

Brook Trout Movement during and after Recolonization of a Naturally Defaunated Stream Reach

CRAIG N. ROGHAIR*¹

Department of Fisheries and Wildlife, Virginia Tech, Blacksburg, Virginia 24061, USA

C. ANDREW DOLLOFF

U.S. Forest Service, Southern Research Station, 1650 Ramble Road,
Blacksburg, Virginia 24060, USA

Abstract.—In June 1995 a debris flow associated with a massive streamwide flood completely eliminated brook trout *Salvelinus fontinalis* from the lower 1.9 km of the Staunton River in Shenandoah National Park, Virginia. Biannual diver counts revealed that brook trout moved several hundred meters into the debris-flow-affected area each year, resulting in complete recolonization within 3 years of the event. We initiated a postrecolonization, biannual mark-recapture survey in 1997 and a radiotelemetry study in 1999 to further examine the movement of brook trout within the Staunton River. Fish that moved less than 100 m upstream or downstream made up 91% of brook trout recaptures; the maximum movement was over 800 m. Telemetered fish showed median seasonal movements of less than 70 m but a maximum movement of nearly 2 km. Despite the limitations inherent in movement studies, we observed postrecolonization movements consistent with those that were the basis for recolonization of the defaunated reach. Understanding the ability of movement to effect population changes is necessary for proper management in the wake of catastrophic events.

In June 1995 a debris flow associated with a massive streamwide flood impacted the lower 1.9 km of the Staunton River, a second-order stream in Shenandoah National Park (SNP), Virginia (Figure 1). Postflood fish surveys revealed that brook trout *Salvelinus fontinalis* had been completely eliminated from the debris flow-affected area, and questions arose on whether brook trout had the ability to quickly recolonize the naturally defaunated reach (referred to here as the “affected area”; Roghair et al. 2002). Phinney (1975) reported that brook trout had recolonized a similar length of a Montana stream within 1 year of an experimental defaunation. However, Moore et al. (1985) found

a “lack of extensive movements” into an experimentally defaunated reach in a Great Smoky Mountains National Park stream and further suggested transplanting fish may be necessary to quickly rehabilitate affected areas. Other studies suggested that salmonids could generally recolonize reaches that had been defaunated by floods and debris flows within 1–4 years (Lamberti et al. 1991; Detenbeck et al. 1992; Propst and Stefferud 1997; Swanson et al. 1998).

Debate regarding the ability of brook trout to recolonize disturbed areas reflects a larger, more general debate on stream fish movement. From the 1930s to the early 1990s, adult stream-resident fish were generally regarded as sedentary (Gerking 1959). Gowan et al. (1994) presented a challenge to this “restricted movement paradigm,” describing methodological limitations and flawed data interpretations associated with previous studies and providing new data from weir and radiotelemetry studies that suggested stream-resident salmonids were much more mobile than previously thought. Several subsequent studies provided corroborating evidence (Fausch and Young 1995; Gowan and Fausch 1996; Young et al. 1997). Others provided more of a middle ground explanation: that fish populations consist of mobile and sedentary individuals, or alternatively, individuals that are mostly sedentary with occasional bouts of movement (Harcup et al. 1984; Hilderbrand and Kershner 2000; Rodriguez 2002).

Beginning one month postdisturbance in June 1996, we used biannual diver counts to monitor the recolonization of the defaunated reach by adult (all fish older than age 0) brook trout. Our objective was to describe the recolonization pattern and document the magnitude of movement of adult brook trout during recolonization. Movements detected during recolonization of the affected area prompted us to initiate movement studies on brook trout in both the affected area and in a section of

* Corresponding author: croghair@fs.fed.us

¹ Present address: U.S. Forest Service, Southern Research Station, Center for Aquatic Technology Transfer, 1650 Ramble Road, Blacksburg, Virginia 24060, USA.

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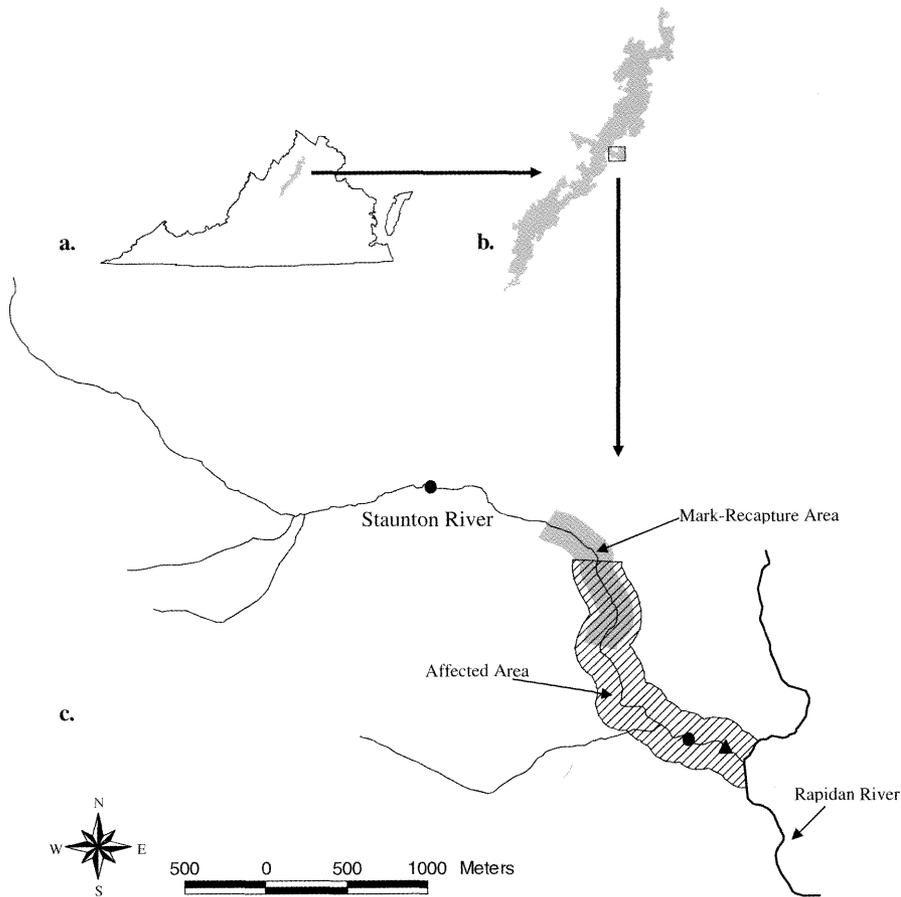


FIGURE 1.—(a–c) Map of the Staunton River, Shenandoah National Park, Virginia, showing the debris flow-affected area (hatches) and mark–recapture study section (gray). The circles show the upstream and downstream extent of the brook trout radiotelemetry study; the triangle denotes the location of a bedrock cascade.

the Staunton River immediately upstream of the recolonized reach that had not been impacted by the debris flow (referred to here as the “unaffected area”). The objective of our postrecolonization study was to determine whether brook trout movements of the magnitude detected during recolonization could be observed in the postrecolonization population through the use of standard techniques.

Study Area

The Staunton River flows east from an elevation of 975 m through the central district of SNP to its confluence with the Rapidan River (Figure 1). The coldwater stream is approximately 6.3 km long, has an average width of 3.5 m, and an average channel gradient of 10%. The channel consists of pools separated by step pool cascades, small (less than 2 m in height) waterfalls, and bedrock slides.

For most of its length, the Staunton River contains mainly two species of fish: brook trout and eastern blacknose dace *Rhinichthys atratulus*. American eels *Anguilla rostrata* are found throughout the stream at very low densities, and a warmwater fish assemblage occupies the Staunton River from its confluence with the Rapidan River (river meter [rm] 0) to the base of a steep bedrock cascade approximately 150 m upstream of the confluence. Most of the Staunton River watershed was cleared before it became part of SNP in the 1930s. The watershed is now completely forested; chestnut oak *Quercus prinus* forests occupy the higher slopes and tulip poplar *Liriodendron tulipifera* is the dominant species near the stream (Karish et al. 1997). The stream has an acid-neutralizing capacity ranging from 50 to 100 $\mu\text{eq/L}$ and a pH typically ranging from 6.3 to 7.0 and is considered moderately acid sensitive (Newman 1996).

Methods

Recolonization

The distribution of brook trout before the June 1995 debris flow was known from a previous study by Newman (1996), who used diver surveys to sample the Staunton River each spring and fall from June 1993 through June 1995. During the surveys, a diver counted fish in every 5th pool and every 10th riffle from the confluence with the Rapidan River to the upstream extent of fish distribution (typically 6 km). An approximation of the distribution of brook trout was obtained from these data. Post-debris flow surveys were performed in October 1995, May 1996, October 1996, June 1997, October 1997, and May 1998 to describe recolonization patterns and movements of adult brook trout.

Postrecolonization

Mark-recapture.—The mark-recapture area spanned a continuous 965-m reach of the Staunton River: 575 m in the affected area and 390 m in the unaffected area of the stream (Figure 1). Brook trout were first marked for the study in May 1997. Subsequent mark-recapture surveys took place in October 1997, June 1998, October 1998, June 1999, and October 1999. The entire reach was sampled during each survey.

Before each survey, the mark-recapture reach was divided into riffle-pool complexes. Each complex consisted of a continuous 10- to 40-m reach of stream that encompassed several pools and riffles and terminated at major breaks, such as boulder cascades or small waterfalls. Brook trout were captured by making a single pass through each complex with a backpack electrofishing unit. Captured fish were checked for marks from previous surveys, and their length (mm), weight (g), and location of capture (m) were recorded. Fish longer than 100 mm without marks were anesthetized with tricaine methanesulfonate (MS-222; ~200 mg/L), given a passive integrated transponder (PIT) tag (11.5 mm × 2.0 mm; 0.06 g), and their adipose fin was clipped. The PIT tags were injected inside the body cavity by means of a 12-gauge hypodermic needle attached to a syringe. Each tag had a unique 10-digit alphanumeric code that allowed us to individually identify recaptured fish. Fish were returned to the pool-riffle complexes from which they were captured.

Telemetry.—Telemetry equipment consisted of a scanning receiver, a three-element folding Yagi antenna, and radio transmitters. The entire trans-

mitter, antenna included, was contained within an epoxy capsule (1.7 g; 9 × 7 × 20 mm) that was surgically implanted into each anesthetized fish's body cavity. Signals were transmitted in the 149,000–150,000 MHz range at 40 pulses/min. Battery life for the transmitters averaged 69 d (range, 55–89 d).

Fifty-three transmitters were implanted between May and October 1999. Between May and July, 15 fish were implanted with transmitters in the affected area of the stream and 17 were implanted in the unaffected area. Between September and October, 10 fish were implanted with transmitters in the affected area and 11 fish were implanted in the unaffected area. Two of the fish implanted during the summer were recaptured and their transmitters were replaced for continued tracking during the fall. All implanted fish were captured and released between rm 590 and rm 3,125 (Figure 1). Fish averaged 86 g (range, 59–163 g) and 215 mm (range, 183–283 mm) at the time transmitters were implanted.

Summer (May–August) and fall (September–December) ranges were determined by locating all fish once every 3–7 d. The location of each fish (stream meter) was determined from the stream-bank by triangulation. In most cases it was possible to determine the occupied unit (pool or riffle) without approaching the stream closely. The distance to the upstream end of each unit had been recorded during a stream habitat survey performed before the movement study (Roghair et al. 2002). Seasonal range is defined here as the distance between the upstream end of the most upstream unit and the upstream end of the most downstream unit occupied by the fish during the entire season.

A rank-based linear model was used to examine seasonal-range data. This nonparametric approach does not assume normality and is very robust to nonsymmetrical data distributions (Hettmansperger and McKean 1998). The sole assumption of rank-based linear models is a continuous distribution of error terms. The approach was used to test for differences in range-size by location (affected area, unaffected area) and by season (summer, fall). Eleven fish were excluded from the analysis owing to a lack of observations. Interaction between season and location was not significant ($F = 1.03$; $df = 41$; $P > 0.05$) for the seasonal data; therefore, main effects (seasons and locations) could be examined with the model. Fish weight and length were included as covariates.

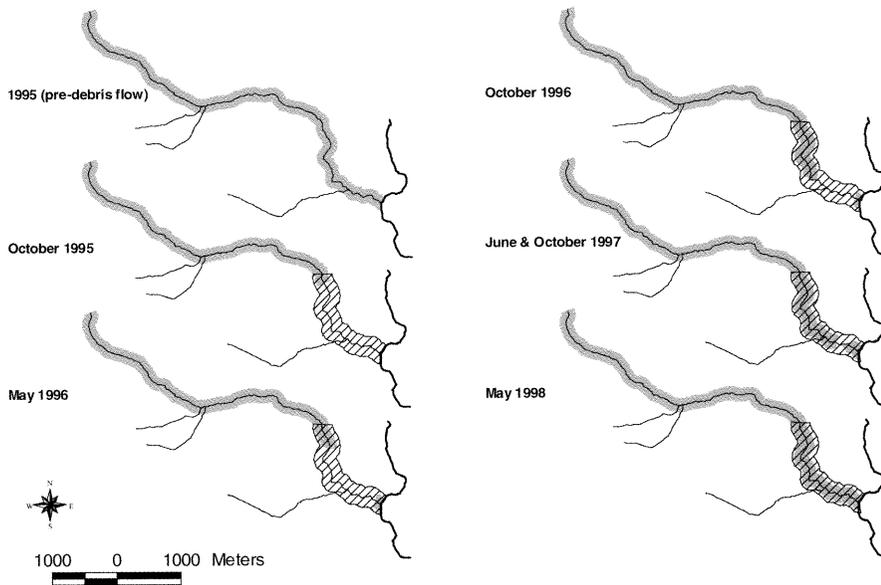


FIGURE 2.—Recolonization of the debris flow-affected area of the Staunton River by adult brook trout, 1995–1998. The shaded areas indicate sections of the stream in which brook trout occupied the majority of inventoried habitat units. Fish were sporadically distributed outside the shaded areas in May and October 1996. Hatches mark the debris flow-affected area.

Results

Recolonization

Adult brook trout were distributed throughout the Staunton River during all diver surveys before June 1995 (Figure 2). In October 1995, 4 months postdebris flow, only five adult brook trout were counted in the debris flow-affected area and all were within 150 m of the upstream end of the affected area. The distribution of brook trout up-

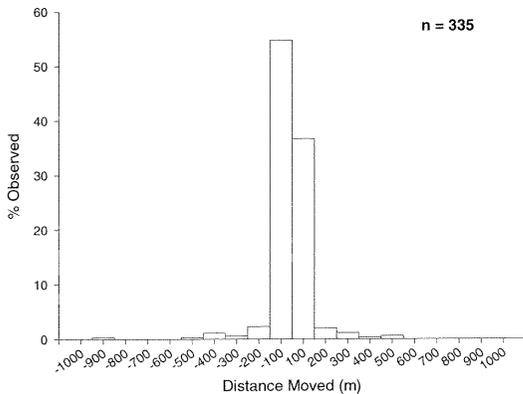


FIGURE 3.—Distribution of the detected movements of recaptured brook trout during the 1997–1999 mark-recapture study in the Staunton River, Virginia, following a flood event.

stream of the debris flow was essentially unchanged.

Recolonization progressed mostly from upstream to downstream (Figure 2). Adult fish were observed in the majority of habitat units (pools and riffles) as far as 400 m from the upstream end of the affected area in May 1996 and 800 m in October 1996. In addition, two adult fish were found in pools 500–800 m from the upstream end of the affected area in May 1996, and three fish were observed in a single pool more than 1 km from the upstream end of the affected area by October 1996. Less than three fish were observed in the downstream-most 200 m of the affected area in both May 1996 and October 1996. The June 1997 and October 1997 surveys revealed that adult brook trout were only absent from a 200–250-m reach beginning approximately 200 m upstream from the confluence with the Rapidan River. Adult brook trout were common throughout the Staunton River by May 1998. In total it took 2.5–3.0 years for adult brook trout to recolonize the 1.9-km debris flow-affected area.

Postrecolonization

Mark-recapture.—Fish that moved less than 100 m upstream or downstream made up 91% of brook trout recaptures (Figure 3). The maximum

TABLE 1.—Summary of brook trout mark–recapture data for postflood recolonization of a debris flow–affected area in the Staunton River in May 1997–June 1999. Total recaptures is recaptures from the first postmarking survey plus the sum of recaptures during subsequent surveys. Percent missed is the percentage of total recaptures not captured during the first postmarking survey but captured at a later date. Percent missed is reported as a minimum because it does not account for fish that either left the mark–recapture area, remained but were never captured, or lost their PIT tag. Missing tags is the number of fish with an adipose clip that did not contain a PIT tag. Postmarking surveys is the number of surveys a group of fish experienced after being marked.

Date marked	Marked (<i>N</i>)	Recaptures (<i>N</i> [%])		Minimum missed (%)	Missing tags (%)	Post marking surveys (<i>N</i>)
		First	Total			
May 1997	83	18 (22)	39 (47)	54		5
Oct 1997	316	61 (19)	99 (31)	38	59	4
Jun 1998	268	72 (27)	87 (33)	17	42	3
Oct 1998	301	51 (17)	56 (19)	8	25	2
Jun 1999	438	64 (15)	64 (15)		29	1
Total	1,406	266 (19)	335 (24)			

detected upstream movement was 410 m and the maximum detected downstream movement was 873 m. Recapture percentages during initial recapture events ranged from 15% to 27% (Table 1). Total recaptures for each marking event increased as fish that initially eluded recapture were caught during subsequent mark–recapture surveys. For example, for fish marked in May 1997, the percentage of fish recaptured increased from 22% during the first recapture event to 47% when all four mark–recapture surveys that followed the first were included (Table 1). The percentage of fish that had lost their PIT tags (captured with adipose fin clip but no PIT tag) ranged from 25% to 59% of recaptures in a given recapture event (Table 1).

Telemetry.—The median seasonal range was

0 m for the summer-affected area, 14 m for the summer-unaffected area, 39 m for the fall-affected area, and 68 m for the fall-unaffected area (Figure 4). No significant difference was found between affected and unaffected areas ($F = 3.80$; $df = 41$; $P = 0.058$), whereas a highly significant difference was found between summer and fall ($F = 15.55$; $df = 41$; $P = 0.0003$). None of the covariates (weight, length) were found to be significant ($F < 0.05$; $df = 41$; $P > 0.400$). The maximum range was 130 m for summer affected, 90 m for summer unaffected, 530 m for fall affected, and 340 m for fall unaffected. The largest range detected was 1,950 m for one fish that moved during fall from the affected to the unaffected area.

Discussion

In the Staunton River, the proper conditions for recolonization existed, including a nearby source population, no insurmountable physical barriers, and suitable habitat in the affected area. Biannual postevent diver counts showed that brook trout recolonized the affected area at a rate of several hundred meters per year (Figure 2). Within 3 years, the reach was recolonized by adult brook trout and the population density increased above levels observed before the event (Roghair et al. 2002). Pre- (1993) and postevent (1995 and 1999) streamwide habitat surveys showed that by 1999 instream habitat conditions were similar to pre-event conditions (Roghair et al. 2002).

The pattern observed during recolonization (mainly from upstream to downstream) was not surprising for three reasons: (1) the existence of a steep, 20-m-long bedrock cascade 200 m upstream from the confluence with the Rapidan River (Figure 1); (2) the state of the Rapidan River brook trout population after the debris flow; and (3) the

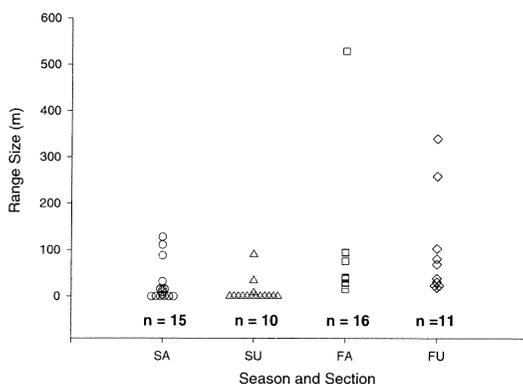


FIGURE 4.—Seasonal-range sizes for adult brook trout in the Staunton River as observed with radiotelemetry during summer and fall 1999. Abbreviations are as follows: SA = summer, affected area; SU = summer, unaffected area; FA = fall, affected area; and FU = fall, unaffected area. One fish that had a 1.9-km range spanning the affected and unaffected areas during fall was omitted.

relatively intact brook trout population in the upstream unaffected area. Although a bedrock cascade is not necessarily a barrier to fish movement, it can at least be an impediment to movement (Adams et al. 2000), especially at base flow. Portions of the Rapidan River both upstream and downstream of the confluence with the Staunton River were affected by debris flows, and brook trout were certainly depleted, if not eliminated, from the Rapidan River near the confluence. The population in the Staunton River upstream of the affected area was immediately available for recolonization, and by October 1995 had moved into the upper 150 m of the affected area.

Movement of brook trout from the unaffected area into the defaunated reach allowed us to make inferences about individual fish movements. Since the debris flow occurred in June 1995 and brook trout spawn only once per year (in the autumn; Jenkins and Burkhead 1993), all fish classified as adults (older than age 0) found in the debris flow-affected area during the October 1995, May 1996, and October 1996 surveys had to have moved there from outside of the affected area. In situ reproduction could not have accounted for any adult fish in the affected area until the June 1997 survey. Adult fish had moved into the majority of habitat units (pools and riffles) up to 400 m downstream from the unaffected area by May 1996 and 800 m by October 1996, and individuals were observed in pools more than 800 m downstream in May 1996 and 1 km downstream in October 1996. This not only illustrated the ability of brook trout to move several hundred meters within a year, but also demonstrated the magnitude of movements needed to support the observed rate of recolonization.

The majority of the fish in our postrecolonization mark-recapture study showed limited movements; over 90% of recaptured fish moved less than 100 m between surveys. In addition, the median seasonal range of all telemetered fish was less than 70 m. The apparent disparity between our postrecolonization movement study and movements observed during recolonization could be explained, in part, by well-known study design and technological limitations. We repeatedly marked and recaptured fish within the same continuous reach of stream, which biased our mark-recapture study toward detecting short-distance fish movements (Rodriguez 2002; Albanese et al. 2003). Tag loss and low recapture rates can further complicate interpretation (Gowan et al. 1994). In addition, using radiotelemetry to monitor a small proportion of the largest individuals in a population during

summer and fall may not accurately depict movements of smaller individuals (Clapp et al. 1990) or movements related to seasonal habitat shifts (Jakober et al. 1998).

The ability to individually identify fish during repeated mark-recapture surveys provided us with unique information on the fate of nonrecaptured fish during the mark-recapture study. For example, in May 1997 we marked 83 fish, 18 of which we recaptured in October 1997. We recaptured another 21 fish during subsequent surveys to bring our total recaptures to 39 fish (Table 1). Although we used single-pass electrofishing, it is unlikely that we missed 54% of the fish available for recapture during the October 1997 survey. Kruse et al. (1998) had an 83% first-pass capture rate in a high-gradient trout stream, and during two-pass depletion estimates performed on the Staunton River in June 2000 we showed an average 73% first-pass recapture rate (Roghair 2000). If we assume that the 18 fish we captured in October 1997 represented 73% (our first-pass capture efficiency) of the marked fish present in the reach, then 18 divided by 0.73, or 25 marked fish were present in the reach at that time. This means that $39 - 25$, or 14 marked fish were outside the mark-recapture reach and unavailable for recapture in October 1997. A closer examination of our May 1997 data revealed that 14 fish were marked within 100 m of the upstream or downstream extent of the mark-recapture reach. It is plausible that a number of marked fish moved out of the reach before October 1997 and then returned at a later date. The major implication is that recapture efficiency and fish movement both played roles in low recapture rates during our study. Past studies typically blamed low recapture rates on high mortality and seldom considered movement as a factor (Gowan et al. 1994).

Because of the limitations listed above, a classic interpretation of our mark-recapture data does not appear to accurately describe the movements associated with the recolonization that we observed in our diver counts. Specifically, the observed recolonization patterns seem to be better explained by focusing on the movements of single individuals rather than on population means or medians, which are inherently biased by the methodology. We detected movements of over 800 m during the mark-recapture study and nearly 2 km during the telemetry study, showing that at least some portion of the population continued to make movements consistent with those we observed during recolonization in the postrecolonization period. As demonstrated during the recolonization of the de-

bris flow-affected area, such movements are necessary to ensure persistence in a highly variable and constantly changing stream environment. Transplanting fish to speed population recovery was considered a viable option after the 1995 debris flow and would have probably taken place were it not for the identification of the Staunton River population as genetically unique within SNP (Poompuang et al. 1997). Transplanting would not have substantially decreased population recovery time, but would have cost time and money and possibly destroyed the genetic integrity of the population. Clearly, understanding the ability of the mobile component to effect changes in populations is necessary before we can make sound management decisions in the face of catastrophic events.

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