

Christine Guthrie (1945–2022): a tribute from her trainees



Christine Guthrie. (Photo courtesy of Wendy Gilbert.)

Family, friends, colleagues, and former trainees around the world are mourning the passing of Christine Guthrie, PhD, Professor Emeritus in the Department of Biochemistry and Biophysics at UCSF. Christine was a giant in the field of RNA biology, and a singular leader in the field of pre-mRNA splicing. She passed away on July 1, 2022 after a battle with breast cancer at the age of 77. She is survived by her husband, John Abelson, also Professor Emeritus in the Department of Biochemistry and Biophysics.

As former trainees, Christine showed us how to think about science, how to frame hypotheses, how to interrogate ideas, and how to present those ideas so others could understand. She exemplified how to be a scientist and inspired generations to follow in her footsteps, some very closely as professors in the RNA field, and others as they have applied what they learned from her to other fields and professions. She set a tone of inclusiveness and openness that permeated everything she did.

In 1973, Christine was the first woman to join the faculty of the UCSF Department of Biochemistry and Biophysics. She helped recruit faculty capable of conceptualizing basic biochemical processes in novel but rigorous ways who were interested in sharing ideas and approaches. She was instrumental in the development of what is now the prestigious Tetrad graduate program at UCSF, a model for many leading graduate programs around the world. A

founding member of the RNA Society, she helped establish it as a uniquely open society willing to interact with anyone interested in RNA biology that continues to feature unpublished, cutting-edge research and that promotes trainees. Christine also helped define a path for women in science, speaking candidly about the sexual harassment and discrimination that she experienced. Sharing these struggles and her successes paved the way for so many women.

Christine openly recounted her personal history and her contributions in the piece “From the ribosome to the spliceosome and back,” published in 2010 in the *Journal of Biological Chemistry*. Realizing that understanding RNA splicing required the use of the genetic power of baker’s yeast *Saccharomyces cerevisiae*, in the early 1980s, the laboratory painstakingly identified the critical snRNA components of the yeast spliceosome, which led her laboratory to identify key interactions between these RNAs and the intron substrate that underpin how introns are recognized by the spliceosome. Showing that the human U2 snRNA could functionally replace the yeast U2 snRNA demonstrated a profound conservation of the splicing machinery. Her group also discovered that a massive RNA rearrangement occurs during splicing that builds a network of conserved RNA interactions that was proposed to be the active site of an RNA enzyme or “ribozyme.” This proposal was confirmed biochemically and then in detail with the arrival of high-resolution structures of the spliceosome in 2014 made by cryo-electron microscopy, a method pioneered at UCSF. Her laboratory also identified and analyzed the protein components of the spliceosome that mediates its many dynamic rearrangements (such as Prp16, Prp28, and Brr2), forming much of the foundation of the field as it exists today.

Known for being unafraid to interrogate the data and see where that interrogation led her, Christine conceptualized proofreading clocks in the spliceosome. On a remarkably minimal data set, she defined a model of splicing fidelity wherein DEAD-box ATPases inspect each splicing step and can discard mistakes, and linked this process to rearrangements in ribonucleoprotein structure. She was initially criticized for “trying to do kinetics by genetics”; however, work over the subsequent decades validated her initial concept as correct.

These skills served her well. Christine earned a place in the National Academy of Sciences in 1993, received the Genetics Society Medal in 1997, the Women in Cell Biology Senior Career Recognition Award in 1998, the

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Panel discussion RNA Society 2015. (Photo courtesy of David Brow.)

RNA Society Lifetime Achievement Award in 2006, and the American Society for Biochemistry and Molecular Biology-Merck Award in 2011. A prolific writer, she published over 200 papers, many in top journals such as *Cell*, *Science*, and *Nature*.

Finally, Christine was uniquely talented at bringing people together and giving them what they needed to flourish. Below are some remembrances from those she trained over the last five decades.



Working with Christine Guthrie was a huge opportunity, great fun and an amazing experience. Her insights and advice had an enormous influence on my future research directions and approaches. It is an honor to be a member of the unofficial Guthrie lab alumni community. Such is her scientific legacy, that fellow alumni are to be found at almost any moderately sized, RNA-related meeting or conference. Even though Christine is so sadly gone, her spirit lives on in the careers of the many researchers who shared the good fortune of working in the Guthrie lab and interacting with her.

—David Tollervey

Christine Guthrie was my PhD mentor, and with Chris, that meant she was my “scientific mom” for life. One of her great talents was making me, and many other young scientists, feel an accepted and valued member of her scientific family, providing the confidence for success. Christine also infused me with her clarity of thought and communication and provided me with my love of the RNA community and science. I will always be indebted to Christine for her mentorship and friendship. I will miss her greatly.

—Roy Parker

I was a postdoc in Christine’s lab for three years, 1986–1989. I learned a lot in that time, both from Christine and the other lab members. She created an exceptionally excit-

ing and supportive environment for doing science. My earlier mentors had taught me how to do science, but Christine taught me how to thrive in the academic research ecosystem. And she continued to support my development as a faculty member, at one point holding up a manuscript for a month so we could co-publish. I will always be grateful for her guidance and encouragement.

—Dave Brow

I was a postdoc in the lab from late 1986–1989, when it was expanding. Others have spoken of the high level of science and Christine’s push for excellence, which goes without saying. She also encouraged team bonding. Who can forget the annual cassoulet dinners (we were all aghast when a new postdoc complimented her on the “nice beans”), the ski weekends and the departmental retreats in Monterey? In turn, we surprised her with what has to be the best lab video ever: “She Blinded Me With Science.” Christine, we miss you!

—Beth Shuster

I was a postdoc, then a senior scientist in Christine’s lab for a long time (1986–1995), partly because I really didn’t want to leave. Her lab was filled with exciting rigorous science and fun, caring lab mates. Group meetings sometimes went on and on if there was some mechanism still to be pondered, which Christine welcomed. Practice talks could be painful at times, but no one was leaving the room until there was the potential for a really strong talk, because telling your story right was paramount. Christine was an incisive thinker and highly articulate communicator, a supportive mentor with high expectations and a big heart, and had, as everyone who knew her will say, an incredible wit. She enjoyed the farcical videos made by her lab members (e.g., “The Sounds of Splicing” and “Splice Trek”), with her little chuckle, a smirk and sometimes an eye roll. Christine appreciated that the videos reflected our camaraderie as well as our devotion to the lab, and of course, our silliness. The world is a lesser place without her.

—Shelly Haltiner Jones

I was a graduate student in Christine’s lab from 1988–1993. My rotation in the Guthrie lab was my fifth! (I was an MD-PhD student.) The environment of the lab that Christine had created and cultured was impossible to walk away from and I found my scientific home. Her support over the next six years was unwavering. The freedom she gave us to explore our crazy ideas was incredible and resulted in me learning to have the confidence to pursue out of the box science. She was intimidating in many ways, and so loving in others. I fondly remember the hugs we would get upon leaving her house after one of the many unforgettable lab parties that she hosted, a

chance for us to experience her softer side. I also remember her sharing her office with us, and not just for the pursuit of science and access to a computer. Christine and I shared a love of cats and while on sabbatical, she let me use her office during the day to house a young kitten that had survived the Oakland fire and needed to be kept in front of a heater and fed every three hours. Lastly, despite all of the issues she encountered as she established her career, I am thankful to Christine for protecting us and empowering us to move forward. Once, early on in my faculty career, when speaking with Christine to request a letter of reference, I said to her that she never told us that running a lab would be so hard. To which she responded if I told you that, would you have done it? I remain thankful to her for shielding us and enabling us to focus on embracing science, as I am ever grateful for her role in making me who I am.

—Cammie Lesser

I was a graduate student in Christine's lab from 1987–1993. As for many first year UCSF students, I first encountered Christine while taking the Biological Regulatory Mechanisms course, or "Bioreg," where she gave inspirational lectures on translation and mRNA splicing. Her presentation of the material was creative and elegant, resulting in no less than a cult-like following among her students. She impressed upon us the elegance of the Ninio-Hopfield kinetic proofreading mechanism to "discard" noncognate tRNAs coupled to a "clock" timed by GTP hydrolysis by EF-Tu. This intellectually appealing concept deeply influenced the notion that ATP hydrolysis by the DEAD/H box helicases could promote the fidelity of spliceosome assembly and disassembly. Her lectures on the use of phylogenetic analysis of primary rRNA sequences to predict RNA secondary structure highlighted its utility in identifying the yeast snRNAs as well as the discovery that mutually exclusive base-pairing within and between the snRNAs and the message could point to the "catalytic core" of the spliceosome. While there is no way I can match her delivery, these lessons are woven into my own lectures given to thousands of UC Davis undergraduates over the last 20 years.

It was clear from her lectures that there was much to learn about the spliceosome, and multiple students wanted to join her lab each year. I was thrilled to join her lab that spring (I was worried she would pick Cammie over me, and she picked both of us!). I remember spending countless hours in Christine's office puzzling over the apparent link between splicing fidelity and ATP hydrolysis that we uncovered by studying the Prp16-1 phenotype. We finally came up with a model that seemed to explain all the data and submitted the paper to Cell. Fast forward, I came to her office to tell her our paper was accepted. She looked at me and said "Reeeeeaaalllly?" I think we

were both kind of surprised. I am forever grateful to Christine as a role model and mentor.

—Sean Burgess

Christine Guthrie was a fixture in my life, serving as my PhD advisor and then, after my postdoctoral time, my departmental faculty colleague. With her passing, I have been flooded in grief by a stream of memories too numerous to relate in this brief remembrance. I will highlight two episodes.

During graduate school, after an abstract deadline for a Keystone meeting in early 1992, I obtained the results that would unexpectedly become the centerpiece of my PhD thesis. Christine and I were both excited about the result, so she worked to get me (not her) added as a short talk to the program, which normally would be impossible. Although I was wrecked with stress and mountain sickness, I managed to get through the talk. I heard indirectly at that meeting that she had given me all the credit for the finding, despite the fact that it was her lab's decade-long quest to identify the essential yeast spliceosomal snRNAs and her strong belief that the snRNAs were catalytic that made it possible. With her students, Christine was patient, supportive, dedicated, and generous.

Years later, after having good luck with grant proposals as an assistant professor, the day came when I obtained an unfundable score on an NIH R01 application. I entered Christine's office, which was adjacent to mine, and let her know of this calamity. Her response was swift and clear: "Sweetie, you have never failed at anything in your life. This will be good for you!" Encapsulated in this response was (1) her belief that I had never failed at anything—while untrue, I took it as a sign of respect (although there was a veneer of scorn), and (2) her ability to put things into perspective, even if it involved "tough love." This is not to say that Christine did not have a soft side, which I experienced often as I walked into the common office area toward my office to often see her reading a journal article from which she would lift her gaze to smile and wave.

—Hiten Madhani

I was a PhD student in Christine's lab from 1988–1995. I thought I knew what I wanted to do when I entered graduate school, and then I rotated in Christine's lab and became completely enthralled by her lab's application of yeast genetics to gain mechanistic and often paradigm-shifting insights into molecular mechanisms of pre-mRNA splicing. Christine's lab was like her family, and that really came through in how she invested in the scientific development of her mentees. Her mentorship always involved high expectations. She pushed me to do things I didn't know how to do, gave me the space to struggle and figure things out, and supported me

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when I needed help. One day she dropped a manuscript on my desk and asked me to do the peer review, which I had never done before. My review was probably longer than the draft manuscript, but Christine read it through and gave me just the right guidance to revise it into a more concise and far more useful critique. Her carefully crafted writing was one of her many gifts that I still try to emulate. One thing I loved about Christine was her wry sense of humor. I had a pretty contrarian and argumentative streak as a graduate student and was not shy to challenge my peers or even Christine, who might have perceived me as a bit of a pain in the neck. One day in a lab meeting, we were having an animated discussion with several lab members about a topic that I don't remember at all; but I do remember clarifying to Christine at some point that I was for once agreeing with her. To that she immediately responded "Great! Now you can graduate." Thank you, Christine. You are gone but the love and support you gave me and the rest of your mentees lives on in our own careers.

—Jim Umen

Christine was intimidating. She did not suffer fools and this was often belied through wordless gestures, such as the way she swirled her iced latte or flipped her flip flop. But she also used words with great wit and skill. She would roll out biting but witty quips that would make all of us laugh, including the target of the criticism. While intimidating, this was also really inspiring. She naturally expected us all to do our best. So that is what we did. Her bluntness also made her support meaningful and real. And it was real. I was helped by her mentorship and support in many ways, some of which I didn't realize until years later. Thank you, Christine. It was a privilege to learn from you and the Guthrie lab, and to experience one part of your amazing legacy.

—Cathy Collins

I was a postdoc between 1988 and 1991. Being in the Guthrie lab was an extraordinary experience. I realized quickly how truly unique the spirit and culture of Christine's lab was. Just as an example, she assigned me the bench right next to the lab's phone so I had to answer calls for the whole lab. A challenge for me, freshly arrived from France, but it helped to improve my English. Christine was a wonderful person and I have been fortunate to work with her, in a great scientific environment.

—Remy Bordonne

When looking for a postdoc after studying protein folding as a graduate student, I investigated a number of labs, all protein folding labs but one—Christine's lab, given my curiosity in RNA rearrangements. After visiting, I was

sold, and my experience in her lab exceeded my greatest expectations. Christine attracted an exceptional group of curious, ambitious, and fun-loving individuals. She guided us with her uncanny biological instincts reflected in regular model-building on the nearest whiteboard and with her enthusiasm sometimes conveyed through unconventional means (e.g., by a sticky-note at our desk indicating she had sent us an email). She helped us communicate our scientific stories in a clear and compelling manner and of course with appropriate usage ("streaked yeast" not "struck yeast"). She was a master communicator herself. As a Haselkorn Lecturer at the University of Chicago, she presented an overview of her contributions to the splicing field, at which point I realized that I would never present a lecture to my own students on splicing that would rise to her level of virtuosity and that I should just present a recording of her lecture instead. Christine was also generous, from sharing Priest Lake to supporting our careers. I will forever be indebted to Christine and always thankful that I ventured beyond the protein folding field and into her lab.

—Jon Staley

When I met Christine days back in Trieste at a meeting, I was a student finishing my PhD. I asked her whether I could join her lab as a postdoc, not the least knowing what an exciting world of science I would thrive into, entering her world and her lab.

As an Austrian scientist I was allowed to experience science at the highest level. When I remember Christine, I see her in front of my eyes with faded jeans, large earrings, short hair and sandals. Her casual appearance paired with that sharp intellect was fascinating to me. I'm grateful to her that she took me up; I would never have become the person I am now, without that period of time I was allowed to share with her. She made a great person out of me, by radiating confidence—you can do it!

—Anita Jandrositz

During my graduate research, Christine inspired in me great fascination for a deep understanding of the mechanistic aspects of dynamic ribonucleoprotein machines of the cell like the spliceosome. As many have highlighted here, her rigorous approach to this work was formidable, and her eloquence and piercing logic could be quite intimidating. However, I always found this counterbalanced by her warm compassionate support and her infectious enthusiasm and delight in talking science as we carried out our research. This was especially the case when surprises arose along the way—data from a particularly clever or elegant (or even a random one-off) well-controlled experiment that happened to yield a result that altered our current models for some aspect of the spliceosome function. Or, when two different people in the lab

ostensibly working on distinct aspects of splicing identified converging results that together further elucidated the mysterious ways of the spliceosome. Her responses to these surprises were some of my favorite memories of Christine and her love for science: she would pause, raise her eyebrows conspiratorially, smile and exclaim, "Intriiiiiiiiing!"

—Amy Kistler

As the postdoc who never left, I was with Christine from 1991–2018, through her repeated bouts of illness where she showed her enormous strength and resilience and through the waves of amazing people she brought together in the lab. The environment of the Guthrie lab that drew so many and inspired our loyalty and memories was built on her innate judgment both of science and people, her unfailing commitment to intellectual curiosity and integrity, and her compassion. Her scientific generosity and conviction that there is plenty of interesting science to go around is not found everywhere, and I feel profoundly grateful for the intellectual environment she created. Among my favorite memories of Christine are the times when, with a dry but puckish humor, she dispensed some pearl of wisdom. One of my favorites: "If it were easy, it would be magic, not science."

—Anne de Bruyn Kops

During the 1990s, Christine attracted an annual series of intense, brilliant, quirky graduate students and postdocs, as closely knit as an eccentric sitcom family. The Guthrie lab culture was one of unfettered intellectual curiosity, scientific rigor mixed with silliness (see all the Guthrie lab videos). We celebrated her many professional triumphs—Vice Chair of the Department of Biochemistry, American Cancer Society Professor, elected to the National Academy of Sciences. But her personal grit was revealed through her cancer diagnosis. I recall one day a message was passed; all her students and postdocs crowded into her small office. John Abelson sat beside her. As she disclosed the news, she looked straight at each one of us in turn, projecting an air of determination and confidence that she would be just fine, that we would be just fine. Wiping tears away, we drew on inner reserves, modeling hers. Her crisis spurred us—the senior students rallied to mentor the younger ones. And she was right: we all somehow forged ahead. She recovered and returned to work.

Christine was an elegant, concise writer and an exacting editor. The floor to ceiling bookshelves in her Noe Valley Victorian were stocked with fiction, including her mother's best-selling novels. Her literary heritage may have partially explained why Christine reworked draft manuscripts so meticulously, her signature cursive penciled above the double-spaced text.

Late in my graduate career, when experiments finally yielded results, I left a draft abstract on her desk with some trepidation. A few hours later a sunny Christine appeared in my bay, smiling broadly. With a flourish, she handed the page back to me: a single penciled correction. "I regret to inform you that 'data' are plural," she beamed. My relief and elation lasted until the abstract expanded into a manuscript, whereupon it received the full CG treatment: she crossed out whole sections, cut the paragraphs apart with scissors, and stapled and taped the pages back together. What emerged was a more compelling narrative that told the story in the most logical order, with exactly the right words.

I learned so much from Christine as a scientist and a person: how to construct a scientific hypothesis and follow its experimental arc, how to speak and write with clarity, how to persevere. She was bravely vulnerable. She soldiered through scientific and personal setbacks, savored her successes with her students, postdocs, beloved friends, and colleagues.

In the Guthrie lab, we experienced the intoxicating thrill of discovery mixed with tribulations, joy and laughter, fragility and mortality, the highs and lows. Christine was generous in revealing how to handle hardships as well as acclaim. All those jumbled pieces pasted together: she showed us the rich full narrative of life.

—Pratima Raghunathan

Christine was the most important teacher in my life. That's a lot to summarize in one short paragraph that will be read by strangers. I'll lean into two of the values I learned from Christine—communication and transparency—to get this done.

Most of what I have done well as a scientist and a mentor can be summarized as "doing my best to live up to Christine's expectations." Listening to Christine discuss branch site reporter assays of Prp8 point mutants in a lab meeting, I had the impression that she knew every snRNA crosslinking result ever generated. Her knowledge was deep. Models were revised and refined until they perfectly encapsulated what was known and called out what still needed to be done. As others have noted, she did not shy away from doing hard things. She modeled being openly afraid and doing it anyway.

This afternoon, one of my students is giving a practice talk. In proper Guthrie style, the whole lab will turn out to dissect the talk, ripping away anything disingenuous or superficial, taking it apart and putting the good pieces together again. We'll do this twice if we need to. I'll drink an iced latte in honor of Christine, and love my student with some brutally honest feedback and dedication to her growth and success.

Thanks for it all, C. I miss you.

—Wendy Gilbert

Tribute to Christine Guthrie

Christine's beautiful papers were one of the decisive factors that led me to join her group as a postdoc. When I arrived in 1995, Christine was in the middle of one of her several fights with cancer. Yet, her fortitude and ability to keep up with everyone's projects while receiving treatment was nothing but amazing. Christine's lab was full of very talented scientists, but she also managed to attract genuinely nice people who deeply cared for each other and liked to have fun. As an example, whenever a lab member would graduate or leave, students and postdocs would spend hours shooting and producing commemorative videos (the famous "One shot productions"). Although my stay in the lab was short (1995–1997), Christine had a major impact on my career and on the way I think about science. My most personal memory of Christine was a dinner with her in 2004; at the time I was an Assistant Professor, and she offered some very personal insights on the struggles of being a young Faculty in academia, and how to cope with these struggles. She will be sorely missed but she left behind an exceptionally strong offspring of scientists to the RNA community.

—Guillaume Chanfreau

I arrived as a postdoc in Christine's lab in 1997 as a protein biochemist and structural biologist, so I felt rather out of my depth in an RNA and yeast genetics lab. Nevertheless, I gamely started RNA work, and produced my first northern with enormous help from Pratima, probably using her extracts and certainly with her guidance at every step. I proudly showed it at my first lab meeting, whereupon John said, "Why are there so few samples on that gel?" Deflated, I was taken aside by Christine, who said something along the lines of, "That may have sounded harsh, but what John is trying to say is that every gel counts and you need to squeeze in as many experiments per day as you can."

This was the first of many scientific insights that Christine shared with me during my time in her lab, a time, I might add, in which she struggled repeatedly with health issues, but never lost her passion for us and the work we were doing. Where I had previously focused on technical skills, Christine taught me to think about the logic of the story and how the pieces fit together. Thanks Christine, for all of those lessons in the art and practice of science.

—Stephen Rader

Christine always demanded that we clearly define the question. It is amazing how hard this is to do for young scientists without practice. All my undergrads' talks include a BIG QUESTION slide, to the point that they make fun of me by choosing ridiculously large fonts. Importantly, this exercise in defining one's question translated or spliced over well to our career and personal lives. Christine often

asked of me, "What do you want?" when thinking about project directions and post-graduation steps. This prompted me to identify that I had always loved teaching and led me down the path to my dream job at a primarily undergraduate institution.

Christine's scientific curiosity, even in times of adversity, carries with me today. In 1992, when Christine underwent breast cancer surgery, I remember how she and John Abelson had the wherewithal to store away a sample of her tumor. Just in case. Notably, this was kept not in our minus eighty freezer, but Keith Yamamoto's, presumably because his was compliant with human samples. This was also a good idea so as not to get accidentally included in a yeast RNA prep or splicing extract experiment!

Christine's warmth continues to resonate. The first time I did chemo, Christine mailed me her chemo teddy bear to keep me company while sitting in the infusion chair. Soon "Pigs of Power," both literal and figurative, started pouring in from my friends and colleagues in the Guthrie Lab community. They are traditionally pig figurines that Christine gave us graduate students to bring with us to our oral exams to give us strength. Thank you, Christine, for developing and caring for us and cultivating our curiosity and power!

—Maki Inada

I still remember interviewing with Christine when I applied to graduate school at UCSF in 1999. She was interested in my undergraduate research about cell cycle checkpoints because it related to one of her favorite topics: how cells maintain fidelity. I left the interview feeling excited; here was someone who would care what I thought, and who would both challenge me and encourage me. Suffice it to say, I joined her lab the next year. In addition to her keen insight as a scientist, Christine had a knack for attracting good people to the lab and encouraging community among us. Some of my fondest memories of the Guthrie lab are of RNA Camp; each summer, Christine and John invited the members of their labs to their home in Idaho for a few days of boating, hiking, picking huckleberries, cooking good food, and discussing science. Whether we were in the lab or by the side of a lake, Christine nurtured us as both scientists and as people.

—Tamara Brenner

I was still a student at the beginning of my thesis when I saw a lecture by Christine at a yeast genetics course in Italy. I was completely fascinated by this tall, very stern-looking woman who was telling with enormous passion and incredible prose how much genetics could enable the understanding of such a complex machine as the spliceosome. I think that was the day I more or less consciously decided to try for a postdoc position in Chris's

lab. After an atypical interview during a meeting in Madison and her acceptance fax, a naive and freshly graduated student landed in an exceptional lab in 1999. Of Christine I will always carry the memory of a rigorous scientist, unabashed at times when criticism was needed, equally loving and attentive to the needs of us as people, not just scientists. In Chris's lab, students and postdocs were peers and equals to principal investigators, in burdens as well as honors. Chris was able to create a lab capable of being an incubator of excellent scientists, as serious and dedicated as she was, and a family where we could share moments of great bonding and fun, such as during the "One shot production" film shooting, or at the wonderful retreats at Priest Lake. Personally, Chris also supported me when I explored the possibility of leaving her lab to become a science editor, and she supported and spurred me on when I decided to continue at the bench instead, even offering me the invaluable opportunity to extend my stay in her lab and work together with John. What good times we had! What I am today as a scientist and my passion for communicating science both properly and clearly are a direct inheritance from the wonderful mentor that was Christine. Chris, you will be sorely missed by all of us, but your legacy will remain solidly with all who had the privilege of knowing you.

—Tommaso Villa

I once went to Christine for advice on what I at the time felt would be the greatest challenge in my academic life. Christine's reply was: "You know what the problem is. Good, now you just need to focus on learning how to do it." No pity, brutal honesty and said with a smile. At the time I probably did not fully appreciate the advice. Looking back, however, what encouragement when someone like Christine tells you that, of course, you can overcome any obstacle if you put your mind to it! Christine was the proof of that again and again in a fascinating but also extremely competitive research world. What a role model!

—Mette Lund

As I neared the end of my graduate studies in Olke Uhlenbeck's lab and contemplated where I would do my postdoctoral studies, I had grown accustomed to (and appreciative of!) the independence that I had to follow the scientific problems that most interested and intrigued me. And so as I interviewed for a postdoctoral position with Christine, one of the most important questions that I asked of her was whether I would have that freedom in her lab, to which she replied, with that wry smile of hers, something like "Sweetie, you don't have to worry about me ever telling you what experiment you should do." Of course, while her lab was not run in a "top-down" fashion,

during my time there she was nevertheless full of suggestions for what I should be doing (and often at a much faster rate!), and I will forever be grateful for the insights, guidance, and mentoring that she provided. Christine often talked about science as family, and I feel immensely lucky to have been a part of hers, and to have had her as a part of mine.

—Jeffrey Pleiss

I was a PhD student in Christine's lab from 2003–2010 and in many ways her model of how research should be done has profoundly impacted my views on science. She did not shy away from a question because it was hard, or because no one had yet invented the tools that were needed to tackle it. She did not choose approaches because they were popular or politically expedient. She wanted to put in the time and effort that was needed to achieve a deep understanding and convey it in an elegant story. Together, these habits do not always make for the easiest path, and Christine knew better than most that there is a cost to doing hard things. She was there to provide support to the people in her lab. She placed her true, genuine trust and confidence in us, which was an invaluable gift. I still can't believe that I can't go visit the next time I am back in San Francisco, but I will always carry things I learned from her with me.

—Megan Bergkessel

Christine brought us together. She created a scientific community that cherished the intellectual intensity of tackling a biological puzzle and arriving at a graceful solution. She created an extended family, opening her home to us for elegant celebrations in the city and for magical retreats in the Idaho wilderness. In a way, we were all her children—she encouraged; she was at times proud, at times less so; she cared deeply. It's too soon, too hard to imagine that the intensity and force of Christine has passed.

—Quinn Mitrovich

There are so many memories of my time in Christine's lab that it is hard to think of only a few to share. I was a postdoc in Christine's lab from 2004–2009, and I was lucky enough to be there at a time when John was also carrying out research in the lab. One of the first things that comes to mind when I think of Christine is how she would sit and draw with a notebook and an ultrafine sharpie during our weekly subgroup meetings; I marveled at her ability to create elaborate models from a few genetic interactions. One of the lab mantras that I learned during my time in the Guthrie lab, and I now share with my own research students, is to "do both" when deliberating which of the two possible next experiments one can try to move a project forward. Finally, I, like many others, will always

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fondly cherish the many wonderful memories from the “RNA camps” that she and John hosted each year at their cabin in Priest Lake, Idaho. Christine had a knack for bringing people together to discuss science and to enjoy life.

Christine was a great mentor and role model for me and for many, many other women in science. Her passion, creativity, tenacity and perseverance were awe-inspiring. She was always very supportive of her students and postdocs, no matter our chosen long-term career paths. She taught us all to be better scientists, educators, and communicators; I would not be the scientist or teacher that I am today without her guidance and support. She will truly be missed.

—Tracy Kress

I joined Christine’s lab as a postdoc, because she had an amazing ability to use genetics in a such keen way. Christine had high expectations, but she gave the resources to develop the skills needed to meet it. She applied a certain pressure with her “tick-tock” tap of her watch, but also showed patience when experiments stalled. Christine pushed me out of my comfort zone. She asked more of me than had been asked, but the challenge made me a better researcher.

Christine’s excitement toward new findings was contagious. In subgroup meetings, nothing would excite Christine more than new data. After looking at the new findings, Christine would ask only a handful of questions, but those questions would hit to the core of the problem. She also had an uncanny ability to identify the impact of any small finding on the entire field. Undoubtedly, a new idea would pop up from our subgroups, and I would be left to decide if it was something I wanted to pursue. Those decisions, and the freedom to make them, were part of my growth as a scientist.

Christine was a strong female role model for many of us. I remember Christine saying that she didn’t know how her current postdocs were managing being both moms and scientists. What she didn’t acknowledge is that she had built a community in her lab that was richly supportive. Christine had a unique ability to gather bright scientists together. That community persists even when you leave the lab. Thank you, Christine. You are missed, but you remain with all of us!

—Corina Maeder

Christine was my graduate mentor between 2007 and 2014, and what attracted me to her lab was her invitation to be thoroughly and honestly myself—whether I was struggling or excelling, she and her lab would support me through it. What I see more clearly, the longer I am in science, is her amazing clarity of thought and ability to tell a scientific story. As a graduate student, one of the

hardest things is to write your first paper—usually you start with the methods and results, and only once you’ve better understood what you have in front of you, fumble through an abstract and title. What sticks the most for me about Christine was her ability to take a blank manuscript and craft the final abstract and title, because she already knew and understood its essence. Christine continues to inspire me to this day, and I am grateful for the time I spent with her.

—Erica Moehle

I was a graduate student in Christine’s lab from 2007–2014, and she profoundly influenced my perspective on what it means to conduct scientific research. My first introduction to Christine was through a talk she gave, in which she painted this beautiful picture of how splicing, transcription, and export were interconnected in responding to different stresses. Only after I joined the lab did I learn that she had described work from several different projects, using her amazing ability to synthesize different ideas into one big picture. This insight was reflected in her mentoring: she would always ask “What’s your question?” or “What’s your model?” to push us to identify and investigate the key questions in our research and connect them to a bigger picture. I will also always appreciate her mentoring approach of allowing us to make the decisions about experimental design while guiding us to think about the important questions. She was also a master at creating a collaborative lab environment, where everybody was expected to explain their decisions (so even young graduate students were treated as equals), and each lab member became a resource for different aspects of technical and conceptual expertise.

—Argenta Price

When I think of Christine, I think of the power of her words. She was well-known for being an excellent writer and her edits to an abstract were always revelatory. The words she spoke were equally powerful and intentioned. When Christine said “Tick tock” to you in a lab meeting, it was of course meant to push you to work faster. But it also meant that Christine was excited to know your results. And that she thought that you were on the right path. One afternoon toward the end of my postdoc, I met with Christine to talk about what was next for me—I told her I was toying with the idea of jobs in editing or teaching. Christine gave me a very perplexed look and said “Oh really? You should be a PI; I think you’re good at this.” That sentence echoed in my head for months. Soon enough, I realized all the things that Christine meant when she said it. I’m where I am today in large part because of those words. Thanks for the push, Christine.

—Kristin Patrick

I was looking for a PhD home and after attending my first group meeting, I knew that I had found it. Christine led the group by allowing everyone in the room to share ideas and perspectives, then she would weigh in on how to move forward, oftentimes with more questions to the group. I felt confident in where she was leading us. She created an environment that was akin to an intellectual salon and taught me the aesthetic value of good ideas. She would always encourage me and pushed me to find ways to pressure test my more unconventional ideas. She supported me unequivocally when I had problems and we bonded because she was a wonderfully sensitive person. She is a beautiful person and will forever be a light that inspires greatness.

—Bellos Hadjivassiliou

Christine established an amazing environment that instilled independence in every one of her trainees at all levels. Somehow she knew when to provide crucial mentorship when needed for success. My research interests changed

while in Christine's lab, and I was fully supported and encouraged to pursue teaching experiences. This enabled me to move to a smaller undergraduate-only faculty position (PUI) after finishing my postdoc in her lab. I am forever indebted to her mentoring and support and use her model of mentoring when possible with my own students.

—Michael Marvin

I was Christine's last postdoc who, together with Anne, turned out the lights when the lab closed in 2018. I learned much from Christine and the Guthrie lab. Christine was a naturally gifted writer. Her edits on my work were minimal, but they immediately identified the crux of the problem—where my tone was off, where I was overcomplicating things—in such a way that it was immediately apparent how to fix it. I can hear her comments in my head as I write now. I wish I'd had more time to work with her.

—Megan Mayerle



Christine and her trainees at her 70th celebration. (Photo courtesy of Jeff Pleiss.)

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