Long-Term Trends in Ecological Systems:
A Basis for Understanding Responses to Global Change

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Cross-Site Comparisons of State-Change Dynamics

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Changes in the state of a system—for example from grassland to shrubland or from dominance by one fish species to another species—with associated changes in other parts of the system, are often irreversible. These state changes are related to changing climatic conditions (chapter 11) interacting with human activities (MEA 2005b). State changes can lead to positive effects on ecosystems; but more frequently, such as with the invasion by an exotic species, the changes are negative and result in altered levels of biodiversity, shifts in rates of nutrient cycling, changes in air and water quality, and increased losses of soil and nutrients to wind and water erosion (Scheffer et al. 2001, Scheffer and Carpenter 2003).

Examination of the dynamics of state changes across a variety of ecological systems can identify common interactions among patterns and processes that can provide new insight into the drivers of these dynamics (Bestelmeyer et al. 2011). It is only through the use of long-term data that we can identify persistent changes in states, the drivers influencing these shifts, and potential reversals or modifications of shifts through time.

Here we illustrate common features of state changes for six systems with a diverse set of organisms (plankton, invertebrates, fish, plants, or penguins).

Vegetation state changes in deserts. In the American Southwest and throughout arid systems globally, large areas of land have converted from perennial grassland to shrubland over the past several centuries (Reynolds and Stafford Smith 2002). This state change is self-reinforcing as positive feedbacks between shrubs and soil properties allow continued shrub survival and promote grass mortality (Schlesinger et al. 1990, Rietkerk et al. 2004). The result is a discontinuous cover of shrubs and unvegetated areas that increases movement of soil and nutrients from bare areas to beneath shrub canopies. In arid systems where average

annual precipitation is typically less than 300 mm, one consequence of this shift from grassland to shrubland is a reduction in above-ground net primary production (figure 3-5).

Although this process of desertification has been well studied (MEA 2005a), little is known about the conditions which affect rate and pattern of shrub dominance or variation in grass survival at patch to landscape scales (Peters et al. 2006). Researchers at the Jornada ARS/LTER (JRN) and Sevilleta LTER (SEV) sites have documented this shift using long-term observations (figure 4-1) and are using experimental manipulations to test the importance of biotic and abiotic processes to threshold behavior through time and across space (Peters et al. 2004, 2009).
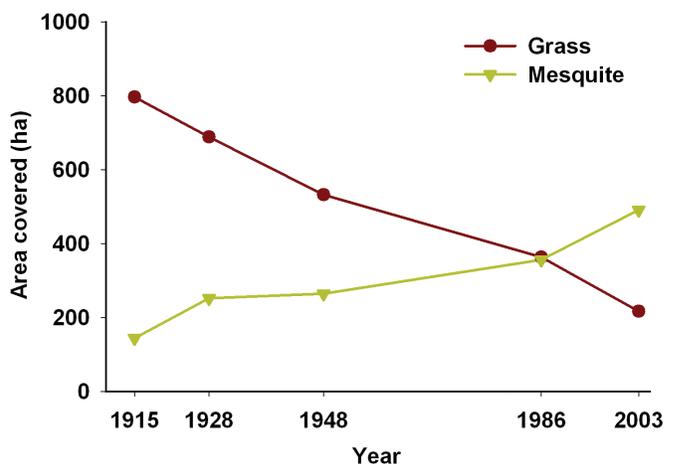
Figure 4-1. State change from grassland (brown) to mesquite shrubland (green) in the Chihuahuan Desert based on changes in area of each ecosystem type through time (Peters et al. 2004). Reprinted with permission from the National Academy of Sciences, USA.

Penguin dynamics in Antarctica. Along the rapidly warming western Antarctic Peninsula (Vaughan et al. 2003), southward climate migration is driving replacement of Adélie penguins by Gentoo and Chinstrap penguins (Ducklow et al. 2007, McClintock et al. 2008). Adélie penguins are a true polar species, with a life history that is critically dependent on the availability of sea ice, especially during winter (Fraser et al. 1992, Ainley 2002). In contrast, the other two species originate in sub-Antarctic latitudes and are ice-intolerant (Fraser et al. 1992, Williams 1995). The population trends shown in figure 4-2 are unprecedented, with the paleo-record indicating that neither Gentoo nor Chinstrap penguins have occupied the region over the past 700 years (Emslie et al. 1998). The changes in penguin abundance and species
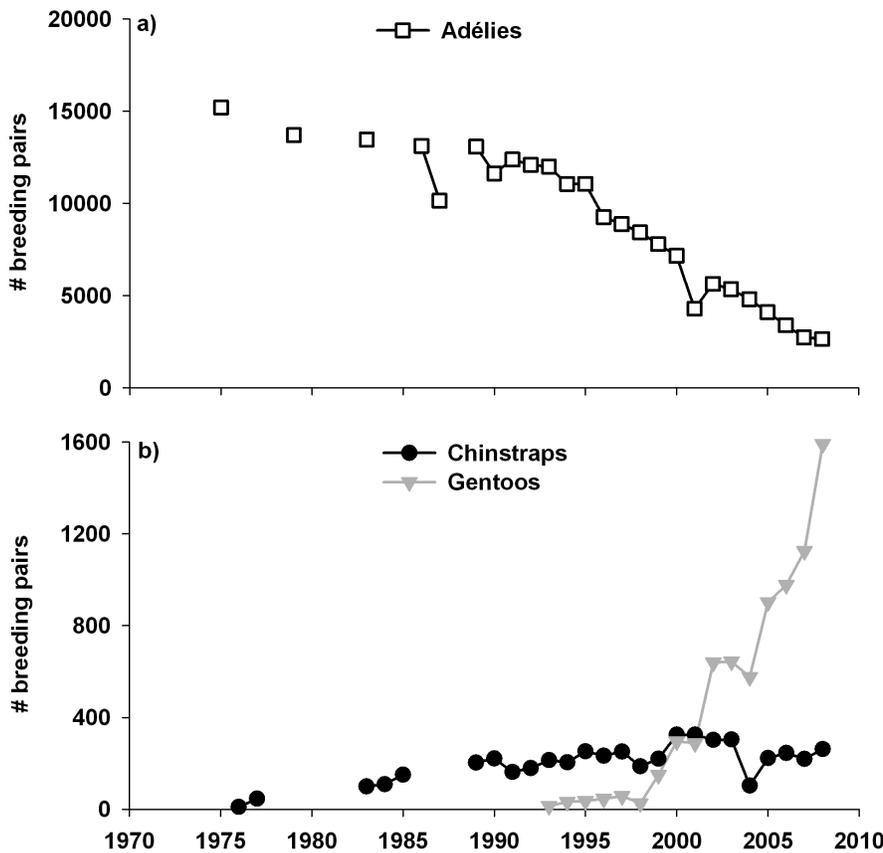
Figure 4-2. State change based on number of breeding pairs of birds from dominance by (a) Adélie penguins, a polar species, to (b) dominance by the ice-intolerant Gentoo and Chinstrap penguins in Antarctica. (Updated from McClintock et al. 2008.)

composition near Palmer Station LTER (PAL) reflect a reduction in the extent and duration of sea ice cover in the area (Ducklow et al. 2007), which is related to the positive Southern Oscillation Index during warm El Niño conditions (figure 3-1).

Fish dynamics in Wisconsin lakes. Similar state changes have been observed in lakes in Wisconsin (figure 4-3). The non-native rainbow smelt became established in Sparkling Lake in the mid 1980s and caused major changes in the lake's fish community (Hrabik et al. 1998, Wilson and Hrabik 2006). Cisco were extirpated by smelt predation on juveniles. Yellow perch also have been greatly reduced because young-of-year smelt out-compete young-of-year yellow perch for prey. Recent declines in rainbow smelt catch per unit effort may be attributed to a harvesting program intended to reduce abundance of this harmful non-native species. It is unclear whether these changes are irreversible. Scientists from the North Temperate Lakes LTER (NTL) are conducting a decade-long experiment that combines manual harvesting of smelt with enhanced stocking and regulatory protection of its predators to reduce smelt to low numbers or possibly remove them from the lake. It is unclear whether the abundance of cisco (if reintroduced) or yellow perch

will increase when smelt abundance is experimentally reduced.

Plankton dynamics in the Pacific Ocean. Along the coast of southern California, variations in plankton populations are closely linked to long-term changes in physical conditions in the ocean environment. A
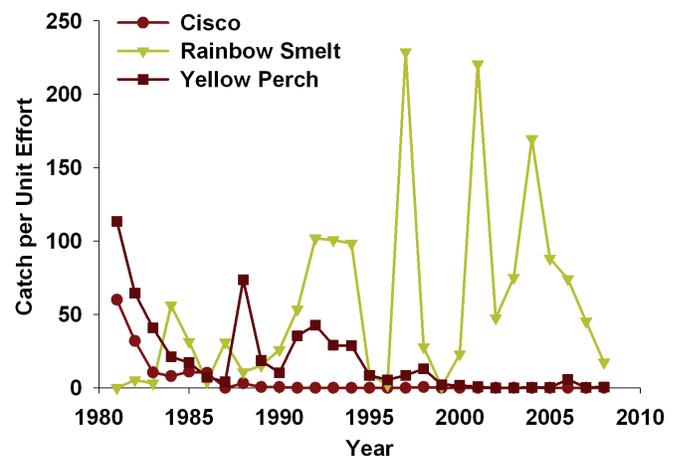
Figure 4-3. State change in lakes in Wisconsin based on fish catch data from dominance by native cisco and yellow perch to dominance by the introduced rainbow smelt. (Updated from Hrabik et al. 1998, Wilson and Hrabik 2006.)

relatively abrupt change occurred in the mid 1970s in sea surface temperature (figure 3-6) (reflected by the Pacific Decadal Oscillation (PDO) index in figure 4-4), with accompanying changes in several members of the plankton assemblage. For example, a subtropical species of krill *(Nyctiphanes simplex)* increased in abundance in the mid 1970s (figure 4-4). Other types of suspension-feeding zooplankton known as salps, one group of which typically enters the study area from higher latitudes, decreased abruptly in biomass at this time (Ohman and Venrick 2003). Following the major El Niño of 1997-98, there was a decrease in sea surface temperatures in the northeastern Pacific Ocean with accompanying reversals of the changes in some plankton populations.

The nodal points of these ecosystem transitions are associated with changes in ocean circulation, but the persistence of the altered communities for two to three decades at a time appears to be related to biotic responses. Whether these ecosystem changes represent cyclical variations is under investigation by the California Current Ecosystem LTER (CCE) site.

Subtidal dynamics off the Pacific Coast. Rocky reefs are known to exhibit sudden changes in state in which one type of benthic community is replaced by another. Scientists at the Santa Barbara Coastal LTER (SBC) have documented a particularly dramatic example of this shift on shallow subtidal reefs at Santa Cruz Island: The density of a small filter-feeding sea
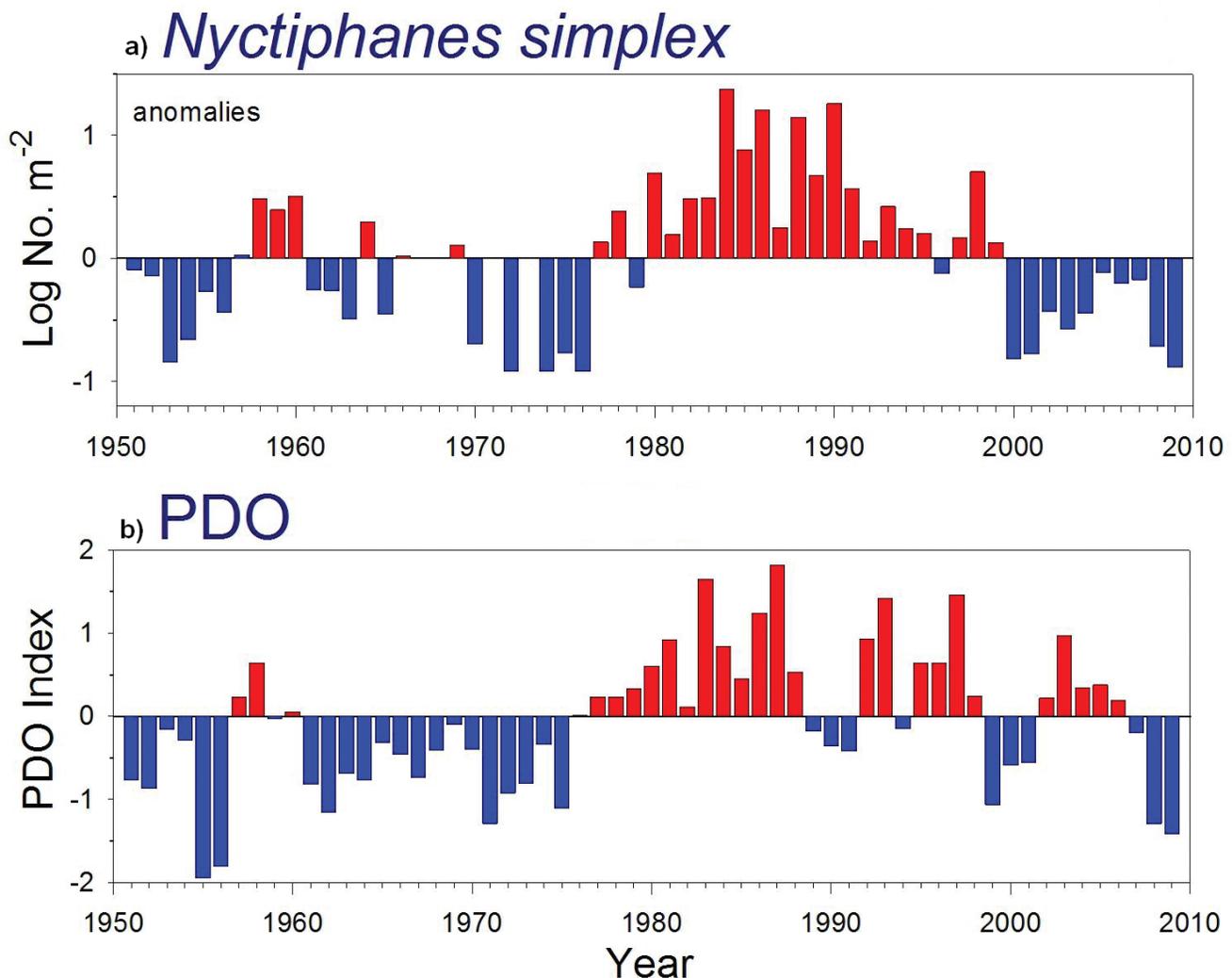
Figure 4-4. Long-term variability in the northeastern Pacific Ocean off the coast of southern California: (a) anomalies of springtime abundance of the euphausiid *Nyctiphanes simplex* and (b) annual averages of the Pacific Decadal Oscillation (PDO) index. (M. Ohman, updated from Brinton and Townsend 2003.)

cucumber, *Pachythyone rubra,* increased from near zero to thousands per square meter (figure 4-5). This change occurred within 2 years and resulted in *P. rubra* covering more than 90 percent of the bottom at many sites (Rassweiler 2008). Manipulative experiments show that *P. rubra* competes for space with understory macroalgae, which had dominated these sites prior to the increase in sea cucumber density. For more than a decade, macroalgae were unable to recover at these sites, in part because sea cucumbers consume algal spores in the water column.
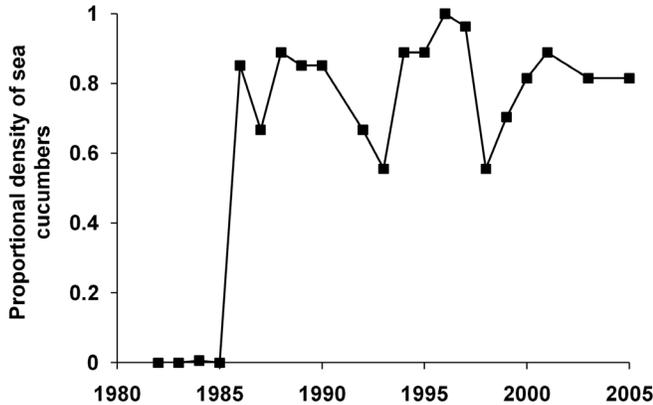

Figure 4-5. State changes in subtidal reefs off the coast of southern California. Sea cucumber biomass increasing over time. (Redrawn from Rassweiler 2008.)

Once the filter feeders reach a high enough abundance, they can reduce settlement rates of macroalgal spores to levels that are low enough to prevent reestablishment of macroalgae. Shifts from an algal-dominated state to one dominated by invertebrate filter feeders represents a major change in the trophic structure of the benthic food web, as energy is derived from captured plankton instead of from primary production by macroalgae. The decline in macroalgae has reduced the abundance of a wide variety of organisms that use the algae for food and shelter, including small crustaceans, which are a key food resource for many reef fishes.

Shifts in coastal fish assemblages in the Pacific Ocean. Similar to the dynamics of plankton along the coast of southern California, communities of rocky reef organisms in the same region underwent dramatic changes in response to the abrupt shift from the cool phase to the warm phase of the PDO in the mid 1970s. This climate shift brought warmer, nutrient-poor surface waters to nearshore regions, as well as increases in the intensity and frequency of El Niño Southern Oscillation episodes. Composition of reef fish assemblages changed

in response to this abrupt shift in physical conditions of the nearshore ocean environment. For example, at coastal sites near Los Angeles, CA, dominance of the assemblage shifted from cold-affinity, northern species to warm-affinity, southern species following the abrupt warming of surface waters (figure 4-6). In addition, by the mid 1990s abundance of nearly all fish species had declined by an average of 69 percent (Holbrook et al. 1997, Brooks et al. 2002).
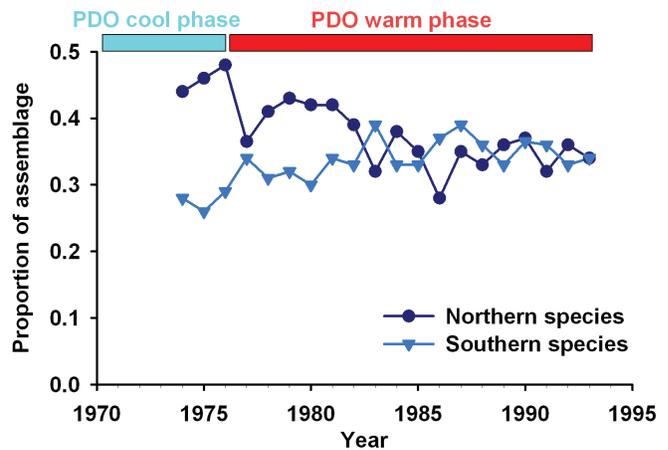
Figure 4-6. Temporal patterns in composition of the fish assemblage on reefs in the Southern California Bight. Shown are the proportions of the annual total species present that were northern species (cold water affinity: circles) and southern species (warm water: triangles). (Redrawn from Holbrook et al. 1997.)

The lower productivity of the coastal marine ecosystem was also accompanied by large effects on population abundance and reef trophic structure. At the SBC study sites on Santa Cruz Island, CA, declines of a similar magnitude were observed for several linked trophic levels in a model food web (several species of surfperches [Pisces: Embiotocidae], the standing stock of their crustacean prey, and the biomass of understory macroalgae on which the prey reside) (Holbrook and Schmitt 1996, Holbrook et al. 1997). The SBC is exploring whether observed changes in composition of the fish assemblage and in trophic structure of the community represent reversible phases driven by cyclical climatic variation.

Conclusions

These examples clearly show the effect of global environmental change (warming, invasive species, altered trophic structure) on the abundance and distribution of dominant and subordinate species in aquatic, marine, and terrestrial systems. In many cases, environmental drivers have shifted to the point that current conditions are leading to threshold changes in species abundance within communities and are altering species range distributions both regionally and globally. However, this era of rapid environmental change is only beginning to be manifested in species responses. Thus, researchers will continue to need long-term data to quantify and predict the nonlinear system responses expected in the future.

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