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CLIMATE VARIATION, REGIME SHIFTS, AND IMPLICATIONS FOR SUSTAINABLE FISHERIES

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ABSTRACT

The term ecosystem regime shift refers to low frequency, high amplitude variation in marine ecosystems involving changes in community composition, species abundances, and trophic structure. Changes occur in the abundance of both exploited and unexploited populations. Temporally coherent changes often occur in other spatially separated ecosystems. Ecosystem regime shifts are thought to be a response to shifts in the ocean and atmosphere climate and hence are relatively coherent with climate changes. However, the mechanisms responsible for ecosystem regime shifts are not well established. Changes in energy flow from the base of the ecosystem is frequently thought to be responsible, but in some cases climate-induced changes in apex predators also result in top-down responses. For example, regime shifts appeared to have occurred in the North Pacific in 1977 and 1989.

This dramatic ecosystem variation presents challenges for fisheries managers. For example, operating in near real time, managers must make decisions as to whether a sharp drop in an exploited stock represents annual variation, overfishing, or a regime shift to a lower level of productivity. If overfishing is the issue, the response is a rebuilding plan. However, if a regime shift has occurred, it will not be possible to rebuild the stock to previous levels. Instead, the stock should be managed at its new lower level of productivity. Management approaches under regime shifts have been explored with various simulation models. Initial work suggested that a constant harvest rate strategy was a robust harvest approach. However, more recent work suggests that regime specific harvest rates are preferable. New research directions to advance ecosystem monitoring, to expand our understanding of the links between oceanic habitat and ecosystem dynamics, and to develop coupled physical and ecosystem models are needed to achieve sustainable fisheries under regime shifts.

In recent years there has been increasing focus on a rather dramatic type of ecosystem dynamics that is termed a regime shift (Steele, 1996; Hare and Mantua, 2000). While there is no single definition of an ecosystem regime shift, the following characteristics have been observed. The abundance of various species covering a range of trophic levels persists around long-term baselines and then suddenly and fairly coherently shifts to new baseline levels where they again persist. The shift in abundance occurs for both exploited and unexploited species. Shifts in ecosystems spanning broad spatial scales including ocean basins are temporally coherent, although the same species may respond differently in different regions. Finally, these sudden ecosystem changes occur concurrently with changes in large-scale atmospheric or oceanic conditions. These low-frequency, high amplitude changes in community composition, species abundances, and trophic structure would appear to present challenges to achieving sustainable fisheries. I will briefly present some examples of ecosystem regime shifts, discuss proposed harvest strategies for fish populations that undergo regime shifts, and discuss research approaches to improve management of fisheries that experience regime shift dynamics.

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Ecosystem Regime Shifts

The concept of an ecosystem regime shift is implicit in many studies of the link between marine ecosystems and the ocean environment (e.g. Cushing, 1982) and is supported by a substantial scientific literature from around the world. I do not intend to provide a synthesis of all this work but rather select a few examples from the Pacific to illustrate several aspects of this concept.

A well-documented example of a dramatic regime shift occurred in the Peruvian upwelling ecosystem in the mid-1970s, including a sharp drop in biomass of anchoveta, bonito, sea birds, and zooplankton and sharp increases in sardines and hake (Fig. 1)†. The ecosystem shifted from a highly productive one that supported a very large biomass of anchoveta to one that was much less productive at high trophic levels but consisting of roughly equal biomasses of sardine and anchoveta (Fig. 1). While most marine ecosystem time series are not long enough to provide evidence of more than one regime shift, in some instances longer dynamics can be gleaned from records in benthic sediments. For example, time series of sardine and anchovy biomass off California appear to have exhibited regime shifts, often at a period of 60 yrs, for 2000 yrs. This is based on biomass estimates obtained from a time series of scales in sediment cores from the Santa Barbara basin (Soutar and Issacs, 1969; Baumgartner et al., 1992). These data provide evidence that regime shifts are an integral part of the population dynamics in at least some ecosystems.

In the northeast Pacific, ecosystem regime shifts in 1977 and 1989 have been documented using a principal component analysis of 31 climate and 69 biological time series covering 1965–1997 (Hare and Mantua, 2000). The 1977 regime shift, represented by the first principal component of these physical and biological time series, was physically characterized by an intensification of the wintertime Aleutian Low, cooling in the central North Pacific and warming in the coastal northeast Pacific and Bering Sea (Hare and Mantua, 2000). Biologically, the 1977 regime shift was characterized by an increase in most Alaskan salmon populations, a decline in Alaskan shrimp populations, and a decline in most North American west coast salmon populations. The 1989 regime shift, represented by the second principal component of the 31 climate and 69 biological time series, was not the end of the 1977 shift back to pre-1977 conditions, but rather a change with different spatial impacts. The 1989 regime shift was physically characterized by winter cooling of the coastal waters in the northern Gulf of Alaska and the Bering Sea and warming in the central North Pacific Ocean (Hare and Mantua, 2000). This regime shift resulted in declines in Bering Sea groundfish recruitment, several species of salmon in western Alaska and British Columbia, and increases in Bering Sea jellyfish biomass (Hare and Mantua, 2000). It is significant to note that in the northeast Pacific more than one mode of physical and biological variability appeared to exist and that both benthic and pelagic species exhibited regime shift dynamics.

In the Hawaiian Archipelago during the 1980s, a dynamic surplus production model was used to provide advice to managers regarding the target harvest level for a developing trap fishery for spiny, *Panulirus marginatus* (Quoy and Gaimard,

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†Fig. 1, page 390 *in* Muck, P. 1989. Major trends in the pelagic ecosystem off Peru and their implications for management. Pages 386–403 *in* Pauly, D., P. Muck, J. Mendo, and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference proceedings 18, 438 p. [*Authors' note:* ICLARM is now known as the WorldFish Center]

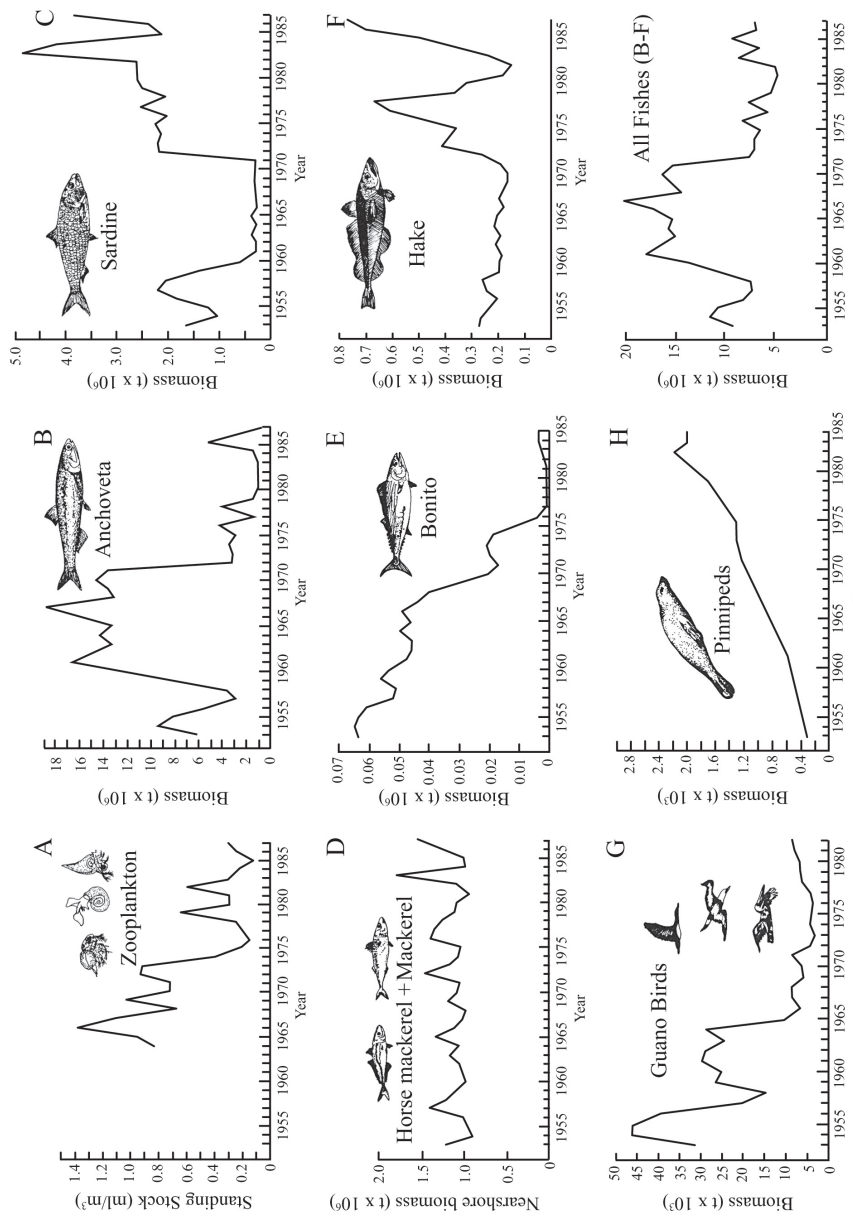

Figure 1. Time series of biomasses of various species in the Peruvian upwelling ecosystem (Muck, 1989) [with permission].

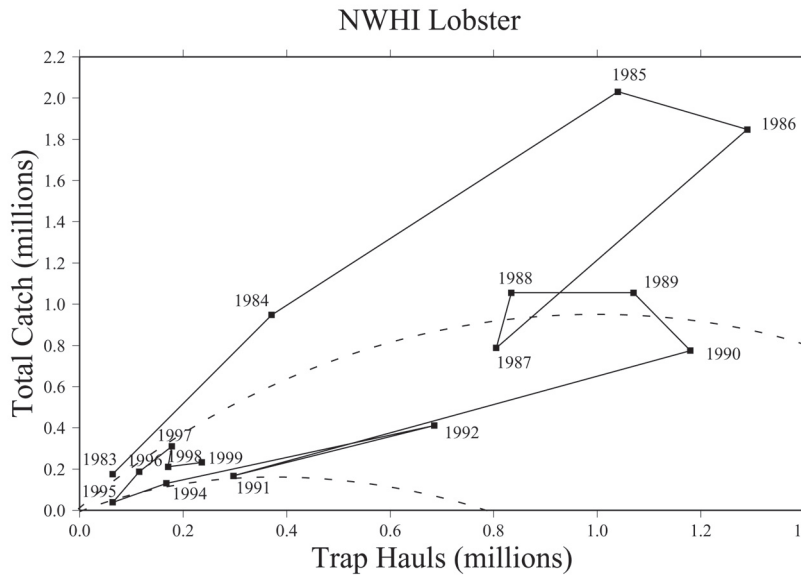

Figure 2. Combined spiny and slipper lobster landings and effort from the northwestern Hawaiian Islands (NWHI) lobster fishery, 1983–1999.

1825), and slipper *Scyllarides squammosus* (H. Milne-Edwards, 1837) lobsters. Using fishery catch and effort data from 1983, when the fishery began developing, through 1989 and a dynamic surplus production model, the maximum sustainable yield (MSY) and effort were estimated at 1 million combined spiny and slipper lobsters with 1 million trap-hauls (Fig. 2). It appeared that the high catches in the mid-1980s represented a process of fishing down a previously unexploited stock, and by the end of the 1980s the fishery was operating at MSY (Fig. 2). However, by the end of the 1989 fishery season there were reports from fishermen that catch rates on the main fishing grounds were declining, with an absence of new recruits to the fishery. Our fishery independent survey in 1990 indeed confirmed an absence of spiny lobsters in all age classes at one of the major fishing grounds. Even though effort has been greatly reduced in subsequent years, there has been no recovery (Fig. 3). Since 1990 slipper lobster have replaced spiny lobsters in the catches at most banks and the fishery has operated at new effort and catch levels of about 200,000 lobsters with 200,000 trap-hauls (Fig. 2). Even Laysan Island, which was never open to lobster fishing, experienced the same collapse in spiny lobster recruitment and subsequent decline in the spiny lobster population (Fig. 4).

We now believe that this collapse of the spiny lobster population was part of a Pacific-wide regime shift that occurred in 1989. Its impact in the northwestern Hawaiian Islands included a decrease in productivity or carrying capacity of several other components of the ecosystem including monk seals and several species of sea birds (Polovina et al., 1994; Polovina and Haight, 1999). It is interesting to note that only spiny lobsters were negatively impacted, while two species of slipper lobsters also harvested by the fishery were not. Spiny lobsters have a 1 yr pelagic larval period compared to the 3 mo pelagic larval period for slipper lobsters. Therefore, physical changes from the 1989 regime shift involving ocean circulation around the Hawaiian Archipelago may have impacted spiny lobsters more because of the species' longer larval periods.

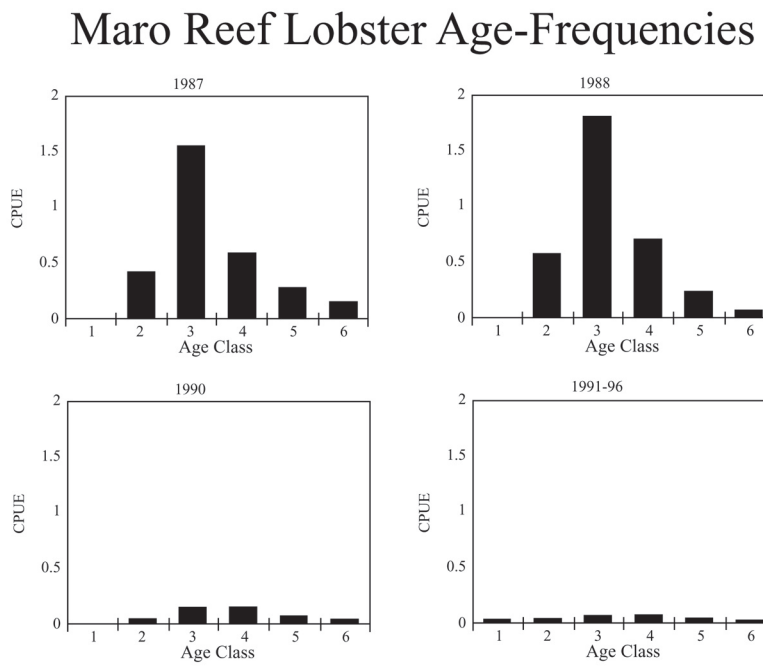

Figure 3. Catch-per-unit effort (CPUE) for spiny lobster by age class for selected years from research trapping at Maro Reef (NWHI).

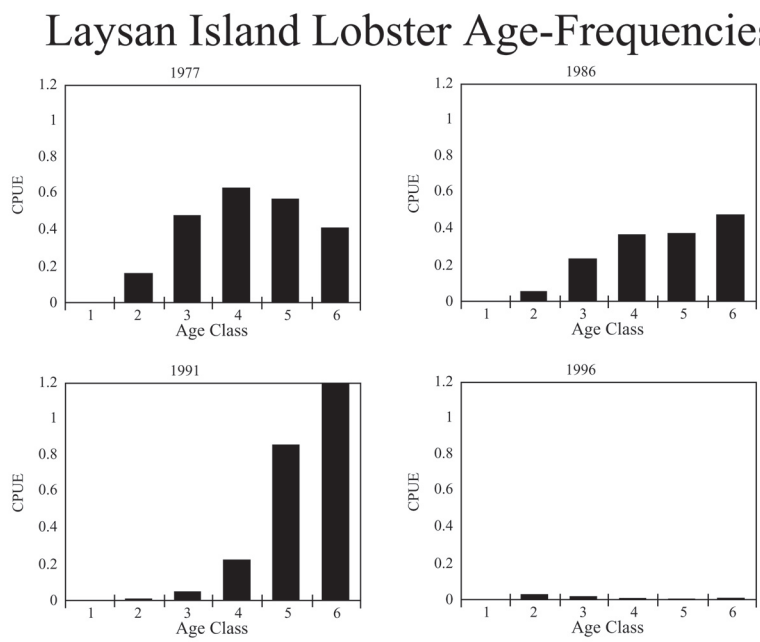

Figure 4. Catch-per-unit effort (CPUE) for spiny lobster by age class for selected years from research trapping at Laysan Island (NWHI), which was closed to commercial lobster fishing.

While in hindsight it is possible to view the sudden drop in spiny lobster in the context of a regime shift with concurrent changes in other physical and biological data, there was considerable uncertainty, confusion, and vigorous debate among biologists, managers, and fishermen over what was happening. Once it was documented that the collapse of spiny lobster recruitment was real, the debate focused on the question of whether this recruitment drop was simply interannual variation, a regime shift, or overfishing. The practical implication of this debate was that if it were only interannual variation, management might not need to change since the existing harvest strategy was robust to interannual variation in recruitment. However, if overfishing were the primary factor, a rebuilding strategy should be developed which substantially, if not completely, curtailed fishing to allow the population to rebuild as quickly as possible to its level prior to the collapse. If this collapse were largely environmentally induced, then it would not be possible to rebuild the population to pre-1989 levels. Rather, management goals should be to manage the fishery to optimize the yield either for this new regime or under a full cycle of environmentally induced population variation. In the northwestern Hawaiian Islands lobster fishery, managers decided that overfishing was not the cause for the decline but that the management objective to target an MSY of 1 million lobsters was no longer achievable under the new regime. And they chose to continue the fishery with a constant harvest rate of 13%. This harvest rate was determined to have a low risk of overfishing the stock based on simulations of a lobster population dynamics model which included low frequency climate-induced recruitment fluctuations (Dinardo and Wetherall, 1999).

Harvest Strategies

Various simulation studies have examined the issue of what constitutes an optimum management strategy for fisheries that undergo regime shifts. Studies have used stochastic population models with strong autocorrelations to simulate low frequency variation in survival and carrying capacity assumed to represent climate-induced regime shifts (Walters and Parma, 1996; Spencer, 1997; DiNardo and Wetherall, 1999; Peterman et al., 2000; MacCall 2001). Two different strategies were recommended by these simulations. The constant harvest rate strategy, a harvest rate that did not change with environmental regimes, generally performed well in some studies (Walters and Parma, 1996; DiNardo and Wetherall, 1999); however, other simulations using different models and assumptions found a regime-specific harvest rate strategy was generally preferred to the constant harvest rate (Spencer, 1997; Peterman et al., 2000; MacCall, 2001).

A simulation of the response of the Pacific sardine, *Sardinops sagax* (Jenyns, 1842), which has a maximum life span of 12 yrs and a natural mortality rate of 0.4 yr^{-1}, under an environmental regime of 30 warm years followed by 30 cold years, will be used to examine constant harvest rate and regime-specific harvest rate strategies (MacCall, 2001). This simulation is driven by a temperature-dependent stock recruitment relationship estimated for Pacific sardine from analyses of historical data (Jacobson and MacCall, 1995). Reproductive rates are much higher during warm years than cold years, and the fishery can achieve large population size and harvest during the warm regime (Fig. 5). The constant harvest rate that achieves the greatest yield over the full 60-yr cycle consisting of a warm and cold regime is a harvest rate of 12.3%

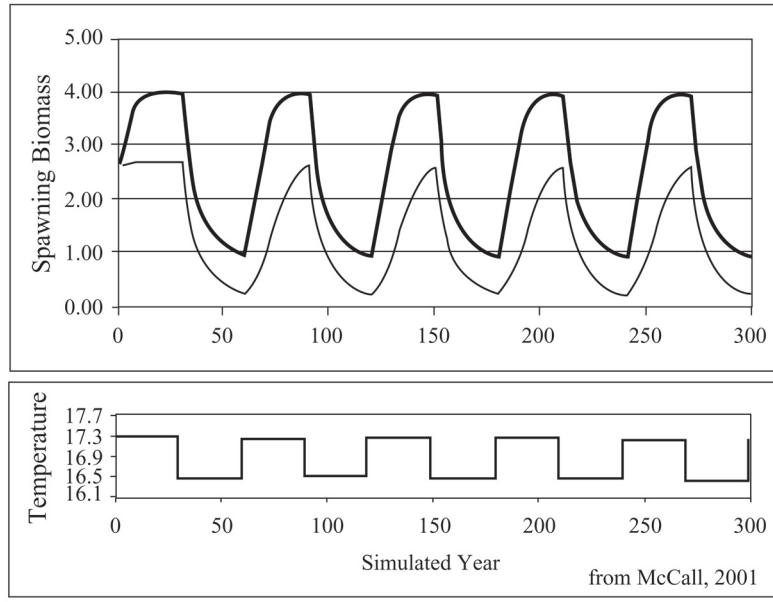

Figure 5. Time series of simulated sardine spawning biomass in the absence of harvest (thick line) and with a constant harvest rate (thin line) and sea surface temperature used to drive the simulation model (MacCall, 2001).

resulting in a mean annual yield of 142,000 t and a spawning biomass ranging from 200,000–2,500,000 t (MacCall, 2001). However, a higher average annual yield and lower variation in spawning biomass can be achieved with a harvest strategy which has a higher exploitation rate during the warm regime and a lower exploitation rate during the cold regime. For example, a harvest rate of 20.9% of the biomass during a warm regime and 3.3% of the biomass during a cold regime produce a mean annual yield of 162,000 t with spawning biomass ranging from 560,000–2,177,000 t. This latter strategy assumes that there is no delay in switching harvest rates when regimes change. However, even better results can be achieved if the switch in harvest rates is delayed some years after the regime shift. For example, if harvest rates change 3 yrs after the regime changes, a mean annual yield of 181,000 t is obtained with a harvest rate of 23.9% of biomass during the warm period but no harvest during the cold period, and spawning biomass ranging from 818,000–1,687,000 t. This yield represents a 27% increase over the mean annual yield of 142,000 t achieved with a constant harvest rate strategy. The finding that a delay in switching harvest rates improves mean annual yield is surprising. Apparently it is effective because the persistence of the high harvest rate for several years after the regime shifts from high to low productivity allows fishing down of the population without reducing recruitment under the spawner-recruit relationship of a less productive regime. Maintaining a low harvest rate for several years after the regime shifts from low to high productivity allows the population to rapidly rebuild to population levels, resulting in more recruits under the spawner-recruit relationship of the more productive regime.

These simulations illustrate several important points. In this example, the optimum constant harvest (F) for a fish population that varies with low frequency environmental variation is 0.123 or about 30% of the natural mortality rate (M). This is well below benchmarks or F = M or even F = 0.5*M typically proposed in fisheries

management. Also for this relatively short-lived fish, the regime specific harvest rate strategy can achieve a substantially greater yield with lower variation in spawning biomass than a constant harvest rate strategy, although the regime-specific harvest rate may result in higher variation in yields between regimes than the constant harvest strategy. However, similar simulations with a long-lived rockfish find the constant harvest rate strategy may work well for long-lived species (MacCall, 2001). Finally, the regime-specific harvest rate performs well when it is applied with a delay of several years. This is very encouraging since it means managers do not have to identify the exact time of regime shift in real time, which can be very difficult. The Pacific Regional Fishery Management Council recently adopted a 3-yr moving average of sea surface temperature (SST) from the Scripps Pier as the indicator of when to switch between harvest rates in the management of the Pacific sardine.

It might seem necessary that any variable harvest rate approach must use a physical or climate index to identify when the regime shift occurs and then determine when to change the harvest rate. It turns out, however, that this is not necessarily the case. This point is illustrated with an interesting approach that estimates annual escapement for Pacific salmon and accounts for climate-induced changes in salmon productivity with only salmon spawner and recruitment data. This result is achieved by employing a statistical approach known as a Kalman filter to annually update the spawner-recruit relationship (Peterman et al., 2000). Since the biological organisms are integrating the climate variation, it may be that if the biological data alone is properly analyzed, it can offer the best indicator of regime shifts.

Research Directions

There are two perspectives on the research needed to improve the management of fisheries that undergo regime shifts. One perspective argues that the most valuable investment of research is to develop ways to actually implement constant harvest rates. Walters and Parma (1996) argue that since a constant harvest rate strategy generally performs well and does not require prediction or understanding of regime shifts, the most useful research will be that which improves annual stock assessments and develops ways to ensure harvests do not exceed the allowable take. Implementing regime-specific harvesting could be especially difficult after a regime shift from a productive to an unproductive regime. When fishing capacity has developed to harvest the large catches associated with high biomass during the productive regime, then scaling back to handle substantially small catches during the unproductive regime could present difficult economic and social problems. Further, if the lower biomass is overestimated, the true constant harvest rate could substantially be exceeded and overfishing of the stock during the low productivity regime could result. Specific examples of this type of research include studies to evaluate time/area closures, tagging studies, and restrictive fishing gears (Walters and Parma, 1996).

The second perspective maintains that research is needed to improve our understanding of the ecosystem dynamics of regime shifts and the physical-biological linkages. Approaches to management are often based on classical single species models that do not incorporate ecosystem and spatial dynamics associated with these regime shifts. In the case of ecosystem dynamics, much of the current thinking about biological responses under regime shifts assumes that the response is driven only from

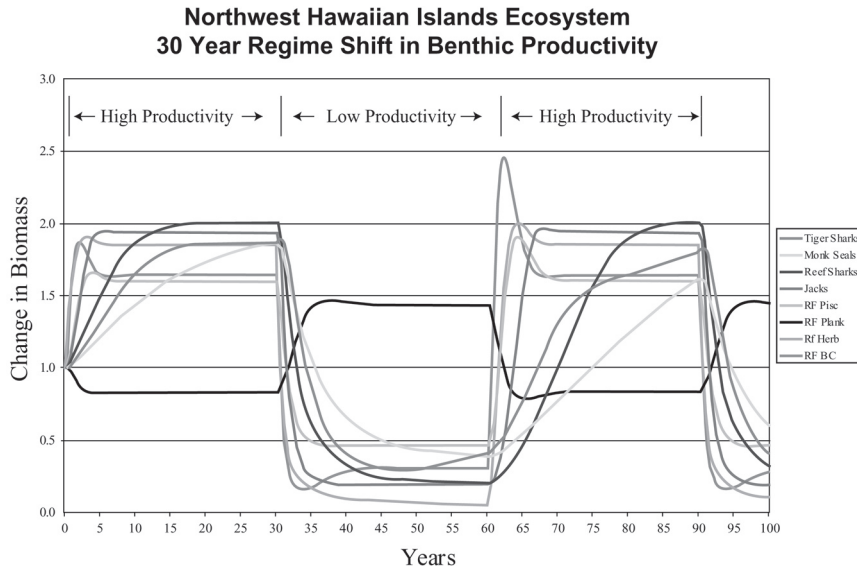

Figure 6. Time series of relative abundances for selected species groups from simulation of the French Frigate Shoals coral reef Ecosim model driven by regime shifts in benthic primary productivity. (RF Pic = piscivorous reef fishes, RF Plank = planktivorous reef fishes, RF Herb = herbivorous reef fishes, RF BC = benthic carnivorous reef fishes).

the bottom of the trophic web; that is, the ecosystem responds to physical changes impacting productivity at the lowest trophic levels. However, simulations of even simple ecosystem models suggest that even when changes in lower trophic levels represent the only driving force, ecosystem responses can include significant temporal lags and top-down responses. For example, simulations of our northwestern Hawaiian Islands coral reef Ecosim model, driven by 30 yrs of high benthic primary productivity followed by 30 yrs of low benthic primary productivity, indicates complex responses (Fig. 6). There are considerable temporal lags, differing by as much as a decade, in how various trophic levels respond both under an increase and a decrease in benthic productivity. There are also top-down responses; for example, planktivorous reef fishes decrease during periods of high benthic productivity in response to increases in their predators (other reef fishes and jacks) even though their prey plankton is unchanged (Fig. 6). Another example of a top-down response is the sharp increase followed by decline in some of the reef fishes, particularly the benthic carnivorous reef fishes, immediately after the change from low to high benthic productivity (Fig. 6). These reef fishes increase in abundance quickly in response to higher prey availability, but 5 yrs later as their predators increase, their abundance declines. The potential exists that ecosystem dynamics can be more complicated and not always coherent with physical forcing. Further harvesting strategies need to take into account top-down as well as bottom-up responses. It is sometimes said that the atmosphere responds quickly to external forcing, but the response dissipates quickly: it has a short memory. The ocean responds slowly to external forcing but the response persists: it has a long memory. It appears that ecosystem responses to external forcing include both quick responses at low trophic levels but higher trophic levels may respond slowly. This also can result in complex trophic interactions including top-down forcing.

To understand the link between large-scale climate changes and local ecosystem dynamics it may be valuable to identify oceanic habitats such as fronts and eddies, that provide spawning, nursery, and adult forage habitat and then monitor the dynamics of these habitats. For example, by deploying Argos-linked satellite tags on loggerhead turtles and from high resolution fisheries data on North Pacific albacore, we have identified a surface chlorophyll front that indexes an important forage and migration habitat spanning the central North Pacific. We have named this feature the Transitional Zone Chlorophyll Front (TZCF) and have monitored its dynamics with satellite ocean color (Polovina et al., 2001; Fig. 7). During the spring of 1998 (an El Niño period) a substantial fishery for albacore developed along this feature in oceanic waters centered between 140 and 160°W, while in the spring of 1999 (a La Niña period) the oceanic fishery for albacore along this feature had greatly lower catches and lower catch rates (Polovina et al., 2001). Significant differences in the TZCF occurred between in the two periods. In 1998 the TZCF exhibited considerable meandering, while in 1999 the feature lacked large meanders and was very stationary (Fig. 7). Meanders in a front create regions of divergence and convergence resulting in the enhancement and concentration of a pelagic food web. We hypothesize, therefore, that the meandering of the TZCF in 1998 created a productive habitat resulting in a food web that attracted foraging albacore and a productive fishery. In 1999, however, the absence of a meandering and dynamic TZCF did not produce such food webs. By identifying and monitoring oceanic habitat, in this case forage habitat, we can better understand the spatial and temporal dynamics of pelagic animals.

Summary

Low frequency, high amplitude variation in community composition, species abundance, and trophic structure coherent with climate variability represent a well-documented aspect of dynamics in a variety of ecosystems. From the aspect of fisheries management it is not desirable or even possible to sustain constant catches for species that undergo regime shifts. It may be possible, however, even in the presence of this dynamic population variation to achieve a sustainable fishery with constant or variable harvest rate strategy. If a constant harvest rate is used, the harvest rate must be relatively low, about 10% of the exploitable biomass, to ensure overfishing does not result during periods of low productivity. If a variable harvest rate is used it may not be necessary to change harvest rate exactly when the regime shifts. Increased yields may be achieved when the harvest rate change follows the regime shift by a few years. The variable harvest rate approach will allow a higher harvest rate during productive periods but may close the fishery during unproductive periods. In some cases it may be appropriate to use climate indices to identify the timing of the regime shift, but it also appears possible to identify the timing of regime shift based only on the biology without using any climate data.

Several areas of research are needed to improve our management under regime shifts. More research is needed to apply the constant or variable harvest rate approaches. For example, the following procedures need to be developed: (1) improvements in stock assessments to ensure biomasses are not overestimated, (2) development of analytic tools to determine when to switch harvest rates, and (3) methods to handle the social and economic difficulties associated with large varia-

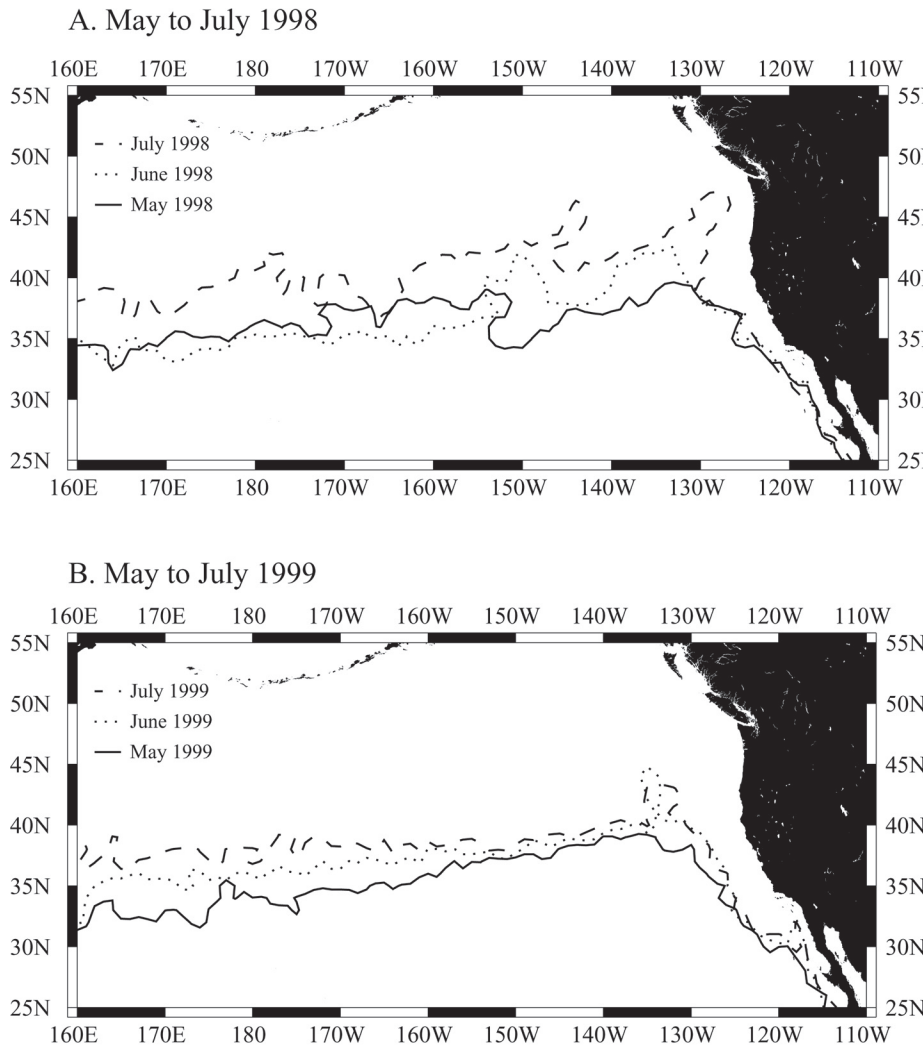

Figure 7. Monthly positions of the Transition Zone Chlorophyll Front in (A) May, June, and July 1998, (B) May, June, and July 1999.

tion in catches. Research is also needed to improve our understanding of ecosystem dynamics associated with regime shifts. This could include development and simulations of dynamic ecosystem and physical-ecosystem models and identification and monitoring of critical oceanic habitat.

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