Abrupt community change on a rocky shore – biological mechanisms contributing to the potential formation of an alternative state

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Abstract
The 1997/1998 El Niño initiated a major shift in the intertidal assemblage on the Washington State outer coast. A 25 year time series (1978–2003) shows stands of dominant canopy algae replaced by mussel beds. A prior experiment had indicated that mussels can become too large to be eaten by starfish; newly initiated starfish removals predict mussel attainment of a size refuge. Such escapes inhibit recovery towards prior community composition and enhance development of alternative community states which may persist long after the originating forcing has lessened or disappeared.

Keywords
Alternative states, Hedophyllum, intertidal, mussels, Pisaster, size escapes, stability.

INTRODUCTION
Lewontin (1969) proposed that shifts in community composition be cast in the language of mathematics governing dynamical space. Lewontin’s framework suggested that alternative states might be identified from long-term studies, and assemblage stability tested by deliberate perturbations of species abundance. Observational (Brooks & Dodson 1965) and experimental (Paine 1966) field studies conducted earlier had identified that dramatic compositional shifts could be forced through alterations of consumer abundance. Slightly later, Sutherland (1974) explicitly cast his fouling community experiments in the framework suggested by Lewontin. Recently, increasing concerns about the biological impacts of climate change (Alley et al. 2003) and regime shifts leading to alternative assemblages (Scheffer et al. 2001, Scheffer & Carpenter 2003, Beisner et al. 2003, Carpenter 2003) have heightened awareness of their sweeping consequences.

This paper provides preliminary details on a physically-forced but abrupt natural change in assemblage composition on an intensely studied marine rocky intertidal shore. The relationships we describe focus on three species: a predatory starfish Pisaster ochraceus (Brandt, 1835) preferentially consumes the mussel Mytilus californianus Conrad, 1837 which in turn can outcompete a brown alga (kelp) Hedophyllum sessile (Setchell, 1901). Although the local species richness is two to three orders of magnitude greater, and spatial structure is known to be important, we believe the essence of the described dynamic is captured by the interplay of just these three dominant species.

Our data meet Connell & Sousa’s (1983) criteria for alternative (multiple) states: (1) Two or more different biological populations or assemblages must be able to occupy the same environment. (2) The novel state should be able to persist indefinitely without maintained biological forcing. (3) The data must meet reasonable temporal and spatial constraints. We argue that for systems fundamentally limited by space, the critical characteristic of persistence or stability (as in alternative ‘stable’ states) is the demonstration of hysteresis. Furthermore, our study may, despite a spatial scale measured as only 1–2 m along a 5 m vertical tidal gradient, meet the regime shift criteria of Carpenter (2003): a ‘rapid modification of ecosystem organization’ with ‘prolonged consequences’.

It is impossible to discuss alternative states without employing certain terms, all with vague or contentious definitional histories. In general, we follow Beisner et al. (2003) and Scheffer & Carpenter (2003). To us, stability implies a dynamic response to a perturbation, one that promotes recovery to the pre-perturbation state. Persistence is simply an acknowledgment that the species of interest did not go extinct during the observational interval and, following Frank (1968), is especially vexing when individuals are long-lived. Hysteresis is revealed when a system can exist in multiple states, and in which the shift or collapse trajectory differs from the recovery one.
METHODS

The research took place on the Washington State (USA) outer coast, on rocky intertidal shores frequently exposed to heavy wave action. The experimental studies at Mukkaw Bay (48°19′ N, 124°40′ W) were conducted from 1963 to 1968; the site has been monitored irregularly since. Research at Tatoosh Island (48°24′ N, 124°44′ W) was initiated in 1968; data acquisition and manipulative experiments began in 1970 and have continued to the present.

Density estimates of starfish were obtained from quadrats or line transects. *Pisaster* removals were manual, with the individuals moved 10–40 m away. Per cent cover estimates of benthic algae and mussels were visual; the Dethier *et al.* (1993) study suggests that such estimates may provide the best representation of relative cover.

Many details of the Mukkaw Bay site have been published (Paine 1966, Paine *et al.* 1985). At Tatoosh, study began in 1978 of six original algal census areas on the heavily exposed north side, each with extensive *Hedophyllum* and few if any *Pisaster* or mussels. These were successfully invaded by mussels by 1999. In April 2000, we initiated a predator removal experiment. To quantify effects of *Pisaster* removal or retention, numbered plastic markers were epoxied as close to the mussel bed edge as possible at the removal and three (of four) *Pisaster* present sites. Because of *Pisaster*'s mobility, we designated only areas separated by significant surge channels as removal (*n* = 1) or sites with starfish (*n* = 4). The procedure required combining three original algal census sites into the single removal site, and combining two others into one of the sites with *Pisaster*. The remaining three in that treatment involved one of the original algal sites and two new ones. The *Pisaster* removal site had an initial perimeter of 45 m; sites with *Pisaster* had perimeters of 16, 18, 20 and 20 m. The distance of the markers to the nearest mussel was measured whenever conditions permitted. However, marker loss, burial under encroaching mussels or hidden under a developing *Hedophyllum* canopy has produced a dataset with numerous gaps and variable durations. Advances or retreats of the bed’s perimeter were calculated as the difference in distance (cm) from initial placement to terminal observation, normalized by duration (months).

RESULTS

The shift in assemblage structure

Photographs dated 1968 and 1970 of the mid- and lower intertidal zone identify the canopy forming alga *Hedophyllum* as the most conspicuous occupant. Quantitative estimates of per cent cover initiated in 1978 substantiate the impression: *Hedophyllum* attains 80–100% cover by late summer, declines to an annual low by early spring and then recovers. Figure 1 illustrates this characteristic pattern for the upper half of the *Hedophyllum* band (+1.0 to +2.0 m above tidal datum). This typical pattern showed signs of change in summer 1997 associated with early stages of an El Niño event, and was fully expressed by early 1998 when per cent cover in spring reached a 20 year low. The spike in *Hedophyllum* per cent cover in 1999–2000 is an artefact of the cover estimation procedure. Mussels outcompete all adjacent species (Paine 1974, 1984), but the process takes time and when the mussels are small, the process is inefficient and some *Hedophyllum* persist. However, as mussels grow larger, they outcompete the algae for space. Figure 1 illustrates the recovery, gradual in comparison with all prior years, because it also takes time for *Pisaster* to eliminate the competitively superior mussels. Where starfish have been removed, mussels dominate and *Hedophyllum* is minimally present.

The role of *Pisaster*

We quantified the cumulative effects of *Pisaster*’s presence or absence by changes in the mussel beds’ perimeters relative to the numbered markers. At the removal site (*n* = 1) there has been no net change (0.0 cm month−1, *n* = 10 markers, maximum months, 28). Where *Pisaster* has been allowed to remain (*n* = 4), net change is significantly different (−1.43 cm month−1, *n* = 27, maximum months, 27; Mann–Whitney *U*-test, *P* < 0.01). At the last observation,
September 2003, mussels had been eliminated from one site with *Pisaster* present, were nearly gone from another, and were dwindling at the remaining two.

**Mussel bed size structure**

Aggregations of mature *M. californianus* have collective properties not dissimilar to those of terrestrial forests. Individual body size renders them immune to consumption by the great majority of consumers whose attacks at earlier life history stages prove fatal. For *M. californianus* to achieve this long-term spatial dominance, three quasi-independent events must occur. First, recruitment must be sufficient to overwhelm a host of consumers, for instance, small carnivorous gastropods (Dayton 1971), and at larger sizes, starfish (Paine 1976). Second, a refuge from predation in large body size must be attainable. And last, the numerical response of natural enemies must be slower than the attainment of the size refuge. Figure 2 illustrates such an escape for the 5 year *Pisaster* removal experiment (1963–1968) at Mukkaw Bay (Paine 1966, 1976, Paine *et al.* 1985). By 1968 a sufficient fraction of the protected mussels were too large to be eaten and therefore coexisted with high densities of *Pisaster* for 30 additional years. Gradual attrition of the matrix individuals eventually lead to their local extinction. Once eliminated, recovery has not occurred, probably due to resident predators maintained by alternative prey. These data and a comparable set from Tatoosh in which a 1970–1995 removal experiment (Paine 1984; R.T. Paine, unpublished data) resulted in mussel matrices composed of 16–24 cm individuals, document both the potential for and reality of size escapes.

**DISCUSSION**

The 1997/1998 El Niño was exceptionally severe (McPhaden 1999) even at Tatoosh’s latitude (~49°N), and is the prime candidate for having forced the observed changes in intertidal community structure. The mechanism(s) remain conjectural, but summer 1997 and early winter 1998 water temperatures appear to have been the highest ever recorded. *Hedophyllum* is a northern kelp (Lüning & Freshwater 1988), and thus seems a likely candidate for stress at exceptionally high ambient temperatures. As a presumed result, both the summer 1997 and early spring 1998 per cent cover estimates were the lowest observed in the prior 20 years, presumably resulting from mortality of adult plants and recruitment failures. Was this physically forced event by itself sufficient? We believe the answer is no. 1982/1983 was another powerful El Niño yet *Hedophyllum* recovered to 80–100% cover within a year (Fig. 1). Rapid recovery also characterized the minor El Niños of 1987, 1992 and 1995/1996. What made the 1997/1998 event different was the associated recruitment events of two other species. The barnacle *Balanus glandula* Darwin, 1854 recruited at exceptional densities (426 per 100 cm², C.D.G. Harley, personal communication), and was followed within a year by mixed mussels, *M. trossulus* Gould, 1860 and *M. californianus*. By summer 1999, the upper *Hedophyllum* zone was being replaced by mussels, thereby meeting successfully the first of the Connell–Sousa requirements.

*Description of Figure 2*:

A mussel bed and a stand of canopy-forming algae are very different biological assemblages. They embody alternative states similar in basic character to those in Maine, USA (Petraitis & Dudgeon 1999, Bertness *et al.* 2002). But are any of these stable? All are, based on the criterion of spatial persistence. On Washington’s outer coast *Hedophyllum* populations can persist for decades as the mid-intertidal canopy dominant (Fig. 1). If it is a biannual species (Widdowson 1965), individuals have turned over many times during our lengthy observational period, suggesting that its populations are stable as well. *M. californianus* characteristically inhabits a belt immediately above this, and although routinely stressed by winter storms, inevitably recovers (Paine 1984). In a dynamical sense, because it always recovers, and no alternative, non-successional states capable of replacing it are known, mussel beds are stable. However, the intertidal distribution of these mussels is limited by *Pisaster* (see also Mengé *et al.* 1994, Robles *et al.* 1995) suggesting that *Hedophyllum* dominance requires *Pisaster’s* presence to constrain the development of mussel beds. In addition, *Hedophyllum* itself is dependent on the identity and density of its consumers, with alternative states of coralline algae (Paine & Vadas 1969) or another kelp (Paine 2002). In this sense, intertidal community structure below the mussel bed is reminiscent of many other
situations (Power 1985, Estes & Duggins 1995) in which a clearly alternative state is maintained by the presence of consumers. All states are persistent under these conditions. However, none are stable because all revert to the alternative assemblage if the consumer guild is substantially altered. In this fashion they violate the second Connell & Sousa (1983) criterion.

What then makes *M. californianus* domination different? The answer is that, granted sufficient time, their growth in size renders them unavailable to most consumers (Fig. 2). The mussel bed, although perhaps not the individual constituent mussels, survived 35 years at Mukkaw Bay (1963–1998) and to date a minimum of 33 years (1970–2003) at Tatoosh. However, maximum longevity and hence turnover of all individuals remains unknown. How does this persistence relate to stability rather than just persistence? If *M. californianus* have mature gonads in their second year (Suchanek 1981), and if we accept Slobodkin’s (1961) clock for ecological time of 10 generations, these aggregations of large and ‘escaped’ mussels are stable. They have been present for 16–18 mussel generations. However, because longevity is unknown they fail the criterion of one turnover of every species in the alternative assemblage (Connell & Sousa 1983). This definition of stability is overly restrictive because longevity of individuals in the initially dominant population is not relevant to organisms comprising the dominant population of the alternative state. Replacement is independent of the lifespan of the current space occupiers; it is dependent on whether or not the space is currently occupied and the related ecological consequences. The appropriate metric is whether the space remains occupied for a sufficient period to prevent or significantly delay recovery (the latter would demonstrate hysteresis), or whether the temporarily novel state simply reverts to the original condition. A biologically sensible, invader-centric, dominance different?

Comparable examples are commonplace in anthropogenically modified terrestrial communities. Most grasslands above a minimal precipitation of 250–1000 mm per year would be forested without human intervention (Milchunas et al. 1988). The lesson is that trees escape by becoming too large; burning and apex predator suppression maintains the grassland alternative state. Once escaped, the tree state is capable of persisting many grass generations, especially if the latter are annuals. Hysteresis aptly describes the situation since the transition from grassland to forest, once a size refuge has been attained, is demonstrably different than the reverse. That is, grazer suppression could well be beneficial to the forest whereas in grasslands it leads to rapid change. A similar inequality characterizes the Tatoosh mussel beds where a combination of stature and longevity permits the establishment of a persistent and therefore stable assemblage, one which coexists without being dependent upon its major consumer.

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**REFERENCES**


