics related to maintaining marine ecosystems in desirable, resilient states.

When sufficient data and knowledge exist to quantify the relationships between drivers and ecosystem states, and to identify thresholds between desirable and undesirable states (data-rich systems), measurable management objectives aimed at achieving resilience of desirable states can be set for the maintenance of drivers and resilience attributes at appropriate levels. This is illustrated in a highly simplified way in Fig. 1.

If quantitative relationships between drivers and ecosystem state are unknown, but a qualitative understanding of these relationships and thresholds is available (data-moderate systems), ecological risk analysis can be used to identify and reduce risks to the attributes that support the resilience of desirable ecosystem states [27].

For poorly understood (data-poor) ecosystems, it may be useful to conduct a qualitative assessment of marine ecosystem vulnerability to help identify priorities for management. Vulnerability can be conceived of as the obverse of resilience (i.e., absence of attributes that contribute to resilience) in concert with the effects

Table 2
Biotic and abiotic resilience attributes and driver thresholds for kelp forests (kelp order: *Laminariales*).

Physical drivers	Zone/process	Qualitative resilience attributes	Quantitative resilience attributes (i.e. thresholds)		
			Minimum	Optimal/normal	Maximum
Substrate	(wavelength)	Hard substrate (e.g. cobble, boulder) Photosynthetically Active Radiation (PAR)		400 nM [67]	
			Light	700 nM [67]	
Light (energy)	Gametogenesis	Moderate light intensity at the surface (sufficient for plant production)	0.2–0.4 E m ⁻² day ⁻¹ [68,69]	350–500 nM [73] 0.4–0.8 E m ⁻² day ⁻¹ (saturation rate, i.e. highest growth rate) [68,69]	
	Gametophytes		0.3 E m ⁻² day ⁻¹ (growth) [70]	2 E m ⁻² day ⁻¹ (saturation rate) [70]	
Light (energy)	Young sporophyte (~1 cm long)	Cold water	0.1 E m ⁻² day ⁻¹ (growth) [70]	1.5 E m ⁻² day ⁻¹ (saturation rate) [70]	
	Juvenile sporophytes (~0.2–1 m long)		0.6–0.7 E m ⁻² day ⁻¹ (growth) [71,72]	2–3 E m ⁻² day ⁻¹ (saturation rate) [71]	
Temperature	Adults	Growth of gametophytes	0.1 E m ⁻² day ⁻¹ (growth) [73]	10 E m ⁻² day ⁻¹ (saturation rate) [73]	
	Gametogenesis			< 12–14 °C (optimal) [74,75] 17 °C (optimal growth temperature for most kelp species, except for <i>Nereocystis Luetkeana</i> for which growth occurred at 15 °C) [77]	~16 °C [22,76]
Temperature	Gametophyte fertility	Nutrient rich (with mainly nitrates) well-up water. Temporal patchy nutrient delivery (e.g., periodic upwelling)—kelp can store nitrogen while other species cannot, perhaps providing a competitive advantage [70,78,79]	5 °C (gametophytes unable to become fertile below this point) [67]	12 °C (optimal in southern California kelp species) [67]	23 °C (growth and fertility decline rapidly beyond this temperature) [67]
	Sporophyte production				16.3 °C [70,75]
Nutrients	Adult kelp	Overall nitrogen concentrations			18–20 °C (the temperature beyond which nutrients are limiting) [68,70,72,77]
	Other nitrogen concentrations		~1 µM of nitrate [80–86]	1–2 µM of nitrate (is necessary to support a typical giant kelp growth rate of 4% increase in wet weight per day) [87] ~2 µM of nitrates (kelp growth is saturated at this point) [88]	
Nutrients	Surface nitrogen concentrations	Bottom nitrogen concentrations	< 0.5–1 µM of nitrate (low for most of the year, higher during winter) [80,89–91]		
	Other nutrients		> 1 µM of nitrate (below 4.5 m depth, (highest during spring upwelling, lowest during summer) [80]		
Salinity	Other nutrients	Moderately saline water			30 ppb of copper reduces <i>Macrocystis</i> growth and fertility [92]; DDT has contributed to the decline or lack of recovery of kelp forests [70]; Zinc is toxic at levels higher than those that are bio-essential [93]
	Gametophyte		25% (cultured gametophytes do not survive salinities below this point) [70,94]	28% (<i>Laminaria saccharina</i> , <i>Costaria costata</i> and <i>Constantinea subulifera</i> grow in the northeast pacific up to and beyond these surface salinities) [95]	
Salinity	Sporophyte	Adult kelp	9% (irreversibly inhibited development of <i>Saccorhiza polyschides</i>) [96]		
	Adult kelp		10% (adult giant kelp transplanted to salinities below this	33% (typical salinity for <i>Macrocystis</i> in eastern Pacific) [70]	The effects of high salinity are compounded by high temperatures [98]

Table 2 (continued)

Physical drivers	Zone/process	Qualitative resilience attributes	Quantitative resilience attributes (i.e. thresholds)		
			Minimum	Optimal/normal	Maximum
Dissolved oxygen	Surface	level suffered damage) [97] 1.43 ml L ⁻¹ (or 2.4 × 10 ⁻¹⁸ nM, below this threshold is considered hypoxic) [99]	0.25 mM [80]	0.14 mM [80] 0.02–0.04 m s ⁻¹ (optimal for uptake of nutrients/ inorganic nitrogen and highest growth rate) [87,100]; ~1 m wave height (nutrient uptake is maximized for surface, subsurface and base of kelp) [87,101–103]	~1 m s ⁻¹ limits the extent of canopy and the distribution of Macrocystis [70]
	Bottom (10–12 m)				
Wave surge	Current velocities	Moderate wave action to facilitate plant nutrient uptake			
Sedimentation		Little land-derived sedimentation (that inhibits photosynthesis)			10 mg cm ⁻³ (0.45 mm thick) (reduce gametophyte survival by 90%) [104]
Biological drivers					
Herbivory		Diverse and abundant herbivores			32 urchins m ⁻² at grazing front; 62 urchins m ⁻² at 9 m behind grazing front; 46 urchins m ⁻² at 18 m behind grazing front (grazing band of sea urchins, <i>Strongylocentrotus franciscanus</i> , <i>S. purpuratus</i>) [105]
Predation		Diverse, abundant, large predators (large enough to prey on functionally important herbivores of most sizes)			

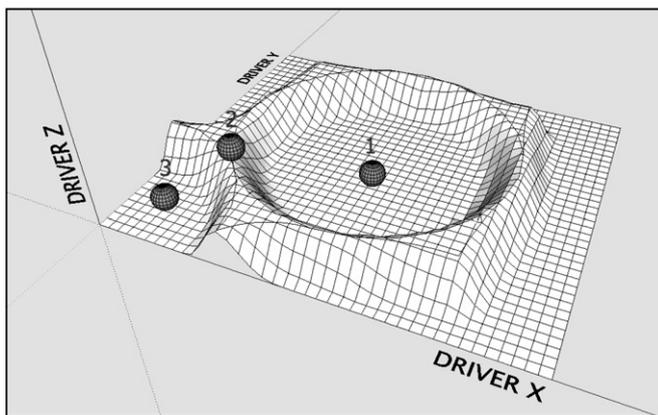


Fig. 1. Alternate ecosystem states and thresholds. Ecosystems can transition from a stable state (1) with multiple ecosystem services to an alternate state (3) with fewer ecosystem services, in response to changes in physical, chemical and biological drivers (drivers X, Y and i) that tip the system over a threshold (2). The wider the basin, the greater the resilience of the system.

of exposure and sensitivity [28,29]. Expert opinion can be systematically analyzed to assess ecosystem vulnerability [29,30].

In lieu of sufficient data to fully describe the relationships between ecosystem state and drivers, a combination of quantitative thresholds for abiotic drivers such as nutrient levels and qualitative thresholds for biotic drivers such as predator and herbivore abundance can be used to maintain marine ecosystems in desirable states. Indicators to be used for tracking change should be chosen carefully so that they are useful for management; for example, highly variable or difficult to measure indicators should be avoided. We summarize some of the available

information on biotic and abiotic thresholds in Tables 1 and 2 for coral reefs and kelp forests, respectively, as interim guidance for managers.

3. Framework for resilience management

3.1. Proactive resilience management

To proactively manage for resilience of desirable ecosystem states, the known attributes that contribute to resilience – including functional redundancy, intra- and inter-species complementarity, and high productivity and recruitment rates – should be monitored and maintained. In practical terms, this translates into setting aside some relatively healthy areas of the ocean for conservation (i.e., within Marine Protected Areas) and maintaining currently healthy areas within a given ecosystem by resisting pressure to maximize one ecosystem service over others (which may be economically attractive, over the short term) and preventing or reducing activities that have significant adverse impacts on these attributes. “Significant adverse impact” can be defined qualitatively (e.g., based on expert opinion), or quantitatively as changes that move the system into a state between the bottom of the basin and the state change threshold (Fig. 1).

3.2. Identify early warning Indicators

The desirable and undesirable states described above for kelp forests and coral reefs are the endpoints on a spectrum of change. By the time coral or kelp cover – often used as indicators of ecosystem state – are significantly diminished, many ecosystem services are likely to have already been lost and recovery is likely

to be difficult [8,31]. Identifying indicators and trends that occur in advance of large shifts in ecosystem state is therefore critical for successful management. For example, fishable biomass may be an indicator of incipient ecosystem state change in coral reefs and is relatively easy to measure [26]. There is empirical evidence for coral reefs based on meta-analysis that variance in the ratio of macroalgae to live coral increases significantly when fish biomass drops below 850 kg/ha, suggesting that this level of fishable biomass, associated with higher system variance, is an early indicator of incipient state change [26]. Similar, rapid changes in the variance of state variables may also be relatively early indicators of incipient change in temperate marine ecosystems [32]. Quantitative relationships between easily measured metrics and non-linear changes in ecosystem state variables like these for coral reefs have not yet been developed for kelp forests or many other marine ecosystems.

3.3. Adaptive management

Monitoring indicators of resilience and early warning indicators of ecosystem state change is of course essential, as is taking corrective action based on continued learning. Determining when action is warranted will depend on the risk tolerance of resource managers, which should be made explicit and transparent.

4. Conclusions

New policy goals, objectives, and management thresholds aimed at maintaining or increasing resilience could provide a sound basis for improving the management of activities that affect marine ecosystems. Specifically, the management framework suggested here is aimed at reducing the risk of ecosystem collapse and the loss of ecosystem services by maintaining ecosystem attributes that contribute to resilience and by keeping drivers of ecosystem change within ranges that prevent ecosystems from transitioning to less desirable states. This approach could also complement existing approaches such as Marine Protected Areas, marine spatial planning, water quality control programs, and fisheries management by improving their alignment with the goal of resilience. More research on the relationships between ecosystem state variables and easily measured metrics for other systems will be necessary for the development of quantitative thresholds for resilience management. In the meantime, proactive risk reduction, risk assessment using expert opinion, and early warning indicators derived from meta-analyses can be used to reduce the risk of ecosystem state change.

Acknowledgments

We are grateful for fruitful discussions with Fio Micheli, Andrea Saenz, Mary Turnipseed, and many other scientists and policy experts that enriched the concepts developed in this paper. We also thank Kendra Karr for assistance in the preparation of the manuscript.

References

- Asner GP, Seastedt TR, Townsend AR. The decoupling of terrestrial carbon and nitrogen cycles: human influences on land cover and nitrogen supply are altering natural biogeochemical links in the biosphere. *BioScience* 1997;47:226–234.
- Vitousek PM, Aber JD, Howarth RW, et al. Human alteration of the global nitrogen cycle: causes and consequences. *Ecological Applications* 7: 737–750.
- Rodhe H. Human impact on the atmospheric sulfur balance. *Tellus Sr.* 1997; A-B 1999;51:110–122.
- Simas T, Nunes JP, Ferreira JG. Effects of global change on coastal salt marshes. *Ecol Mod* 2001;139:1–15.
- Smetacek V, Nicol S. Polar ocean ecosystems in a changing world. *Nature* 2005;437:362–368.
- Harley CDG, Hughes AR, Hultgren KM, et al. The impacts of climate change in coastal marine systems. *Ecol Lett* 2006;9:228–241.
- Levin SA, Lubchenco J. Resilience, robustness, and marine ecosystem based management. *BioScience* 2008;58:27–32.
- Palumbi SR, McLeod KL, Grunbaum D. Ecosystems in action: lessons from marine ecology about recovery, resistance, and reversibility. *BioScience* 2008;58:33–42.
- Millennium Ecosystem Assessment. *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, D.C.
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, et al. Coral reefs under rapid climate change and ocean acidification. *Science* 2007;318:1737–1742.
- Steneck RS, Graham MH, Bourque BJ, et al. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 2002;29: 436–459.
- Hughes TP. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 1994;265:1547–1551.
- Hoegh-Guldberg O, Smith GJ. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper. and *Seriatopora hystrix* Dana. *J Exp Mar Bio Ecol* 1989;129:279–303.
- Knowlton N. The future of coral reefs. *Proc Natl Acad Sci* 2001;98: 5419–5425.
- Gardner TA, Cote IM, Gill JA, et al. Long-term region-wide declines in Caribbean corals. *Science* 2003;301:958–960.
- Bellwood DR, Hughes TP, Folke C, et al. Confronting the coral reef crisis. *Nature* 2004;429:827–833.
- Pandolfi JM, Jackson JBC, Baron N, et al. Are U.S. coral reefs on the slippery slope to slime? *Science* 2005;307:1725–1726.
- Hoegh-Guldberg O. Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshwater Res* 1999;50:839–866.
- Hallock P, Schlager W. Nutrient excess and the demise of coral reefs and carbonate platforms. *PALAI* 1986;1:389–398.
- Done TJ. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 1992;247:121–132.
- Macfadyen A, Ford ED, editors. London: Academic Press, Inc.; 1987.
- Tegner MJ, Dayton PK. El Nino effects on southern California kelp forest communities. *Advan Ecol Res* 1987;17:243–279.
- Konar B, Estes J. The stability of boundary regions between kelp beds and deforested areas. *Ecology* 2003;84:174–185.
- Baskett ML, Yoklavich M, Love MS. Predation, competition, and the recovery of overexploited fish stocks in marine reserves. *Can J Fish Aquat Sci* 2006;63:1214–1229.
- Baskett ML, Saloman AK. Recruitment facilitation can drive alternative states on temperate reefs. *Ecology* 2010;91:1763–1773.
- McClanahan TR, Maina JM, Muthiga NA. Associations between climate stress and coral reef diversity in the western Indian Ocean. *Global Change Biol* 2011;17:2023–2032.
- Hobday AJ, Poloczanska ES, and Matera R. Implications of climate change for Australian fisheries and aquaculture: a preliminary assessment. CSIRO Marine and Atmospheric Research, Report to the Department of Climate Change, Canberra, Australia; 2007.
- Metzger MJ, Leemans R, Schroter D, et al. The ATEAM vulnerability mapping tool. Quantitative approaches in systems analysis no. 27, CD-ROM publication. Wageningen, The Netherlands: Office C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC); 2004.
- Teck S, Halpern B, Kappel C, et al. Using expert judgment to estimate marine ecosystem vulnerability in the California Current. *Ecol Appl* 2010;20:1402–1416.
- Halpern B, Walbridge S, Selkoe KA, et al. A global map of human impact on marine systems. *Science* 2008;319:948–952.
- Hughes TP, Bellwood DR, Folke C, et al. New paradigms for supporting the resilience of marine ecosystems. *Trend Ecol Evolut* 2005;20:380–386.
- Scheffer M, Bascompte J, Brock WA, et al. Early-warning signals for critical transitions. *Nature* 2009;461:53–59.
- Harrison PL, Wallace CC. Reproduction, dispersal and recruitment of scleractinian corals. *Ecosyst World* 1990;25:133–207.
- Birkeland C, Rowley D, and Randall RH. Coral recruitment patterns at Guam. In: *Proceedings of the fourth international coral reef symposium*, Manila; 1982. p. 339–44.
- Hodgson G. Sedimentation on coral reefs. PhD dissertation. University of Hawaii, Honolulu; 1990.
- Dubinsky Z, editor. Amsterdam, The Netherlands: Elsevier Science Publishing Company, Inc; 1990.
- Falkowski PG, Dubinsky Z. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* 1981;289:172–174.
- Dubinsky Z, Berman T, Schanz F. Field experiments for in situ measurements of photosynthetic efficiency and quantum yield. *J Plankton Res* 1984;6:339–349.
- Chalker BW, Dunlap WC, Oliver JK. Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. II. Light saturation curves for photosynthesis and respiration. *J Exp Mar Biol Ecol* 1983;73:37–56.

- [40] Gorbunov MY, Kolber ZS, Lesser MP, et al. Photosynthesis and photoprotection in symbiotic corals. *Limnol Oceanogr* 2001;46:75–85.
- [41] Burris JE, Porter JW, Laing WA. Effects of carbon dioxide concentration on coral photosynthesis. *Mar Biol* 1983;75:113–116.
- [42] Edmunds PJ, Davies SP. An energy budget for *Porites porites* (Scleractinia). *Mar Biol* 1986;92:339–347.
- [43] Vaughan TW. Corals and the formation of coral reefs. *Ann Rep Smithsonian Inst* 1919;17:189–238.
- [44] Skirrow G. The dissolved gases–carbon dioxide. In: Riley JP, Skirrow G, editors. *Chemical Oceanography*. London: Academic Press; 1975. p. 1–192.
- [45] Plath DC, Johnson KS, Ptykowitz RM. The solubility of calcite – probably containing magnesium – in seawater. *Mar Chem* 1980;10:9–29.
- [46] Morse JW, Mackenzie FT. *Geochemistry of sedimentary carbonates*. New York: Elsevier; 1990.
- [47] Jokiel PL, Coles SL. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reef* 1990;8:155–162.
- [48] Bell PRF. Eutrophication and coral reefs—some examples in the Great Barrier Reef Lagoon. *Water Res* 1992;26:553–568.
- [49] Bell PRF, Elmetri I. Ecological indicators of large-scale eutrophication in the Great Barrier Reef Lagoon. *Ambio* 1995;24:208–215.
- [50] Lapointe BE. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnol Oceanogr* 1997;42:1119–1131.
- [51] Crossland CJ. Dissolved nutrients in reef waters of Sesoko Island, 1. Okinawa: a preliminary study. *Galaxea*; 1982 47–54.
- [52] Morris B, Barnes J, Brown F, et al. The Bermuda marine environment. *Bermuda Biol Stat Res* 1977.
- [53] D'Elia CF, Webb KL, Porter JW. Nitrate-rich groundwater inputs to Discovery Bay, Jamaica: a significant source of N to local reefs? *Bull Mar Sci* 1981;31:903–910.
- [54] D'Elia CF. Unpublished data.
- [55] Adey WH, Steneck RS. Highly productive eastern Caribbean reefs: synergistic effects of biological, chemical, physical, and geological factors. In: Reaka ML, editor. *The ecology of coral reefs in symposia series for undersea research*. NOAA's undersea research program, Rockville, MD; 1985. p. 163–187.
- [56] Smith SV, Jokiel PL. Water composition and biogeochemical gradients in the Canton Atoll Lagoon. *Atoll Res Bull* 1978;221:15–53.
- [57] Marsh JA. Terrestrial inputs of nitrogen and phosphorus on fringing reefs of Guam. In: *Proceedings of the third international coral reef symposium*, Miami, Florida; 1977. P. 331–36.
- [58] Crossland CJ, Barnes DJ. Dissolved nutrients and organic particulates in water flowing over coral reef at Lizard Island. *Aust J Mar Freshwater Res* 1983;34:835–844.
- [59] Smith SV, Buddemeier RW. Global change and coral reef ecosystems. *Annu Rev Ecol Syst* 1992;23:89–118.
- [60] Atkinson MJ. Are coral reef communities nutrient-limited? In: *Proceedings of the sixth international coral reef symposium*, Townsville; 1988. p. 157–66.
- [61] Larned ST, Atkinson MJ. Effects of water velocity on NH_4 and PO_4 uptake and nutrient-limited growth in the macroalga *Dictyosphaeria cavernosa*. *Mar Ecol Prog Ser* 1997;157:295–302.
- [62] Hearn CJ, Atkinson MJ, Falter JL. A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. *Coral Reef* 2001;20:347–356.
- [63] Connell JH. Diversity in tropical rain forest and coral reefs. *Science* 1978;199:1302–1310.
- [64] Huston M. Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reef* 1985;4:19–25.
- [65] Barnes DJ, Chalker BE. Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z, editor. *Coral Reefs, Ecosystem of the World 25*. Amsterdam: Elsevier; 1990. p. 109–131.
- [66] Muehllehner N and Edmunds PJ. Effects of ocean acidification and increased temperature on skeletal growth of two scleractinian corals, *Pocillopora meandrina* and *Porites rus*. In: *Proceedings of the eleventh coral reef symposium*, Fort Lauderdale, FL; 2008. p. 57–61.
- [67] Foster MS, Schiel DR. The ecology of giant kelp forests in California: a community profile. *US Fish and Wildlife Services Biological Report*, vol. 82. 1985. p. 1–152.
- [68] Deysler LE, Dean TA. Critical irradiance levels and the interactive effects of quantum irradiance and dose on gametogenesis in the giant kelp, *Macrocystis pyrifera*. *J Phycol* 1984;20:520–524.
- [69] Dayton PK. Ecology of kelp communities. *Annu Rev Ecol Syst* 1985;16: 215–245.
- [70] Dean TA, Deysler L, Thies K, et al. The effects of the San Onofre Nuclear Generating Stations (SONGS) on the giant kelp *Macrocystis pyrifera*: final preoperational monitoring report. *Marine Review Committee*, Encinitas, CA. 1983.
- [71] Dean TA, Jacobson FR. Growth of juvenile *Macrocystis pyrifera* (Laminariales) in relation to environmental factors. *Mar Biol* 1984;83:301–311.
- [72] Dean TA, Jacobson FR. Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera* during the 1982–84 El Niño in southern California. *Mar Biol* 1986;90:597–601.
- [73] Clendenning KA. Photosynthesis and general development in *Macrocystis*. *Nova Hedwigia* 1971;32:169–190.
- [74] Luning K, Neushul M. Light and temperature demands for growth and reproduction of Laminarian gametophytes in southern and central California. *Mar Biol* 1978;45:297–309.
- [75] Dean TA, Deysler LE. The effects of suspended solids and thermal discharges on kelp *Macrocystis*. In: Bascom W, editor. *The effects of waste water discharges on kelp in Southern California*, Southern California Coastal Water Research Project, Long Beach, CA; 1983. p. 114–135.
- [76] Dayton PK, Tegner MJ, Edwards PB, et al. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol Appl* 1998;8: 309–322.
- [77] Vadas RL. Ecological implications of culture studies on *Nereocystis luetkeana*. *J Phycol* 1972;8:196–203.
- [78] Chapman ARO, Craigie JS. Seasonal growth in *Laminaria longicuris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar Biol* 1977;40:197–205.
- [79] Fujita RM. The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. *J Exp Mar Bio Ecol* 1985;92: 283–301.
- [80] Jackson GA. Nutrient and production of giant kelp, *Macrocystis pyrifera*, off southern California. *Limnol Oceanogr* 1977;2:979–995.
- [81] Zimmerman RC, Robertson DL. Effects of El Niño on local hydrography and growth of the giant kelp *Macrocystis pyrifera* at Santa Catalina Island, California. *Limnol Oceanogr* 1985;30:1289–1302.
- [82] Tegner MJ, Dayton PK, Edwards PB, et al. Is there evidence for long-term climatic change in southern California kelp forests? *California Cooperat Ocean Fish Invest Rep* 1996;37:111–126.
- [83] Tegner MJ, Dayton PK, Edwards PB, et al. Large-scale, low-frequency oceanographic effects on kelp forest succession: a tale of two cohorts. *Mar Ecol Prog Ser* 1997;146:117–134.
- [84] Dayton PK, Tegner MJ, Edwards PB, et al. Temporal and spatial scales of kelp demography: the role of oceanography climate. *Ecol Monogr* 1999;69:219–250.
- [85] Hernandez-Carmona G, Robledo D, Serviere-Zaragoza E. Effect of nutrient availability on *Macrocystis pyrifera* recruitment survival near its southern limit of Baja California. *Bot Mar* 2001;44:221–229.
- [86] Graham MH, Vasquez JA, Buschmann AH. Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanogr Mar Biol: Annu Rev* 2007;45:39–88.
- [87] Gerard VA. Growth and utilization of internal nitrogen reserves by the giant kelp, *Macrocystis pyrifera*, in a low nitrogen environment. *Mar Biol* 1982;66:27–35.
- [88] Zimmerman RC, Kremer JN. In situ growth and chemical composition of the giant kelp *Macrocystis pyrifera*: response to temporal changes in ambient nutrient availability. *Mar Ecol Prog Ser* 1986;27:277–285.
- [89] Zimmerman RC. Seasonal patterns in the productivity of a giant kelp (*Macrocystis pyrifera*) forest: the effect of nutrient availability. Los Angeles: University of Southern California; 1983.
- [90] Dayton PK, Tegner MJ, Parnell PE, et al. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol Monogr* 1992;62:421–445.
- [91] Fram J, Stewart H, Brzezinski M, et al. Physical pathways and utilization or nitrate supply to the giant kelp, *Macrocystis pyrifera*. *Limnol Oceanogr* 2008;53:1589–1603.
- [92] Smith SV. Kaneohe Bay: nutrient mass balance, sewage diversion, and ecosystem responses. In: *Proceedings of the U.S. environmental protection agency symposium on advances in marine environmental research*; 1979. p. 344–58.
- [93] Lobban CS, Harrison PJ, Duncan MJ. *The physiological ecology of seaweeds*. New York: Cambridge University Press; 1985.
- [94] North WJ. Personal communication.
- [95] Druehl LD. The distribution of Laminariales in the North Pacific with reference to environmental influences. In: Scudder GGE, Reveal JL, editors. *Evolution today*. Proceedings of the second international congress of systematic and evolutionary biology; 1981. p. 55–67.
- [96] Norton TA, South GR. Influence of reduced salinity on the distribution of two laminarian algae. *Oikos* 1969;20:320–326.
- [97] North WJ, editor. Pasadena, CA: California Institute of Technology; 1969.
- [98] Druehl LD. Distribution of two species of Laminaria as related to some environmental factors. *J Phycol* 1967;3:103–108.
- [99] Grantham BA, Chan F, Nielsen KJ, et al. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northwest Pacific. *Nature* 2004;429:749–754.
- [100] Wheeler WN. Nitrogen nutrition of *Macrocystis*. In: Srivastava LM, editor. *Synthetic and degradative processes in marine macrophytes*. New York: De Gruyter; 1982. p. 121–135.
- [101] Wheeler WN. *Ecophysiological studies on the giant kelp, macrocystis*. Santa Barbara, CA: University of California; 1978.
- [102] Seymour RJ, Tegner MJ, Dayton PK, et al. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in Southern California. *Estuar Coast Shelf Sci* 1989;28:277–292.
- [103] Wheeler WN. Kelp forests of British Columbia, a unique resource. Ministry of Agriculture and Fisheries, Aquaculture and Commercial Fisheries Branch, Province of British Columbia; 1990. p. 91.
- [104] Deviny JS, Volsse LA. The effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Mar Biol* 1978;48:343–348.
- [105] Leighton DL. Grazing activities of benthic invertebrates in Southern California kelp beds. In: North WJ, editor. *The biology of giant kelp beds (Macrocystis) in California*. Nova Hedwigia; 1971. p. 421–53.