



The extraordinary Atlantic silverside and me

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Abstract

My career is inextricably linked to the remarkable characteristics and astonishing insights provided by a simple yet elegant species, the Atlantic silverside, *Menidia menidia*. My initial field and laboratory studies provided the first demonstration of temperature-dependent sex determination (TSD) and its adaptive significance in fish, as well as the first empirical confirmation of frequency-dependent sex ratio selection. This early work then led to the discovery of countergradient variation in growth, evolutionary trade-offs associated with growth, pioneered the study of fisheries-induced evolution, and furthered our understanding of the spatial scale of local adaptation in marine species. Most of these topics are now vigorous areas of research encompassing numerous species and systems. Here I describe how these unforeseen discoveries were made and led to other findings on bluefish (*Pomatomus saltatrix*) and striped bass (*Morone saxatilis*). An interest in leadership during my early years was later rekindled as I took on administrative roles. It all began with an intriguing observation stemming from my MS thesis that I was compelled to follow. My career illustrates the value of exploring deeply the natural history of lesser-known yet easy-to-study species and to follow unexpected observations even if peripheral to a preconceived plan of research.

Keywords: *Menidia*; environmental sex determination; temperature-dependent sex determination; countergradient variation; fisheries induced evolution; coga-dient variation; sex ratio evolution; local adaptation; bluefish; striped bass

Introduction

This memoir is as much about the amazing characteristics of the Atlantic silverside (*Menidia menidia*) as it is about my career. Little did I know as a beginning graduate student in 1976 that the scarcely known yet abundant species I chose to study would point the way to phenomena now known to be widespread. The first of those discoveries landed me a faculty position straight out of graduate school. Many years later, I shifted to leadership roles at university and national levels. Why I decided to study *Menidia* and how lab members and I capitalized on this opportunity is the story told herein. I am deeply indebted to the numerous outstanding students, post-doctoral associates, and technicians who are the heroes responsible for most of this work, many of whom are named in the publications cited below.

Early life history

When I was 10 years old, my family went deep sea fishing off the coast of Miami, FL, USA. We were on the edge of the Gulf Stream on a headboat drifting ballyhoo as bait to catch dolphin-fish. There were huge swells and nearly everyone was seasick and lying in the ship's cabin, but not me. I was determined to catch fish. Suddenly I felt an incredible jolt, and, as line peeled off my reel, I clenched the rod and held on with all my might. About 30 min later, I landed a magnificent 46 lb. 6'1" Atlantic sailfish. I was awestruck. Anglers ardently seek sailfish, but they are usually landed by charter vessels using very sophisticated and expensive gear, surely not by some scrawny kid drifting bait. My dad was so proud that he had the fish mounted, and it has followed me ever since, and to this day it is on the wall of my home. Yet my future inspiration would

come not from an apex predator of the open ocean but from a small, ordinary, easy-to-catch, and ignored shore zone fish known as the Atlantic silverside.

I grew up in Homestead, a small agricultural town on the southern tip of mainland Florida, also known as the gateway to the Florida Keys and the Everglades. There I spent much of my youth on the water fishing and snorkeling with my brother, Michael (now a wildlife biologist at Utah State University). My father was a plant pathologist with the University of Florida Extension Service, and my mother was a botanist. My dad developed varieties of fruits and vegetables that were resistant to diseases prevalent in the subtropics. Local farmers who benefited from his work would often drop off produce at our house as a show of appreciation. I was impressed that research could make such a positive difference in people's lives. It seemed like applied science could be a career path for me.

In high school, I was involved in music, playing trombone in band, and singing tenor in chorus. Something prompted me to try out to be drum major of the marching band. Though not chosen, I was later selected to be the student conductor of the concert band and achieved a superior rating in the state contest. Judges highlighted my "determination to lead." Being a leader was becoming part of my identity and would recur later in my career.

Despite graduating as valedictorian of the South Dade High School class of 1971, I felt unprepared for college. This was the era of forced racial integration in the USA, and during my junior year, the nearby high school for black students was closed and merged into our nearly all white high school, which was unfortunately festooned with confederate imagery (nickname Rebels, fight song Dixie, icon confederate flag,

etc.). Integration did not go well. Riots on campus during school ensued, and, thankfully, the confederate symbolism was eliminated. Afterward, the emphasis shifted to keeping the peace as much as education. At our graduation ceremony, my valedictory address was not the usual “the future is ours” speech. Here was an opportunity to speak on behalf of the students. So, I boldly criticized the educational system that, in my view, had let us down. When I finished the speech no one applauded, which was in that moment terrifying. What had I done? Apparently, the audience did not realize that the speech had ended so the applause finally came only after I returned to my seat. Lesson learned: when giving a provocative talk, always have a strong and easily recognizable finale.

After high school, I wanted a non-traditional approach to education. I chose to attend Eckerd College, a small, then-fledgling, progressive, liberal arts institution in St. Petersburg, FL, USA. I liked that it was among the first colleges to experiment with courses involving independent study and to abandon letter grades in favor of written evaluations. I also liked that there were lots of hippies on campus. My major advisor was ecologist George K. Reid, and my first research experience was working on a US National Science Foundation (NSF) grant with John C. Ferguson, who was doing experiments to understand nutrient reserve dynamics during the annual life cycle of starfish (e.g. Ferguson 1975). My job was to run samples through a gas chromatograph. In my junior year, I devised and carried out my own independent research involving the geographic distribution of an isopod in Florida that was newly reported to be burrowing into the prop roots of the red mangrove, allegedly causing the demise of forests over large areas (Rehm and Humm 1973). In my very first career publication, I found that the prevalence of the isopod was spatially variable (Conover and Reid 1975). The red mangrove forests never collapsed.

I decided to apply for graduate school in marine biology but did not initially get into any of my preferred schools. Despite having a publication to my credit, my standardized test scores were only average and that was the main criterion for acceptance back then. Eckerd’s avant-garde approach to course evaluation did not help. The following year, I applied to schools with marine fisheries programs. I had success, in part, because of a professor who knew George Reid, a lesson in the value of the network.

Graduate school

In 1976, I entered graduate school in fisheries biology at the University of Massachusetts (UMass), Amherst. My initial advisor was James Parrish, an assistant professor who was starting up a new marine fisheries research program. He left UMass a year later and my advisor then became Michael Ross. My fellow graduate students included Bill Kelso, Scott McKenzie, Chris Gledhill, and Fred Sutter. We were all expected to develop MS thesis research involving coastal species. I planned to publish my thesis research and move elsewhere to pursue a PhD.

For multiple reasons, I chose to focus on the Atlantic silverside, *M. menidia*. Little was known about this small forage fish, with only a single publication summarizing its life history (Bayliff 1950). Yet *M. menidia* was one of the most abundant fish inhabiting salt marshes, embayments, and beaches throughout its range from northern Florida to Nova Scotia.

It was also extremely easy to sample. You could catch thousands of them wading from shore with a small beach seine in less than an hour! So, I figured almost any research I did would be publishable.

I was also attracted by the exceptionally simple, annual life cycle of the Atlantic silverside. Reproduction occurs in the spring, with juveniles growing rapidly in summer and fall and reaching adult size by the onset of winter, when an offshore migration was believed to occur. All individuals mature at age 1 upon return to the shore zone and virtually none reach age 2. Hence, *M. menidia* is truly an annual fish, and, even more interesting, it is the only annual fish in the entire western North Atlantic.

How an annual life history could evolve in *M. menidia* puzzled me. In a class on fish ecology, I wrote a term paper on life history evolution. It was inspired by Stearns’s (1976) review, which highlighted the contrast between the two principal theories at that time, i.e. r and K selection vs. bet hedging. Marine fish exemplified the bet hedging strategy (Stearns 1977). The argument was that many marine fish exhibited highly variable and unpredictable year-class success. Hence, life histories that involved delayed maturation and long reproductive life spans were favored because such strategies maximized the probability that an individual would experience at least one good year of reproductive success during its lifetime. How then does an annual life history strategy evolve in the highly variable western North Atlantic? I suspected there must be something unique about *M. menidia* that selects for an annual life cycle.

Another reason for pursuing research on the Atlantic silverside involved patterns of energy flow between salt marsh and offshore environments. In an annual species the entire biomass of a population turns over each year so its relative contribution to production in coastal waters could be large compared with longer-lived species. Moreover, if the presumed offshore migration could be verified, then the silverside could represent an unrecognized means by which salt marsh-derived production was exported to offshore communities. I designed a study that would increase our knowledge of *M. menidia* life history while also addressing the issue of energy flow.

As it turned out, I showed that the Atlantic silverside does indeed accumulate very high levels of biomass by autumn at our study site in Essex Bay, MA, USA (Conover and Ross 1982) and then migrates onto the continental shelf in winter (Conover and Murawski 1982). Only ~1% of the population returns to recolonize the shore zone as reproductively active adults the following spring. Hence, the *M. menidia* life cycle does represent the transport of energy from shallow water, near-shore environments, to the shelf. But it was an unexpected observation, unrelated to the offshore energy transport question, that proved to be pivotal to my career.

Discovery of temperature-dependent sex determination (TSD)

While conducting my MS thesis research, I carefully dissected and determined the sex of all juvenile *M. menidia* that I had collected as year classes recruited to the population during spring and early summer. I noticed that the sex ratio of the earliest recruits was highly female biased while that of late-season recruits was highly male biased. By the time that all juveniles had recruited to the population, the sex ratio ~1:1 (Fig. 1). This unusual pattern, which repeated itself over two separate

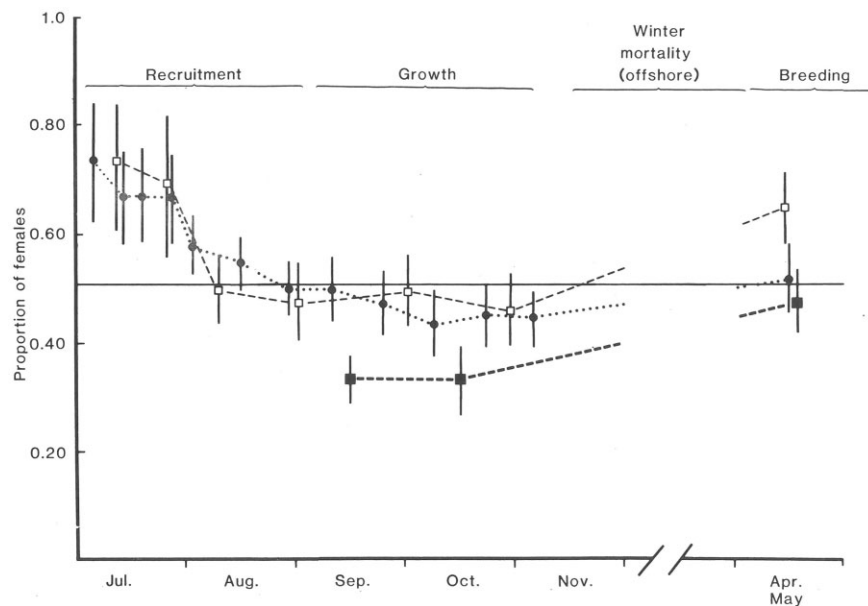


Figure 1 Variation in sex ratios of *M. menidia* during major periods its life cycle in Essex Bay, MA, USA. Since a life cycle is completed in 1 year, each year class represents a distinct generation: solid squares, 1976; solid circles, 1977; and open circles, 1978. Vertical lines indicate 95% confidence limits based on exact probabilities. Sample sizes range from 55 to 442 (mean, 255). The horizontal solid line represents a 1:1 sex ratio. From Conover and Kynard (1981).

years, could be explained in four ways. First, larvae destined to become female may grow faster than those that will become male and therefore appear sooner. Second, parents might be biasing the sex ratio of their offspring as the spawning season progressed. Third, there might be differential mortality between the sexes. Temperatures are much lower at the beginning vs. the end of the spawning season, e.g. so perhaps survival favors first females then males as temperatures increase from spring to summer. Lastly, an environmental factor might directly influence sex differentiation, such as low temperatures inducing female development and high temperatures causing male development. At the time, these four possibilities seemed equally probable because there was no precedent for any of them in the fish literature.

I was now faced with a crucial decision: move to another university for my PhD as originally planned or stay at UMass and do the experiments necessary to determine the explanation for the sex ratio pattern described above. Luckily, at about the same time, Boyd Kynard joined the UMass Fisheries faculty as a replacement for Jim Parrish and was fully supportive of my plan for further research on *Menidia*. He turned out to be a great mentor and his boundless enthusiasm and curiosity inspired me. I learned many things from Boyd, but two bits of his sage advice stood out: (i) choose a research topic that has the potential to make a “big splash;” and (ii) avoid doing “me too” research that simply verifies or replicates what others have done.

Another major influence on my research interests at this time was a course on evolutionary biology I took from an outstanding teacher at UMass, David Klingener, a mammologist in the zoology department. Afterward, I was determined to integrate evolutionary principles into my work and into fisheries science, although I did not yet know how.

My proposed doctoral research on *Menidia* fit the Kynard “big splash” criterion but it also was a huge gamble. There was no way of knowing whether I could deliver a break-

through, and if I failed, I would have done research on a species few people cared about. Despite the risk, I decided to stay at UMass but not without considerable angst along the way.

The first experiments were largely a failure. The plan was to rear embryos from the beginning, middle, and end of the breeding season at both low and high temperatures up to a juvenile stage beyond sex differentiation. Unfortunately, the experiments at low temperature were lost when the thermostat on the incubator seized and all the fish died. I did still get some interesting data from the high temperature treatment: the sexes grew at the same rate, and sex ratios in all three batches of embryos were similar and strongly male-biased. This outcome pointed to either temperature-dependent differential mortality or TSD. I had to wait another year to repeat the experiments, during which I had ample time to second guess my decision to stay at UMass.

In the following years, experiments proved that the answer was indeed TSD. Larvae reared at low temperatures typical of the early breeding season were female biased compared with those reared at higher temperatures. Thermal influence occurred only during a specific period of larval development when mortality was low, and gonads were undergoing differentiation. Our data also showed that sex is not determined purely by temperature but instead by a temperature \times genotype interaction. The Atlantic silverside thus became the first gonochoristic fish species in which TSD was demonstrated and the results were published in the journal *Science* (Conover and Kynard 1981).

At the time I discovered TSD in *M. menidia*, there were very few examples of any form of environmental sex determination (ESD) in other organisms. Only 2 years earlier was TSD conclusively demonstrated to occur in turtles in the wild (Bull and Vogt 1979). One year later, TSD would be reported in an alligator (Ferguson and Joanen 1982). There were also a few instances scattered across the invertebrates.

These cases and many others soon begged the question of whether ESD is merely phenotypic plasticity of a primitive sex-determining mechanism or an adaptive trait molded by natural selection and evolution.

Charnov and Bull (1977) proposed that ESD could be adaptive and would evolve when an offspring encounters an environment that affects its fitness differently depending on its gender. In short, if certain types of environments enhance the fitness of females more than males while other environments do the reverse, then selection favors the evolution of sex-determining mechanisms that match gender to the environment that maximizes relative fitness.

Life history data I had already accumulated on *M. menidia* enabled the first illustration of the adaptive significance of ESD as predicted by the Charnov/Bull model (Conover 1984): I showed that large size benefits the reproductive success of females more than males (fecundity increases more steeply with size in females). Individuals produced at the beginning of the spring spawning season will have higher relative fitness if they become female because they will experience a longer growing season and will therefore be larger as adults. Fish produced at the end of the spawning season are destined to be small as adults and will maximize relative fitness by becoming male. Temperature during larval development serves as a cue predicting the length of the growing season that an individual will experience.

The Science paper got widespread media coverage. I won a “best paper” award at a national conference, and I soon had job interviews on my schedule. I was especially pleased when George Streisinger, whose fame, among other achievements, derived from pioneering the use of zebrafish (*Danio rerio*) as a model organism, wrote me a personal letter thanking me for my discovery. In the same year as our work, he had published the first methodology for artificially cloning fish (Streisinger et al. 1981). But he was puzzled about why his zebrafish clones included both sexes. They should have been unisexual, as are naturally occurring clonal fish species, but he had not considered the possibility of ESD.

So, my gamble paid off. My work on a small fish had made a big splash. But I was not ready for how quickly this success catapulted me into a tenure-track faculty position.

Move to Stony Brook University

My first job interview in the spring of 1981 landed me a tenure-track position at the Marine Sciences Research Center (MSRC) of Stony Brook University. The chair of the search committee was Larry Slobodkin, one of the pioneers of modern ecology. During my job seminar, I mentioned that a goal of mine was to bring evolutionary thinking to bear upon fisheries science. Larry asked me how I was planning to do that. I gave a weak answer. Worse yet, I was so naive that I had not brought enough cash to cover my travel expenses, and I had no credit card (back then students could not qualify for credit). I had to borrow cash from the associate director to pay for the taxi back to the airport. I was sure my unpreparedness would count against me and soon I heard the job had gone to someone else (Jed Fuhrman). But a few months later I got a call from MSRC Director Jerry Schubel, who had wrangled additional funds to offer me a job.

With renowned faculty in ecology, evolution, and marine science, I knew Stony Brook would be an excellent university for me. It was a place where I could continue research

on *Menidia* and it had a marine seawater lab where I could do experiments. But the abrupt transition from the comfortable life of a graduate student to assistant professor on a 5-year tenure-track clock was jarring. I never expected things to progress so fast. I would have benefited from the additional experience a postdoctoral appointment would have provided.

I started at Stony Brook in the fall of 1981 before my PhD was officially awarded in 1982. Back then, there was little institutional support for junior faculty. My start-up package was \$1k and an empty lab. I was so inexperienced I had no idea you could negotiate such things! I was grateful to have a 9-month academic year appointment at a salary of \$19k (barely enough to pay for housing on Long Island) but beyond that I was starting from scratch. I had 5 years to prove worthy of promotion and tenure. It was sink or swim. Luckily, today new faculty hires start off with very generous salaries, start-up packages, and a mentoring plan.

Those early years at Stony Brook were an emotional roller coaster. I became engaged in the late fall of 1981, but then that Christmas eve, my father was killed in a car accident by a drunk driver, and I lost not only a dad but also a mentor. I was devastated and would not have made it without the support of my fiancé, who was completing her PhD in botany at UMass and would become my lifelong partner (Margaret Conover). We were married the following spring, and our two kids were born in each of the next 2 years. Starting a family was wonderful and so too having a job. But with the tenure clock ticking and a family to support, the pressure to achieve on an immediate time scale was intense and it triggered the imposter syndrome. Did my newfound professional success reflect my true capability or was it an illusion?

I was told that my pathway to success at Stony Brook was simple: acquire multiple external grants, use them to financially support multiple graduate students, and publish lots of papers in high impact journals. In the spring of 1982, I submitted my first grant proposal to the US National Science Foundation (NSF) on TSD in *Menidia*. I was so inexperienced in proposal writing and apprehensive about just getting my foot in the door at NSF that I asked for only 1 year of support with a total budget of \$58k. I fully expected it to be rejected as are most first-time NSF proposals (so I was told). As it turned out, NSF awarded my project at \$60k and made it a 2-year grant. While \$30k per year underfunded our annual expenses, this proposal was a rare instance in which NSF provided more funds than were requested. This was the beginning of continual funding from NSF over >30 years, for which I am eternally grateful. That continuity in funding was crucial in keeping my lab running through multiple long-term experiments that required daily attention (see below). Eventually, I did receive tenure and promotion partly due to the many NSF-funded discoveries that emerged from my years at Stony Brook.

Evolution of ESD and the sex ratio

While my hypothesis for the evolution of TSD described above was plausible, it fell short of proving that TSD is adaptive and not merely the plasticity of a primitive sex-determining system. I realized that validation might be achieved by comparing the sex ratio response to temperature among populations from different latitudes. Given the vast differences in temperature and length of the growing season that occur with latitude, the

response of sex ratio to temperature must be adjusted to local thermal regimes to achieve a locally balanced sex ratio. Otherwise, populations would be nearly all males in the south and all females in the north. Plus, selection favoring TSD should be greater in the south, where the spawning and growing seasons are longer than in the north, where these seasons are shorter, and temperatures are more variable.

To address this question, we launched the first of what would become many “common garden” experiments wherein offspring from different locations are reared in standardized environments so that genetic differences in phenotype can be revealed, a technique scarcely used in the fish literature at that time. Indeed, we found the proportion of females at any given temperature and the overall level of thermal influence on sex ratio was greatest at the lowest latitudes and declined at higher latitudes, including one of the northernmost populations (Nova Scotia) that completely lacked TSD. This was the first evidence that TSD is molded by natural selection and evolution in the wild and as such became a cover article in *Nature* (Conover and Heins 1987). Breeding experiments later showed how changes in temperature \times genotype interaction alter the level of thermal influence with latitude. The genetic component of sex determination is polygenic in southern populations, whereas northern populations display a segregating major sex factor, i.e. insensitive to temperature (Lagomarsino and Conover 1993).

Latitudinal comparisons were also instrumental in measuring the effectiveness of TSD in enabling females to be larger than males. We used otolith analyses to back-calculate hatch dates of juvenile silversides from three different latitudes (Conover 2004). At a low latitude location where the level of TSD was high (South Carolina), females' hatch dates were much earlier than males. The same was true but less so at a mid-latitude site (New York) with an intermediate level of TSD. There was no difference in hatch dates of males and females in the Nova Scotia population that lacked TSD. Correspondingly, the proportion of females increases steeply with size in South Carolina and New York but not in Nova Scotia, where both sexes are equally abundant among all sizes (Conover 2004).

There was still another fundamental evolutionary question that the Atlantic silverside could address. Why is a 1:1 sex ratio so common in nature? Theory predicts that frequency-dependent selection favors whichever sex is in the minority until a 1:1 balance is achieved. Yet this foundational principle of sex ratio theory lacked empirical confirmation. I realized we could test that theory by rearing separate lab populations of silversides at opposite thermal extremes during larval development, which would initially create highly skewed sex ratios, thereby triggering frequency-dependent selection in subsequent generations. The selection experiment involved five separate populations from three different latitudes subjected to opposite thermal extremes during the thermo-sensitive period over 8–10 generations. It took over 5 years to complete, including harrowing experiences with disease outbreaks and power outages, but the results were clear. Increases in the minority sex occurred quickly over subsequent generations until each of the initially sex-ratio-skewed populations achieved a balanced sex ratio. The level of TSD also declined. Thus, the Atlantic silverside provided the first empirical demonstration that frequency-dependent sex-ratio selection drives the evolution of 1:1 sex ratios and the underlying sex-determining mechanisms. Moreover, it does so rapidly in response to cli-

mate change, demonstrating that at least some species with TSD can evolve in response to global warming. The uniqueness of this study again warranted publication in *Science* (Conover and Van Voorhess 1990; see also Conover et al. 1992).

I was honored to become the first visiting Mote Eminent Scholar in Fisheries Ecology at Florida State University and used this opportunity to study TSD in *M. peninsulæ*, which replaces *M. menidia* as the dominant silverside along the east and west coasts of Florida. Surprisingly, this species has the opposite latitudinal pattern to that of *M. menidia*: only the northernmost population of *M. peninsulæ* displays TSD (Yamahira and Conover 2003) while southern populations produce a 1:1 sex ratio regardless of temperature. This observation makes sense in terms of adaptation because spawning and growth occur continuously throughout the year in the southernmost populations of *M. peninsulæ* and therefore would derive no adaptive advantage from TSD. Only the northernmost population has distinct spawning and growing seasons. Hence, across the combined range of these two species, TSD is absent or minimized at the latitudinal extremes and maximized at intermediate latitudes, strongly implicating seasonality rather than temperature as the agent of selection driving the evolution of TSD.

There are now many examples of temperature influencing sex determination across diverse fish taxa (Conover 2004, Kitano et al. 2024). Other environmental factors such as pH and photoperiod are also known to affect sex determination in certain species (Brown et al. 2014, Renn and Hurd 2021). There has been an explosion of studies on the genomic and molecular bases of sex determination, largely driven by the desire to manipulate the sex ratio of fish used in commercial aquaculture. Numerous review articles exist for those who wish to explore this literature (e.g. Yamamoto et al. 2019, Kitano et al. 2024). Based on current knowledge, *M. menidia* so far remains unique among all fish in two major respects: (i) it exhibits dramatic among-population variation, from almost complete TSD to purely GSD; and (ii) it is the only fish species in which the adaptive significance of ESD is understood.

Discovery of countergradient variation

In the common garden TSD experiments described above, we reared fish from all latitudes at standardized temperatures, fish densities, and with continuously unlimited food. We expected growth to be standardized accordingly. We were shocked to find that the fish from more northern latitudes grew much faster. Moreover, in our field collections, we were puzzled about why at the end of the growing season fish at all latitudes were about the same size. Other species along the east coast show the same pattern (Conover 1990). How could this be when temperatures are lower and growing seasons shorter with increasing latitude? This is how I stumbled upon countergradient variation (CnGV), a counterintuitive phenomenon that dramatically changed our understanding of how organisms adapt to climate.

CnGV occurs when genotypes are distributed in nature such that the genetic and environmental influences on phenotype oppose one another across a spatial or temporal gradient (Conover and Schultz 1995). In the case of *M. menidia*, fast-growing genotypes are found in northern environments where lower temperatures and shorter growing seasons would

otherwise depress the rate of growth. This spatial pattern of genotypes in nature almost perfectly counteracts environmental influences such that adults are of similar size at all latitudes (Conover and Present 1990). Because CnGV creates phenotypic similarity in nature, it represents a form of cryptic genetic variation that at the time was largely unknown. The opposite of CnGV is cogradient variation (CoGV), which occurs when genotypes that code for a phenotypically plastic character tend to occur in environments that shift the character in the same direction. In silversides, e.g. genotypes that code for more vertebrae are found at northern latitudes, where lower temperatures also tend to cause higher vertebral counts (Billerbeck et al. 1997).

CnGV in growth was surprising because it conflicted with the prevailing view that organisms at different latitudes would adapt to the change in mean temperature with latitude (Lonsdale and Levinton 1985). Were that the case, northern fish would grow faster than southern forms at low temperatures, but southern fish would grow faster than northern fish at high temperatures. In other words, performance in one temperature regime trades off against performance in another, representing a genotype \times environment interaction. But that's not what our results showed. Instead, northern silversides have accelerated their rates of growth across all temperatures but especially at the higher end of the temperature range (Conover and Present 1990), and this enables northern silversides to grow to adult size in only a 3–4 month period. As with TSD, CnGV in *Menidia* therefore represents an adaptation to variation in length of the growing season, not temperature (Conover 1992, Yamahira and Conover 2002).

Adaptation to seasonality rather than temperature is also important because it has major implications for how we think about the consequences of contemporary climate change. Models typically focus on the effect of higher temperatures on physiological processes, but our work suggests that for organisms living in the temperate zone, it is changes in patterns of seasonality that will drive evolutionary responses to climate change.

The existence of CnGV in growth of Atlantic silversides begged explanation. Why do not northern fish simply grow slower and take longer to grow to adult size? The answer is a latitudinal gradient in size selective winter mortality (Conover 1992). In northern populations, only the largest young-of-the-year survive the winter (Munch et al. 2003). This occurs because, like many warm-water temperate fish, silversides rely primarily on lipid reserves as an energy source in winter, and larger fish enter the winter with higher weight-specific lipid content and they burn energy at a lower weight-specific rate (Schultz and Conover 1997). Making it through the winter is an enormous challenge for the northernmost silversides, which must gain enough energy during a 3–4 month summer to make it through an 8–9 month-long winter, including the energetic cost of an offshore migration to the continental shelf (Schultz and Conover 1999). In fact, northern populations typically experience a 99% overwintering mortality rate (Conover and Ross 1982). Hence, at high latitudes there is very strong directional selection on body size every generation in winter, which selects for genotypes that grow very fast in summer.

Yet an enigma remained. Why would southern silversides grow at rates much slower than they can evolve? If southern silversides, throughout their 10-month growing season, grew at maximal rates like those of northern fish, they would at-

tain twice the size that they do (Munch and Conover 2002). Since instantaneous mortality rates in general tend to decrease with size, why would anything but the maximum growth rate evolve? This paradox became even greater when we found that northern silversides grow faster by consuming more food and converting it into tissue more efficiently (Present and Conover 1992), and we could initially find no trade-offs associated with this increased capacity (Billerbeck et al. 2000). Northern fish also store more energy before winter (Schultz and Conover 1997) and as adults produce greater quantities of eggs than their southern conspecifics (Conover 1992). All these traits should be positively associated with fitness. There must be tradeoffs associated with rapid growth but there was scant evidence of it in our work or in the literature.

Many experiments later, we found the answer. Fast-growing silversides suffer from energetic constraints that reduce swimming ability and increase predation vulnerability (Billerbeck et al. 2001, Lankford et al. 2001). This occurs because northern silversides devote a much larger fraction of their metabolic scope to the cost of food processing and tissue synthesis (Arnott et al. 2006). Respiration rate increases dramatically immediately after a meal is consumed and remains elevated for several hours thereafter. During this period, swimming performance declines for all fish but more so for northern silversides, reflecting the cost of processing larger meals with higher efficiency. Even when not feeding, fast-growing northern silversides display lower swimming performance than southern fish, as do fish within both populations that have been phenotypically manipulated to grow fast or slow. As a result, fast-growing fish are more vulnerable to common predators (Munch and Conover 2003). The tradeoff is non-linear with respect to meal size and growth rate (Munch and Conover 2004): it's only when a critical threshold is exceeded that the decline in performance occurs.

CnGV in growth is also reflected in risk-taking foraging behavior. Fast-growing northern genotypes are bolder and more willing to forage for and consume food in the presence of a predator than are the timider southern fish (Chiba et al. 2007). Similar results were found when comparing silversides that were artificially selected for fast vs. slow growth, thereby confirming risk-taking foraging behavior is genetically correlated with intrinsic growth rate.

These studies collectively show that growth rate evolution is a balance between competing sources of selection. Size-selective winter mortality is the overwhelming source of selection at high latitudes. Only genotypes that grow extremely fast will survive the winter. At lower latitudes other sources of selection such as predation favor genotypes with a more conservative growth rate.

Finally, while the Atlantic coast of North America is one of steepest latitudinal temperature gradients in the world, the Pacific coast is quite the opposite (Baumann and Doherty 2013). We used this contrast to show that the magnitude of phenotypic and genetic change with latitude is scaled to steepness of the gradient. Along a similar range of latitudes along the US Pacific coast, the topsmelt silverside (*Atherinops affinis*) displays CnGV in growth and variation in vertebral number but only about half as much as for *Menidia* on the east coast (Baumann and Conover 2011, Baumann et al. 2012), thus confirming that CnGV is driven directly by differences in climate.

Menidia menidia was the first fish in which CnGV was demonstrated (Conover and Present 1990). At that time, the main examples were body size in *Drosophila* (Levins 1968) and development rate in frogs (Berven et al. 1979), both involving altitudinal gradients. There are now numerous examples of CnGV and CoGV in many taxa involving various traits across multiple types of ecological gradients. About 25 papers per year appear on this topic (Web of Science). Reviews of this literature include Conover et al. (2009), Albecker et al. (2022), and Sparks et al. (2022).

Fisheries induced evolution

It was thrilling to have made major discoveries about TSD, sex ratio evolution, CnGV, and the evolution of growth by the midpoint of my career. My work was having an impact in the realms of ecology and evolution, but my long-held goal of applying an evolutionary perspective to fisheries management had not yet been met. I knew another “big splash” was needed to illustrate the potential for rapid evolutionary change in response to fishing.

The lack of attention to evolutionary consequences of harvesting was not because the issue had been ignored. There were some pioneering studies and a book entitled “The Exploitation of Evolving Resources” (see Stokes et al. 1993 and references therein), but these were not garnering much attention, at least in part because growth and other physiological traits were viewed as being so plastic in response to the environment that any genetic variation would be swamped. Moreover, evolution was still largely viewed as requiring time scales much longer than those of management.

CnGV in growth of silverside fish across latitudes stood in stark contrast to this viewpoint. I started with a thought experiment. What would happen if a fishery was imposed on northern populations of silversides (they are harvested as bait) with minimum size regulations that encouraged the harvest of large fish? Local populations would likely collapse because the fishery would be removing the fish that had the best chance of surviving the winter. What if something similar—i.e. harvest selection opposing natural selection—occurred in other fish?

An empirical demonstration that would command the attention of both fishery theorists and managers was needed. Having successfully done a multi-generational selection experiment on sex ratio, we designed a new selection experiment that would show (i) if size-selective mortality was in fact the agent of selection driving the evolution of CnGV in growth and (ii) the impact on yield of rapid evolutionary responses to size-selective harvesting, later to become known as fisheries-induced evolution (FIE).

The experiment involved six separate captive populations subjected to either large, small, or random size-selective harvest of adults over five generations, followed by another five generations where size-selective harvest was relaxed on all populations. The results, published in *Science*, were dramatic (Conover and Munch 2002) and received much media coverage. Harvested biomass evolved rapidly in directions opposite to the size-dependent force of fishing mortality. These shifts were caused by selection of genotypes with slower or faster growth rates and a suite of correlated physiological (Walsh et al. 2006) and behavioral traits (Chiba et al. 2007) that mimicked natural latitudinal variation. When selection was relaxed, there was evidence of a partial reversal of the changes

wrought by size-selection (Conover et al. 2009). Later, we collaborated with Nina Therkildsen and Steve Palumbi to track genomic changes in protein-coding genes that occurred during the experiment. Allele frequency shifts in the lab were like those observed in the wild across hundreds of unlinked variants, a result that also warranted publication in *Science* (Therkildsen et al. 2019). Size-selection in the lab recapitulated variation in the wild at both the phenotypic and genomic levels, thus confirming that our experiments were realistically simulating patterns in nature.

The publication of our initial results (Conover and Munch 2002) did indeed make a big splash judging from some of the positive and negative reactions that followed. Critics claimed that our experiment was not relevant to real fisheries (see Hilborn 2006, Brown et al. 2008; and our counter response in Conover and Munch 2007, Conover and Baumann 2009). Subsequent work has proven otherwise. Our timing was good because independent research on rapid, contemporary evolution was blossoming simultaneously in multiple fields (Palumbi 2001, Stockwell et al. 2003), and the development of probabilistic reaction norms for detecting evolutionary changes in age at maturity coincided with our work (e.g. Olsen et al. 2004). These collective works led to an explosion of research on FIE and there is now a voluminous literature with Conover and Munch (2002) among its most cited papers. Evolutionary thinking is now integrated into fisheries science and continues to blossom.

Spatial scale of local adaptation

The Atlantic silverside has also provided new insights regarding the spatial scale of local adaptation. The need to understand the geographic structure of populations within a species (i.e. its phylogeography) has long been recognized. These distinct homogenous units of a species provide a spatially explicit basis for managing fisheries and conserving genetic variation. It was believed that absence of gene flow among locations is what enabled genetic differences among populations to arise, and, therefore, comparison of genetic markers neutral to selection was the method of choice. However, it is preservation of adaptive genetic variation, molded by selection, that should be the goal of conservation (Conover et al. 2006). What if the geography of neutral genetic variation is not an accurate proxy for the spatial distribution of adaptive genetic variation?

Menidia menidia is continuously distributed along the east coast of NA with no barriers to gene flow and studies of neutral genetic variation suggest homogeneity across much of its range (Johnson 1974, Mach et al. 2011), yet there is tremendous adaptive genetic variation. How is it maintained despite gene flow? To address this question, we first used otolith chemistry as a physical marker to show that the offshore winter migration causes mixing of fish from adjacent latitudes along the east coast with little evidence of site fidelity to the estuary of origin (Clarke et al. 2010). Then, to measure the spatial scale of local adaptation, we performed a massive common garden experiment involving 39 sites drawn from the 3000 km range of *M. menidia*. Not only was there significant genetic variation on extremely fine scales, but also each trait we measured (TSD, growth, rate, and vertebral number) varied in a unique clinal pattern (Hice et al. 2012). Clearly, gene flow does not prevent adaptive genetic variation nor does it cause each adaptive trait to have the same geographic

pattern. At the genomic level, Wilder et al. (2020) found that latitudinal adaptation involves strong signatures of divergent selection across a gradient of neutral differentiation, i.e. across its distribution. *Menidia menidia* displays very low genome-wide differentiation (median $F_{ST} = 0.006$ across 1.9 million variants) consistent with high connectivity, yet there is near fixation of opposite alleles across hundreds of genes. Lack of concordance between the geography of neutral and adaptive genetic variation illustrates the difficulty of defining evolutionarily significant subunits of a species for conservation purposes.

Other research pursuits

Recruitment dynamics of bluefish

Bet-hedging is not just for fish. It can also be a career strategy. Soon after arriving at Stony Brook, and not knowing how far silversides would take me, I looked for gaps in our knowledge of other species that were important to New York. At the time, the bluefish (*Pomatomus saltatrix*) was the top recreational species in terms of US landings and a key piscine predator. With government agencies then mostly focused on commercial species, I surmised that the bluefish was “the most important species we knew the least about.” That catchphrase helped get my first bluefish proposal funded.

Like the silverside, two unique features of the bluefish life history attracted my interest. First, spawning occurred near the edge of the Gulf Stream in the South Atlantic Bight (SAB) in the spring and again in summer in the Middle Atlantic Bight (MAB; Kendall and Walford 1979). Multiple waves of juveniles recruited to near-shore New York waters in the summer. Connections between spawning and recruitment locations were speculative but no other species was believed to use the northward flowing Gulf Stream as a mechanism to disperse offspring from the SAB to the MAB (although strays from other species occur). Second, *P. saltatrix* was the only species known to grow so fast that it entered the recreational catch as 4–6-month-old young-of-the-year (YOY).

We started by initiating a field sampling program on the south shore of Long Island to track the arrival of juveniles and used otolith analyses to back calculate birthdates. Results showed two waves of recruits that represented offspring from the SAB to MAB spawning seasons (Nyman and Conover 1988) but with considerable interannual variability in relative abundance (McBride and Conover 1991). A 20-year research effort to understand the recruitment dynamics of bluefish ensued.

Subsequent research made a connection to silversides. The incredibly fast growth of YOY bluefish is fueled by a switch in their diet from zooplankton to fish immediately after larval development. Couple this with the fact that they move inshore just when the abundance of larvae and juveniles of inshore species like silversides are beginning to peak (Juanes et al. 1994). The timing is crucial because capture success for YOY bluefish is much higher on smaller sizes of prey (Juanes and Conover 1994). Hence, spring-spawned bluefish use advection from the SAB as a tactic to get a head start on the growing season of their principal prey in the MAB (Juanes and Conover 1995). Moreover, YOY bluefish have remarkably high food consumption and digestion rates (Buckel et al. 1995). Accordingly, predation by YOY bluefish has a direct impact on the abundance and mortal-

ity rate of YOY anadromous fish in estuaries (Buckel et al. 1999a) and other species on the continental shelf (Buckel et al. 1999b).

CnGV and winter mortality in YOY striped bass

Two major studies involving striped bass (*Morone saxatilis*) emerged from our work on silversides. First, we showed that CnGV in growth occurs in striped bass along the NA east coast (Conover et al. 1997), and this has potential implications for selecting fast-growing strains for use in aquaculture (Kenter et al. 2018). Second, we explored the impact of size-selective winter mortality on recruitment of YOY striped bass. Indices of year-class strength in striped bass are generally assessed by sampling YOY abundance at the end of summer yet overwinter mortality can dramatically alter year-class strength. We found that the size-dependent allometry of energy reserve storage in YOY prior to and energy depletion during winter interact with the severity of winter to determine overwinter survival and thereby year-class strength (Hurst and Conover 1998, 2002). The impact of winter mortality on recruitment variability is now widely recognized in numerous systems (Hurst 2007).

Keys to success in research and mentoring

Before moving on to discuss my career in administration, I want to summarize some lessons learned about success in research.

Making discoveries

I have had the good fortune to publish several papers in premier journals like *Science* or *Nature*. Such journals mostly publish first-time discoveries or those that upend current dogma. People sometimes ask me what is your secret? Part of the answer is I studied a species with a remarkably simple life cycle that was highly amenable to a deep understanding of natural history through long-term field and lab-based research, and which also turned out to have some amazing characteristics. Beyond silversides, here are some general ideas about doing cutting-edge research that should be universally applicable.

Pursue curious observations

Do not neglect observations that have no obvious explanation or were not what you were expecting. Be willing to adapt your program to follow unexpected leads. In so doing, you might discover something unknown to science.

Read the literature to find knowledge gaps

Being aware of new discoveries and emerging technologies is critical in placing your work in a larger context, but what you glean from the literature matters. The goal is not to emulate or copy what others have done but to identify gaps. What pieces of the puzzle are missing? Once new advances are made, such as TSD, CnGV, or FIE, attention often shifts toward that topic. When that happens, if you want to publish research in top journals, it may be time to move on to new horizons and let others fill in the details. I could have focused my whole career on sex determination, but I preferred to shift to other unexplored topics.

Connect observation to theory

Empirical results have greatest value when they support or refute the predictions of theory. There are two ways of doing so. Some people start with theory and then find a species or system that can provide the critical test. But it can also be done the other way around. I strove to deeply understand the natural history of silversides and then found theories lacking confirmation that my system could address. Keep both pathways in mind.

Experiments are powerful

Well-designed and executed lab and/or field experiments attract attention because they produce empirical results that are incontrovertible within the context in which they were conducted. This is the reason the Conover and Munch (2002) selective harvesting experiment succeeded in drawing attention to the problem of FIE when prior analyses based on modeling and theory did not. Experiments delivered nearly all the discoveries we made, especially common garden experiments, which are now quite common.

Mentorship

A key factor in my success has been the numerous excellent graduate students and postdocs with whom I have worked. Making scientific discoveries is exciting, but there is no bigger thrill than to see a timid, beginning student transform over a few years into a seasoned scientist who leaves the lab believing they are smarter than I am. When that happens, my job as advisor is done, and we become collaborators. Two philosophies guided my mentorship. First, I used a team-based approach, which meant that everyone had a responsibility not just for their own project but to pitch in and help everyone else. This included field sampling and helping maintain fish cultures on weekends and holidays. We all learned from each other's research, including successes and failures along the way, and the camaraderie helped attract prospective students into the lab. Second, I tried to align a student's thesis project with their skills and career goals and to treat all my students as equals regardless of their talent or aspirations. In fact, only a few lab members followed my pathway into academia. Most went on to do important work for public agencies or the private sector. I am equally proud of all of them.

Transition to dean

Few university academicians move from a successful research career into administration, and those who do are often viewed with skepticism by peers. Why would anyone want to leave the comfortable and fulfilling life of a tenured college professor and move to the "dark side" of university administration?

The appeal of leadership that emerged during high school was rekindled when a search was launched for the dean's position at the Marine Sciences Research Center (MSRC) of Stony Brook in 2002. Having had success in acquiring grants, publishing papers, and teaching and mentoring graduate students, I had the mid-career itch to take on a new challenge. Plus, I had a vision about how to expand our mission and raise our profile as the only state-supported marine science center in New York. I was offered the dean's position and began my term in 2003.

The transition from a faculty or research scientist role to organizational leader is a sea change. The talents and skill set

needed to excel as a leader are vastly different from those of a professor. As an advocate for science, e.g. you must develop a new language for communicating with those outside your expertise, especially the public. Doing so requires overcoming "the curse of knowledge," i.e. the tendency for experts to forget how to talk without jargon in terms non-experts can understand. In short, when advocating for science, try not to sound like a scientist.

I benefited from two different leadership training activities offered by the State University of New York and the Aldo Leopold Leadership Fellows program. I also recommend "The Contrarian's Guide to Leadership" by Steven Sample (Sample 2002), a former president of the University of Southern California. Sample emphasizes the importance of developing your own administrative philosophy. Two points stood out. First, know how you will measure success. During my first 20 years at Stony Brook, e.g. I noticed that the true mark of successful leaders was not what they did while in office but whether the initiatives they launched were sustained and thrived after they left. This requires gaining acceptance and transferring ownership of ideas to the people you serve. Second, when your principles are compromised as they often will be, "know what hill you are willing to die on." I relied on this advice multiple times in the years that followed.

The role of a university dean is the epitome of middle management. You are sandwiched between the faculty and senior leadership, who often do not share the same point of view. To succeed, you need to be a trusted communicator up and down the ladder, which means your integrity is paramount. Before making decisions, listen to all points of view and resist the temptation to see issues as black or white. There will always be people who disagree with you, but it's crucial that all voices know they have been heard. Also, be consistent on where you stand on the issues that matter to people because this is what builds trust.

During my 7-year term as dean, one opportunity stood out as both the most challenging and impactful. In 2004, Long Island University decided abruptly to close its Southampton College campus on the south shore of Long Island and asked MSRC to adopt its undergraduate marine science program. Knowing that Stony Brook at that time was focused on improving undergraduate education, this seemed like a golden opportunity for MSRC to expand into the baccalaureate realm, but we lacked the waterfront teaching facilities to do so. Working with a faculty planning committee, we proposed to SBU campus leadership that we should acquire Southampton's waterfront campus and use it to support marine science but also to create a bold, new undergraduate college focused broadly on environmental sustainability. The president loved the sustainability concept and immediately took full ownership of it, soon thereafter marshalling the resources to purchase the residential campus. Meanwhile, I lobbied successfully for funds to build a new marine laboratory there on the Southampton waterfront. Almost overnight, MSRC was transformed from a purely graduate research center to a comprehensive School of Marine and Atmospheric Sciences (SoMAS).

I was eventually asked by the president to head the new sustainability program. Working with our faculty, we developed a plan to immediately hire a core of leading tenured faculty in sustainability who would take up residence on and ownership of the new college. The president told me that was a terrible idea. She wanted to pursue a less expensive option of

hiring temporary adjuncts and directing things from the main campus, which in my view would leave the new sustainability program in a vulnerable position. We were at an impasse. I had to decide what hill to die on. When you are in middle management, it is extremely hard to decline a request from senior leadership, but sometimes you must. The president found someone else to lead the new campus although I remained in charge of marine science. It was disappointing for me personally but, sure enough, a few years later, severe state budget cuts forced the next SBU administration to shut down much of the Southampton campus (but not marine science) and move the sustainability program to the Stony Brook campus. In the end, it worked out well. SoMAS continues to thrive on both campuses and is now the permanent home for the sustainability program.

By virtue of my Aldo Leopold training, I developed a new passion for science communication, which led me to work closely with the dean of Stony Brook's School of Communication and Journalism, Howard Schneider, to help him found the Alan Alda Center for Communicating Science. The opportunity to work alongside Alan Alda to facilitate training sessions for graduate students and workshops at Brookhaven National Lab and Cold Spring Harbor are memories I will always cherish. Coincidentally, both of my kids pursued careers in the knowledge communication realm. Emily Conover is a physics journalist for Science News and Adam Conover is a professional comedian who uses humor to convey knowledge.

Director of ocean sciences at NSF

I loved my 7 years as dean of SoMAS but I again felt the urge for a new challenge. When the chance to become the Division of Ocean Sciences (OCE) director at NSF arose, I embraced it for multiple reasons. Nearly all of my funding for research on *Menidia* came from OCE and I wanted to give back to an organization that I depended upon and admired. I also wanted experience outside of academia in a key federal science agency that would broaden my knowledge of ocean sciences and the interface between science and policy. The timing seemed right. It was the early years of the Obama administration when scientists, rather than politicians, were being appointed to head federal science agencies, and there was much enthusiasm about making progress on ocean policy. I accepted the position as a rotator, which meant I was on leave from Stony Brook while being a term-limited employee of the federal government.

I began as director of OCE in July of 2010, and two unprecedented events that occurred that summer demanded my immediate attention and would continue to do so throughout my nearly 4-year term. The first was a massive oil spill, which resulted from the blowout of the Deep Water Horizon oil rig in the Gulf of Mexico on 20 April 2010. I represented NSF on an interagency task force that was mobilized in response to this catastrophe. NSF's key role was to enable researchers to quickly get into the field. We did this by repositioning research vessels in the Gulf of Mexico, allowing Principal Investigators (PI) with existing grants to reprogram their work plans, and by issuing numerous "Rapid Grants," which require only a few days to process. This team effort among NSF program officers made these things happen at lightning speed and it was gratifying to be part of it. There was huge media coverage of this event and, after the well was capped, much public attention was focused on ecosystem recovery. Soon NSF-funded PIs

were holding press conferences to discuss initial findings, but what they reported was not always in line with the official government position. I remember being asked at a task force meeting if NSF could manage what our PIs said to the press. I explained politely that, no, they are supported by grants, not contracts, and they have academic freedom. This encapsulates a vital difference between NSF and many other federal agencies.

The second major event of 2010 was the signing of an executive order by President Obama on 19 July 2010, creating the framework for what became the US National Ocean Policy (NOP). One of my first duties was to attend the official announcement and then, over the ensuing years, to be the NSF lead on the interagency committee tasked to create an implementation plan. An important accomplishment of NOP was to bring together all the federal agencies that operate or play a role in ocean research or policy to coordinate efforts and engage in strategic planning. Throughout our work, the Gulf oil spill served as a vivid reminder of why such interagency harmonization was needed. Interagency coordination is now accomplished by the Ocean Policy Committee, which traces its roots back to the original NOP.

The biggest challenge I faced as OCE director, however, was not about policy. It was about budget. The core mission of OCE is to fund ocean science through investment in shared-use infrastructure and grants to individual PIs (via a home institution) to directly support the costs of their projects. A division director's challenge is to allocate funds across the many programs that need support and to get input on and communicate with the scientific community about our decisions. When I arrived at NSF, there were increasing demands for OCE to support more infrastructure, i.e. build more ships, expand ocean drilling, revitalize submersibles, and pay for the cost of operating a massive new real-time ocean observing system into future base budgets. The large institutions that benefited from the contracts to operate this equipment were especially vocal, but the proportion of the total OCE budget devoted to infrastructure was already going up rapidly and destined to exceed 50%. Conversely, the budget allocated to support individual research grants was decreasing, yet principal investigators did not have a collective voice. To make matters worse, OCE had been opaque about the problems it was facing.

I realized that action must be taken early during my term in office. I had not created the budget problem but if I avoided it, I would become party to it. The first thing I did was to be transparent about the crisis faced by OCE. I openly discussed the problem at town hall meetings across the USA and I asked for ideas about solutions. Soon a group of directors of the leading oceanographic institutions, including Mark Abbott and Susan Avery, met with me to advocate for a decadal survey for renewal of the fleet. I liked their idea of a decadal analysis, but it needed to be about more than just vessel construction.

I developed a decadal survey design that would assess the current state of ocean science knowledge, define the research priorities for the coming decade, and identify the needed resource investments. But I added a twist. The plan must assume that the OCE budget over the coming decade would not increase over inflation. Difficult trade-offs would have to be made. This was a departure from previous US ocean research priority planning efforts where costs were unconstrained and therefore produced an unattainable wish list.

OCE contracted with the National Research Council (NRC) to put together a diverse blue-ribbon panel of leading scientists to conduct the survey. People warned me that the effort would fail because it is impossible to get 20 members of the community to agree on priorities under a restricted budget. Luckily, they were wrong, and the resulting plan (National Research Council 2015) became the guiding light for OCE covering the years 2015–2025. In fact, it was so successful that a new decadal survey for the years 2025–2035, also administered by the NRC, is now in progress.

Towards the end of my term at NSF, the president of Stony Brook University asked me to return and step in as interim vice president for research. I agreed to do so and eventually moved to a similar role at the University of Oregon, where I am now an emeritus professor. In each of my four senior administrative roles, I have been challenged to grow in numerous ways but, most importantly, in being stretched to encompass a wider range of disciplines. This broadening of perspective near the end of my career harkened back to where my education started in the liberal arts as an undergraduate. Reconnecting to a wide array of disciplines was an unexpected benefit of being a university administrator.

At many institutions, good senior leadership is a gap yearning to be filled because few are willing to take this step. For me, it has been an extremely rewarding experience, but the satisfaction derived from serving others must come from within. Unlike research, which is forever memorialized via publication, there is no certainty that your administrative accomplishments will be cited or remembered by others in the future. Instead, your legacy is determined by whether the initiatives you developed are carried on by others after you leave. Leadership is like running a relay race. You pick up the baton from your predecessor and run with it until it is time for you to pass it on. You want your successor to seize that baton and continue moving forward. My satisfaction comes from knowing that the initiatives I championed as Dean, NSF Division Director, and research VP continue to thrive.

Concluding remarks

How fortunate I was to have chosen the Atlantic silverside for my graduate thesis research 48 years ago. Back then, I had no idea it would prove to be an exceptional model, revealing unknown or neglected phenomena of general significance. It all started with the unusual seasonal changes in sex ratio I observed as an MS graduate student (Fig. 1). Had I not decided to focus my doctoral dissertation on the causes of that sex ratio pattern none of the rest of the discoveries we made would have emerged. Looking back, I realize now that *Menidia* was leading the way, and I merely followed the path it illuminated, including the linkage it provided to our work on bluefish and striped bass. The reputation I established created the opportunity to take on senior administrative positions.

Why has *M. menidia* been such a seminal species? The answer, I believe, is what attracted me to this species in the first place: its annual life history pattern. Evolution happens on generational time scales, so an annual life cycle lends itself to rapid adaptation on calendar time, and the steep selection gradient caused by spatial climate change along US and Canadian east coasts accelerates the rate of evolution even more. This is probably why trait variation within *Menidia* is so exceptionally high. No other species displays greater levels of among-population variation in sex determination, somatic growth

rate, and vertebral number. Yet despite its exceptional nature, the phenomena revealed by silversides have proven to be common in numerous taxa.

Much can be learned about general principles germane to marine harvested species from easy-to-study, short-lived, model species even if they do not comprise a major fishery. Most harvested species are much more difficult to study than silversides owing to long life cycles and difficulties in collecting and culturing all life stages in the field and in the lab, respectively. Fisheries science has excelled at developing mathematical and statistical models for interpreting fisheries data, but it has not often employed an empirical model approach. There are likely to be other species that could produce new insights and serve as models of general patterns, especially those with short life cycles distributed across strong environmental gradients, were their natural history to be explored.

Lastly, never sell yourself short. As an obscure graduate student at UMass, I could not, in my wildest dreams, have imagined that my career would result in an invitation to publish a memoir alongside such luminaries as have appeared in this series. The key was to take it one step at a time and not look too far ahead. Becoming confident after each step will compel you to take the next. Challenging yourself to continually pursue new opportunities will assure you have a rewarding career.

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Data availability

No new data were generated or analyzed in support of this research.

Notes

Food for Thought articles are essays in which the author provides their perspective on a research area, topic, or issue. They are intended to provide contributors with a forum through which to air their own views and experiences, with few of the

constraints that govern standard research articles. This Food for Thought article is one in a series solicited from leading figures in the fisheries and aquatic sciences community. The objective is to offer lessons and insights from their careers in an accessible and pedagogical form from which the community, and particularly early career scientists, will benefit. The International Council for the Exploration of the Sea (ICES) and Oxford University Press are pleased to be able to waive the article processing charge for these Food for Thought articles.

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