THE DECLINE OF THE CUT-LEAVED ANEMONE, *ANEMONE MULTIFIDA,* AT WINOOSKI FALLS, VERMONT, 1988–2010

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Summary

A small population of the cut-leaf anemone has been known at Winooski Fall, Winooski, Vermont, since 1829. We began monitoring it in 1987 when the site was proposed for hydroelectric development, and did the first full mapping of the plants in 1988, at which time there were 541 clumps, which we call plants but do not represent genetic individuals. Subsequently 19 plants were removed in 1992 and given to nurseries before the power plant was built, and another 7 that were lost during construction of the hydroelectric plant in 1992. These 26 plants are not included the analysis here.

The remaining 515 clumps are what we call the original 1988 plants. We have made 28 full counts of them since 1988. At our latest count, in June 2010, there were 117 plants, a decrease of 77%. Other metrics–the number of leaves, the population area, and the number of flowers–shown comparable declines.

An analysis of the decline shows that direct human impact has had little if any effect. The decline is driven by an excess of mortality over recruitment. This in turn is climate-controlled: mortality peaks in summers that are exceptionally hot or exceptionally dry.

Currently, the winooski anemones seem to at the edge of their climate envelope. In good years they hold on but do not prosper; in bad years they suffer. The result is a staircase decline, with periods of little change separated by sharp drops. In the 16 years for which we have data they have had 12 years with population declines, the largest of which were 28% and 30%. They have had only four years with population increases, the largest of which were 11% and 3%.

With this kind of excess of mortality over recruitment, the population is already functionally extinct, though, since the plants are long lived, it may persist for several decades more.

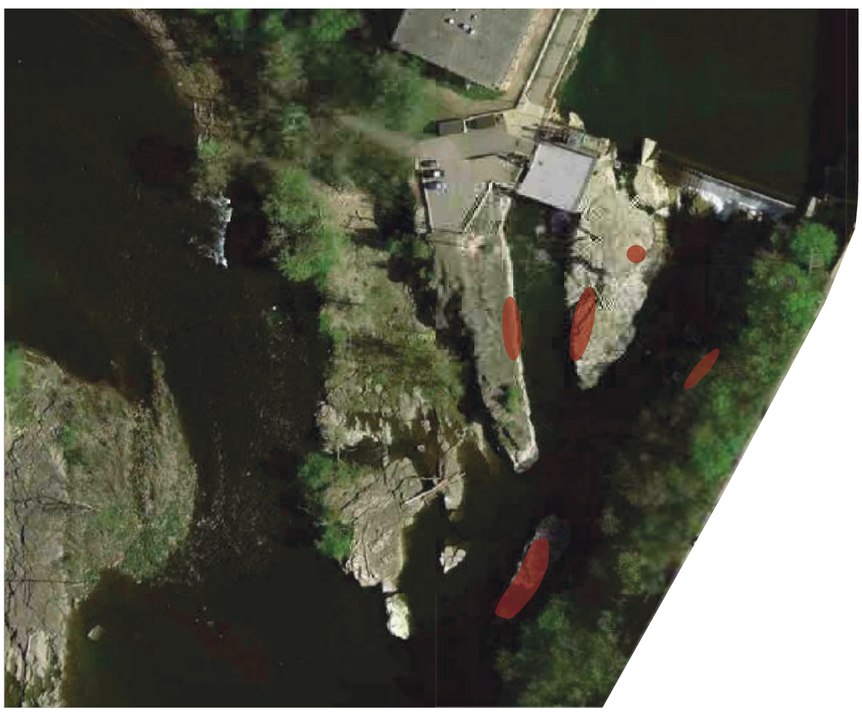
The decline of the cut-leaved anemone is probably a good model for the way that other northern species may decline, or are already declining, as the climate warms and their reproduction fails. We have many other northern species in our biota. It is likely that, if we look around, we, will find that we have other anemones as well.

Background

For more details on *Anemone multifida* and the monitoring project see my 1998 report, *The Monitoring of Cut-Leaved Anemone at Winooski Falls, 1994–1998.*

Acknowledgements

This project originated with an agreement between the Vermont Agency of Natural Resources and the Winooski One Hydroelectric Company in 1987. The Winooski One Hydroelectric Company has been the principal supporter of the project; the White Creek Field School and the Wildlife Conservation Society's Adirondack Program have supported additional fieldwork and analyses of the effects of climate change on the anemone. I thank John Warshow and Mat Rubin of Winooski One for their support over 24 years, and Debbie Benjamin for her invaluable help in the field, also over many years.



The Study Site

Winooski Falls is a rock gorge on the Winooski River, between the cities of Winooski and Burlington. It was first dammed in 1835. A larger dam was built in 1876, downstream of and submerging the former dam. This dam fell into disuse; a flood in the 1950s removed the upper 8 feet of the dam, lowering the spillway and upstream pool.

The Winooski One dam was built in 1992, just below the 1876 dam and incorporating some of the 1876 footings. It restored the pool to its original height, and, because water spills all along its crest, greatly increased the amount of mist and spray in the upper parts of the gorge.

The anemones occur in 5 small populations, all less than about 100 square meters, shown in red in the diagrams. Another 19, which occurred in area where the power plant and tailrace were constructed, were removed and given to nurseries during construction. They are not included in any of the graphics which follow. Another 5-10 were observed once in the middle 1990s on a vertical wall east of the Island. They are apparently a transient population and no longer exist; in any event, they are not in the database or the graphics.

All of the 5 study areas receive some human use, but only the West Bench gets regular use. The East Bench is at the foot of a steep wooded slope and is difficult to access. The Island can only be reached by boat or swimming. Access to Transect 1 and the Northwest Bench is blocked by a locked gate and a security fence; a few fishermen climb the fence, but rarely seem to go to the face where the anemones are. Only the West Bench is open to the public; it gets moderately heavy summer use, and we have, in the past, lost anemones there to trampling and fires.

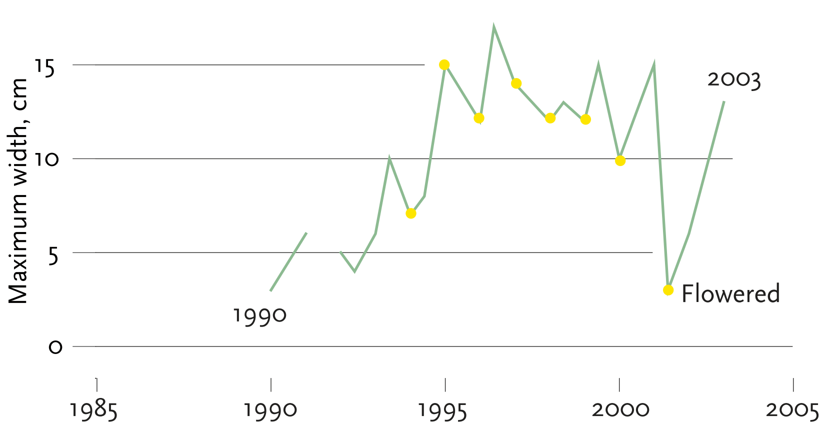
The Cut-leaved Anemone

The cut-leaved anemone is a wide-ranging species of boreal and montane habitats, often on calcareous soils. It is widely distributed in western North America but local in the east, where it is currently known from Vermont, northern Maine, Quebec, Newfoundland, and Labrador. It formerly occurred in 3 other river gorges in Vermont and at least one in New York. All of these populations seem to be gone, and Winooski Gorge is the only currently known eastern U.S. population south of the St. John's River.

The Winooski anemones were first reported by James Robbins in 1829; there were subsequent reports by Cyrus Pringle in 1877, L.R. Jones and W.W. Eggleston in 1894, L.A.Charette and M. Smith in 1961, L.A. Charette in 1962, and Peter Zika in 1981. I first examined the site in 1986, did a preliminary estimate of the plants in 1987, and the first full count in June, 1988.

The anemone is a semi-colonial plant that grows from an erect underground stem, producing basal leaves and erect flowering stems. The underground stems don't really creep, but can branch repeatedly, producing large clumps. At Winooski Gorge the stems are almost always in cracks in rocks. In consequence it is impossible to tell where one clump ends and another begins, or whether two adjacent plants are one individual or two. As a result, any population census is, by necessity, a count of tufts or clumps, and not a count of the number

SIZE OF PLANT 76A



of individuals. (We call the tufts "plants" here, but this is just for convenience.) The true number of genetic individuals, which is unknown, is certainly less than the number of clumps.

Anemone plants can very greatly in size and in the number and size of their leaves. The graph on p. 4 shows a typical life history. Plant 76A was first observed in 1990, when it was 3 cm wide and had 2 leaves. It first flowered in 1994, when it was 7 cm wide and had 9 leaves. It vanished in the drought fall of 1991, and reappeared in June 1992. It was at its peak size from 1996 to 1999 and typically produced 35 to 50 leaves and 3 or 4 flowering shoots with 7 or 8 flowers. After 1999 it declined in its number of leaves and flowers, perhaps because it had exhausted the nutrients in its crack. It flowered for the last time in 2002, produced 10 leaves in 2003, and then disappeared.

Because the anemones are variable, and because individual clumps can disappear for a year or two and then return, we have to be careful how we count them. In particular, to get the best possible estimates of how well the population is doing, in this study we:

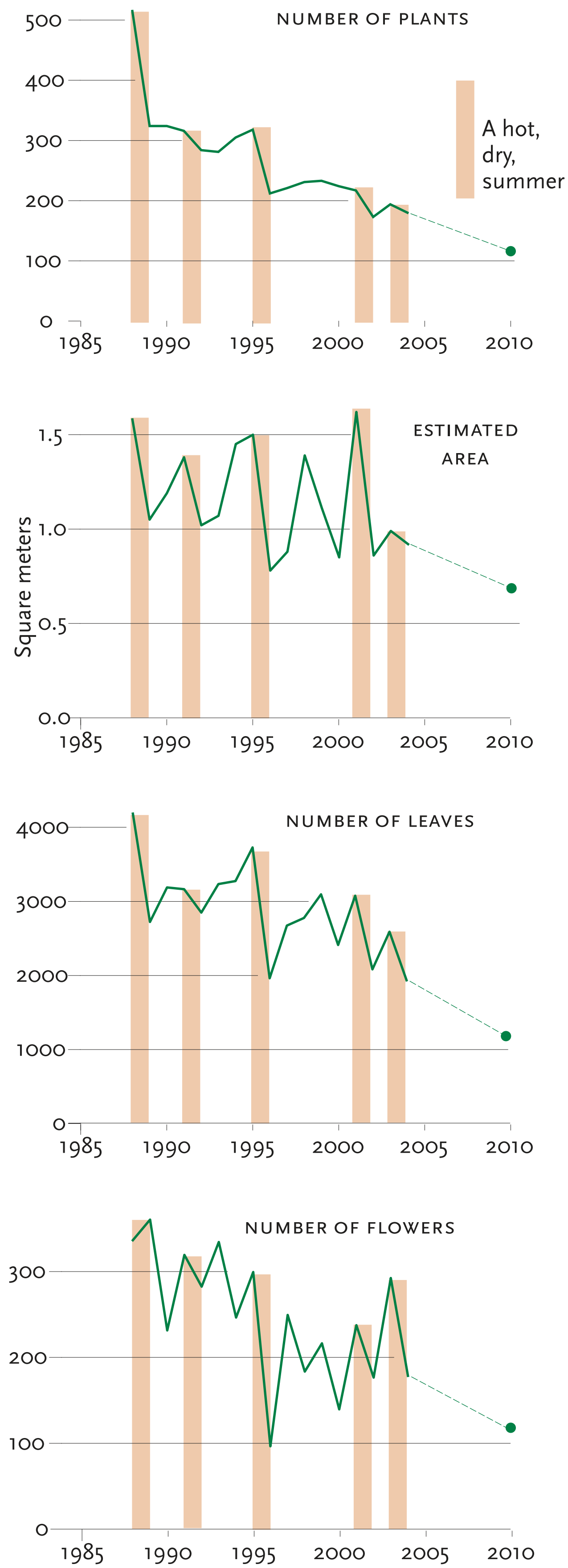
1 Used four different metrics–number of plants, number of leaves, summed area of plants, and number of flowers–to estimate population success.

2 Measured recruitment and mortality by noting the first and last appearance of plants in our databases. Temporary disappearances, in other words, do not count as mortality, and returns after temporary disappearances do not count as recruitment.

Population Trends

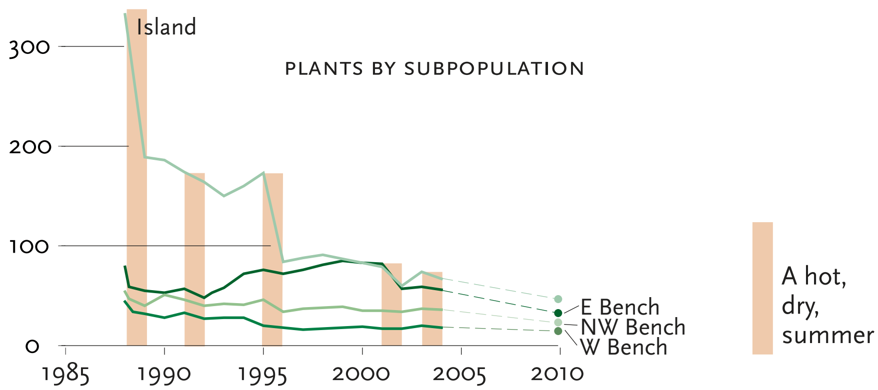
Between 1988 and 2004 we counted the plants once or twice each year. We made no counts from 2005 to 2009, and then returned and made a full count in June 2010. Altogether we have now made 29 full counts, recording 7,883 plants, 81,173 leaves, and 4,307 flowers.

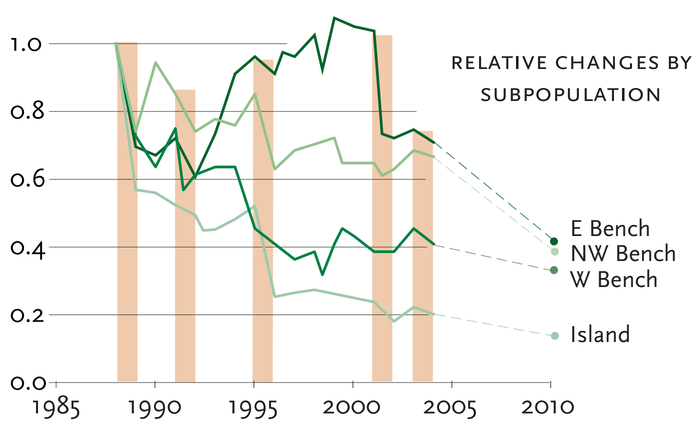
All the metrics–plants, area, leaves, and flowers–show a continuing decline from 1988 to 2010. The number of plants has decreased by 77%; the number of leaves by 72%; the estimated area by 66%. and the number of flowers by 65%. Further, all show steep declines in years with hot dry summers, and either hold steady or recover in between.



The metrics differ in the amount of recovery between declines. Size, leaf number, and flower number are plastic and increase strongly between declines. The number of plants, in contrast, increases only slowly, because of the limited numbers of seedlings and their high mortality. Thus this population faces a reproductive bottleneck. It lose plants rapidly when conditions are bad, but can only gain them slowly when conditions are good.

Despite the differences all the metrics show the same pattern: an overall decline of about 3% per year, with the steepest declines coming in the hottest and driest years.





Declines by Subpopulation

Neglecting the small group of plants on Transect 1, the Winooski anemones divide into 4 subpopulations, as shown in the maps on p. 3. The trends in number of plants for the subpopulations, shown in the graphs above, are interesting because the shed some light on the relative magnitude of human and natural impacts.

The subpopulations fall into two grounds.The NW Bench, W Bench and Island have all declined, with the upstream NW Bench declining more slowly than the downstream Island and W Bench.

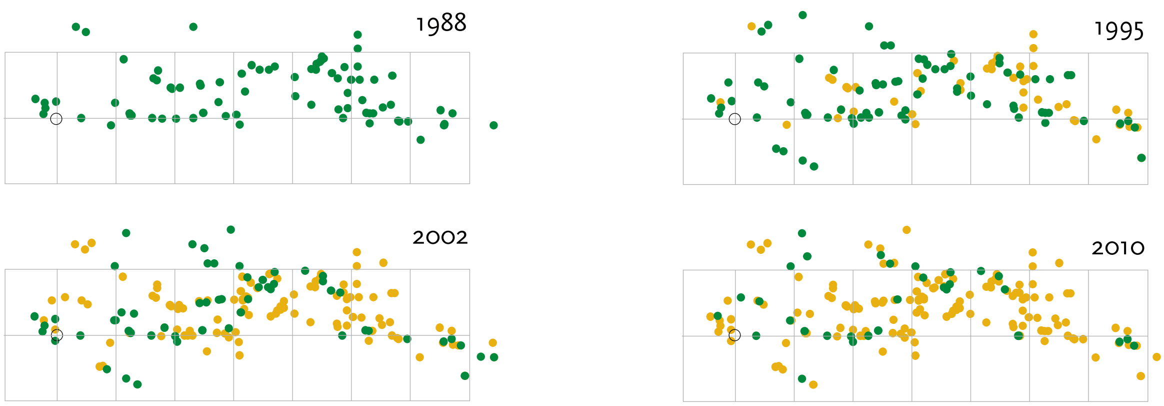
This is interesting because the W Bench receives moderately heavy human impact and the other two very little. Clearly, steep declines can occur in the absence of direct human impact. This does not show that human impact has no affect, but it does suggest that it is not the main factor driving the declines.

The East Bench, in contrast had a dramatic increase in the number of plants between 1991 and 1999, followed by an equally dramatic decline since then. The increase began when the new dam raised the upstream pool, and we suspect that the spray from the crest of them dam, which has made this bench much wetter than before, was responsible. Why the anemones decreased so rapidly after 2001 we don't know. On our latest visit we noticed an increase in shrubs and overhanging trees. Anemones don't like shade, and it is possible that the same water that benefited them has now benefited their competitors even more.

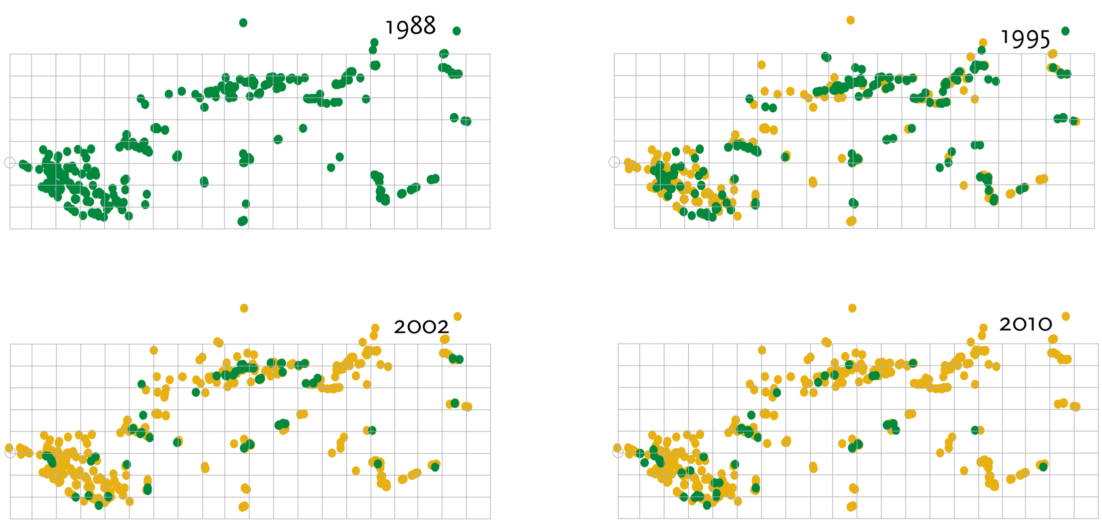
Spatial Patterns of Decline

Spatially, the declines of the subpopulations have all be contractions. Each subpopulation has thinned and lost peripheral plants, becoming restricted to areas where the population was originally densest. The changes thus appear to be retreats to the most suitable microhabitats rather than a shiftings of the populations toward new ones.

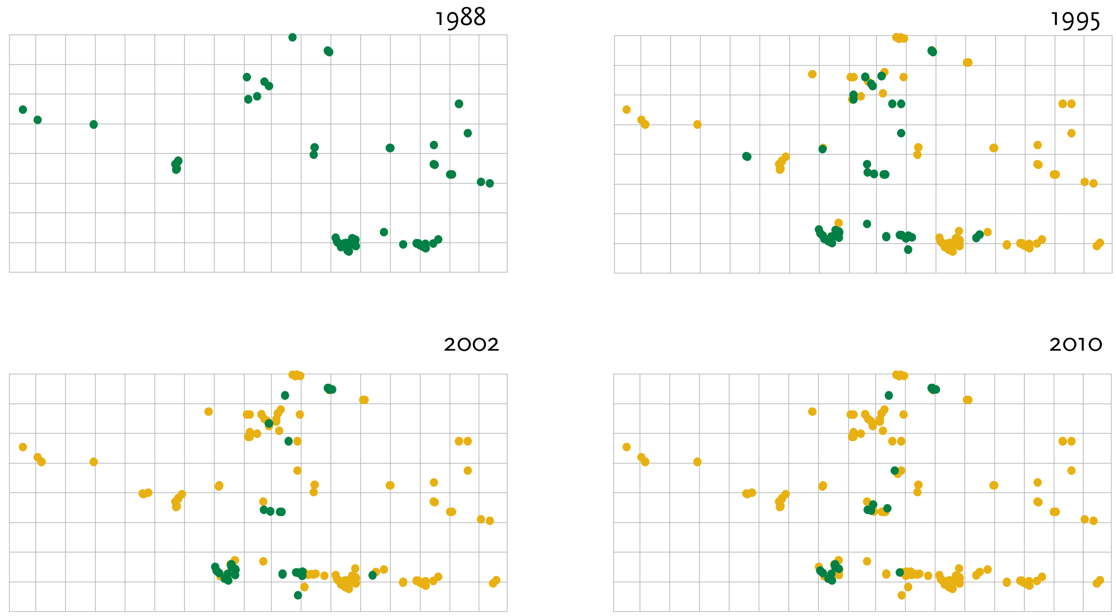
POPULATION CHANGES, EAST BENCH



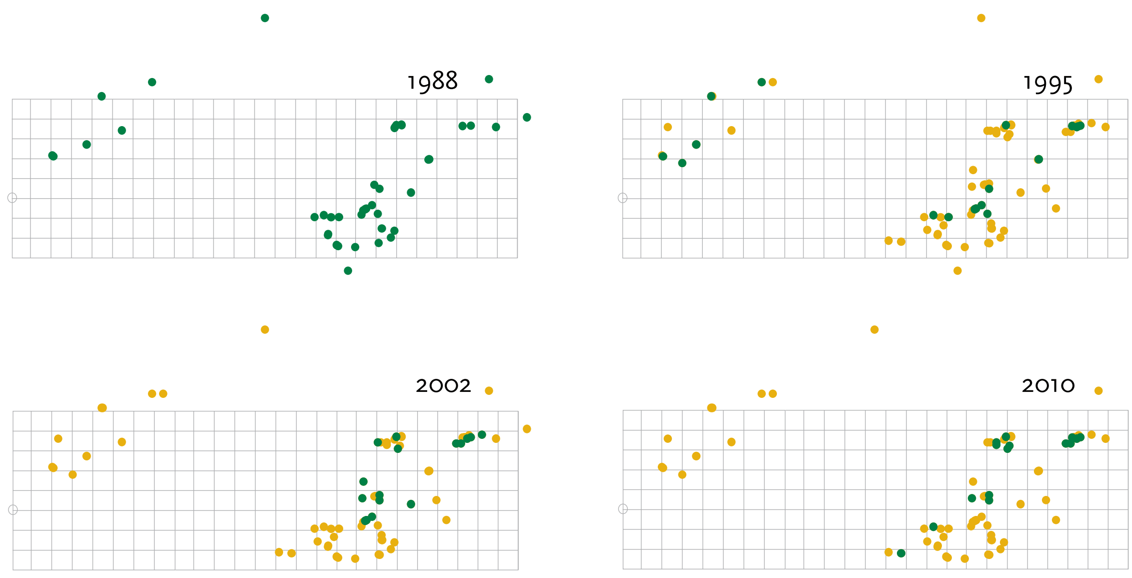
POPULATION CHANGES, ISLAND



POPULATION CHANGES, NW BENCH



POPULATION CHANGES, W BENCH

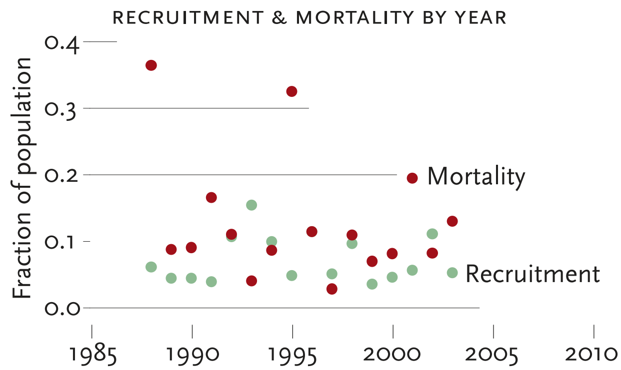


This is shown in the sequential maps above and on the previous page. Each map represents one survey. The green dots are plants that were extant during the survey, the tan dots plants that had disappeared. Each grid square is 1 meter by 1 meter.

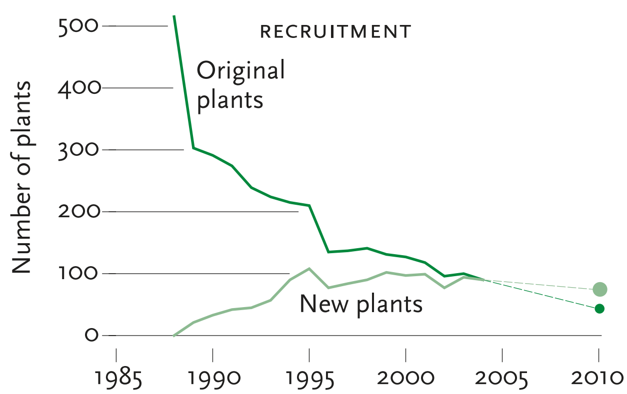
Mortality and Recruitment

Population changes reflect the balance of recruitment–the appearance of new plants–and mortality–the disappearance of old ones. To separate the two, you have to track individual plants rather than just count the whole populations.

Our study did this, taking care, as noted above, only to count the first appearances and last disappearances and not temporary disappearances followed by reappearances. Because we don't know how many genetic individuals are in the population, we are still looking at the recruitment and mortality of clumps rather than individuals. But still it gives an important window into what is driving the population dynamics, and, in particular, into the role of climate.



The graph shows the results. Mortality is high and variable; it averages 15% per year, reached over 30% in dry years, and exceeded recruitment in 12 of the 16 years for which we have data. Recruitment was about half mortality, averaging 8%, and more constant. It never exceeded 15%, and only once exceeded mortality by more than 3%. Thus the population, as suggested above, faces a reproductive bottleneck. It crashes quickly and often. It grows rarely, and then only slowly.



The effects of the imbalance of recruitment and mortality can be seen by following the cohort of plants originally mapped in the 1988 survey. That cohort has declined rapidly, reflecting the high mortality rates. Even though *Anemone multifida* is, in theory, a long-lived perennial, only 37% of the plants have survived the 22 years from 1988 to 2010.

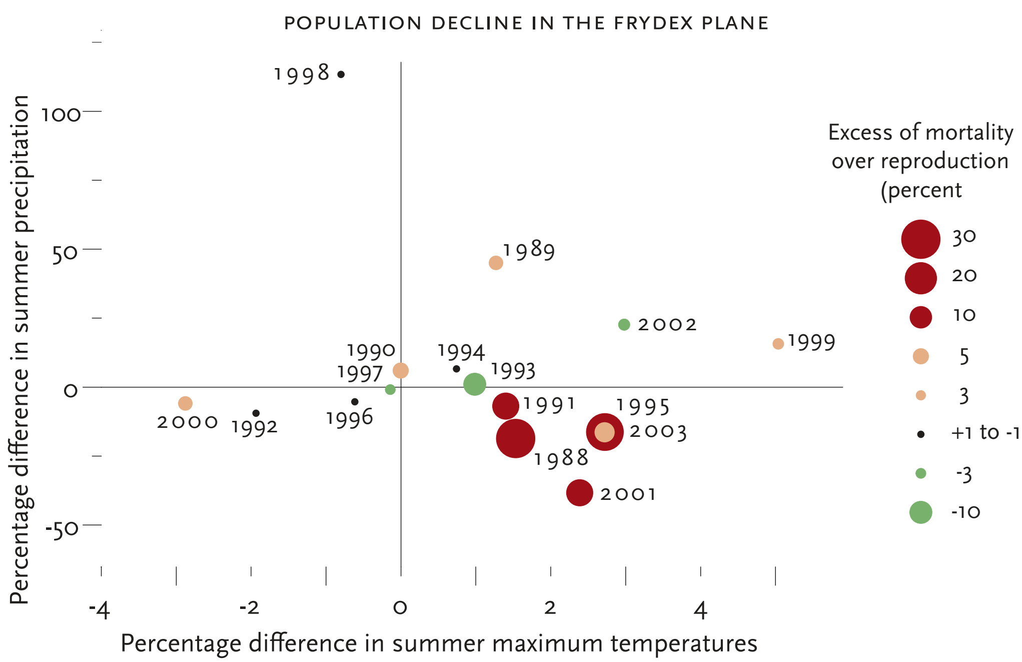
The lower line on the graph shows the new plants that have arrived to replace the originals. From 1988 to 1995 the number of new plants grew, though at a slower rate than the number of individuals was reclining, again reflecting the excess of mortality over recruitment. After that the declining number of flowering plants and the new plants' own mortality catch up with recruitment, and the number of new plants held steady for a while and then started to decline.

All of this suggests that mortality, and in particular the spikes in mortality shown in the upper graph, is driving the population trends. What then is driving mortality?

And Climate

I suggested above that there were general correlations between population declines and hot dry summers. In 1988, the year of our largest population declines, the Champlain Valley was so dry that red cedars and marginal wood ferns were drying from drought, and so hot that I had to spit on my hands to scramble up ledges.

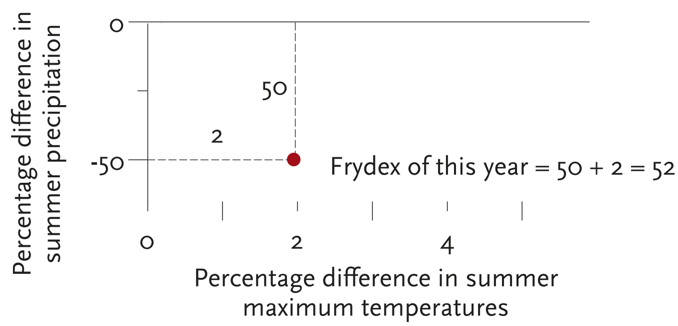
This can be made more precise by examining how the population changes, measured as the excess of mortality over regeneration, compare to the average June to September precipitation and maximum temperatures. The graph below shows the result. The axes are the percentage deviation from the long-term (1895 to 2010) climate means for Burlington. Hot is to the right, and dry downward. The resulting excess of mortality, measured as a percentage of the June population, is shown by the size and color of the circle.



The results are striking; the five years with the largest excess of mortality all fall in the lower right quadrant, where rainfall is low and temperature is high.

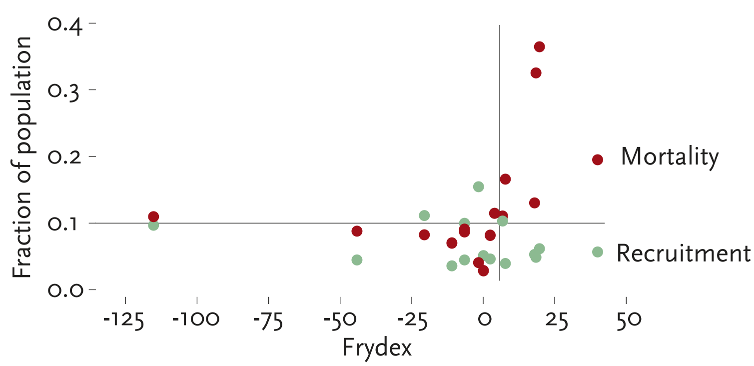
This suggests using a simple index, the sum of the percentage by which rainfall is high and the percentage by which rainfall is low, as a measure of climate stress. The diagram at the top of p. 11 illustrates the definition.

DEFINITION OF THE FRYDEX



Since precipitation is more variable than temperature, this definition is weighted towards precipitation. It could easily be fixed by using the ratio of the exceedance to the variance. I haven't done that and use the simple form here.

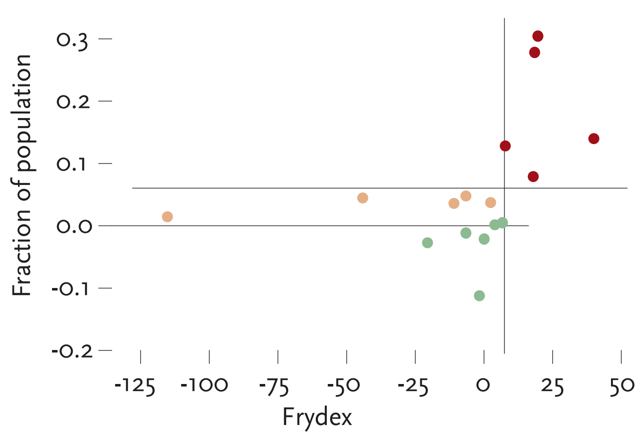
RECRUITMENT & MORTALITY VERSUS FRYDEX



Even in the simple form, the FRYDEX seems to represent a biological threshold. When it is above about 5, mortality is always over 10%, and recruitment around 5% or less. There is excess mortality, and the population declines.

Combining morality and recruitment into a single measure, the excess mortality, the pattern is even clearer.Whenever the FRYDEX is over about 5 the population crosses a threshold. Mortality exceeds reproduction by 7% or more, and again the population declines.

EXCESS MORTALITY VERSUS FRYDEX



Conclusions

The Winooski anemone population is declining, and may already be functionally extinct. Mortality is high and seems to be climate controlled. In ordinary years recruitment is low, and only rarely exceeds mortality. In bad years mortality peaks, and the population declines abruptly.

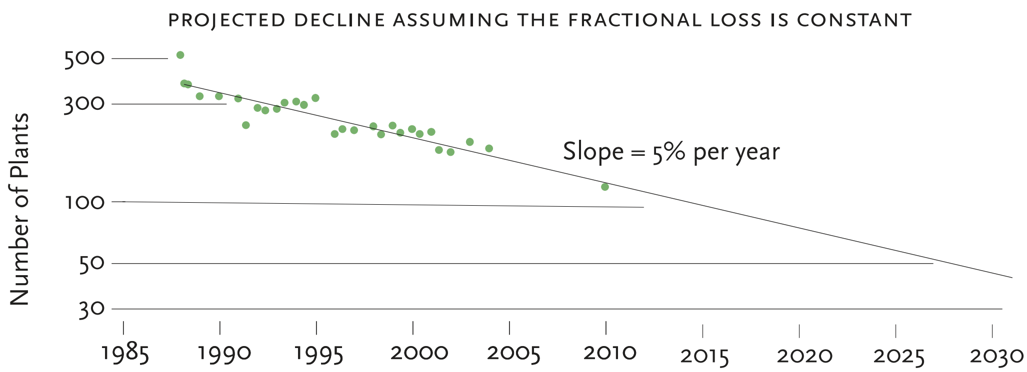
My analysis suggests that the anemone has two problems.

The first problem is the bad years, when the summer is hot and dry and mortality peaks. We have observed five such peaks since 1988, and the climate record suggests that there was also a peak in 2007 which we didn't observe directly.

The second problem is that there are no good years. Under average conditions and even under wet and cold conditions, mortality is close to recruitment, and the population holds steady or declines or increases slightly. There are no peaks in recruitment that would make up for the peaks in mortality.

The prospect is thus for continuing decline. From 1990 to the present the population lost about 9 plants per year. There are 117 plants now, and if this rate remains constant, the population in 2020 will be down to around 30 plants.

If, on the other hand, the percentage loss, currently around 5% per year, remains constant, then the population will do a bit better.



If we plot the decline as a straight line on a log scale, which is equivalent to assuming that the percentage loss is constant, the population will approach 30 plants sometime in the 2030s.

Rates of loss, as our data show, are never constant, and small populations are always vulnerable to sudden losses. As the population gets smaller, a single event–a drought, a flood–could wipe most of the plants out in a few weeks. The only thing that seems certain is that, given the small number of flowering plants and the climate stress they seem to be suffering, the population's ability to recover from losses is low. The 180-year run of the Winooski anemones may or may not be nearing its end. But it seems very unlikely that we will, in our lifetimes at least, ever see a population of hundreds of anemones here again.