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Paul A. Montagna

Texas A & M University - Corpus Christi, paul.montagna@tamucc.edu

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HOW A SIMPLE QUESTION ABOUT FRESHWATER INFLOW TO ESTUARIES SHAPED A CAREER

Paul A. Montagna

Texas A&M University–Corpus Christi, Harte Research Institute for Gulf of Mexico Studies, 6300 Ocean Drive, Unit 5869, Corpus Christi, Texas 78412 USA; Author email: Paul.Montagna@tamucc.edu

ABSTRACT: Chance and good luck led to a career studying how freshwater inflow drives estuary processes. In 1986, someone asked me: How much fresh water has to flow to a bay for it to be healthy? The question shaped my career. There is probably no better place on Earth to compare effects caused by inflow differences than the Texas coast, because the major estuarine systems lie in a climatic gradient where runoff decreases 56-fold from the Louisiana border in the northeast to the Mexico border in the southwest. This estuary–comparison experiment was used to study inflow effects. The science evolved from the idea in the 1990’s that organisms responded directly to inflow rates to the domino theory in the 2000’s of indirect effects where inflow drives estuary conditions and that organisms respond to those habitat conditions. Today it is hypothesized that climate drives hydrology, which drives estuary dynamics; and thus, climatic factors can indirectly shape estuarine structure and function. Assuming change along the inflow gradient is analogous to effects of altering estuaries over time, we can now predict ecosystem change with changing climate or land–use change.

KEY WORDS: benthic ecology, biogeochemistry, environmental flows, freshwater inflow, invertebrates, salinity

BEGINNINGS

I was born in New York City. In a way, becoming a scientist, especially a marine ecologist, was more an accident than a choice. I was a house painter, home remodeler, and pizza maker. I would have continued a blue–collar life and not gone to college except for the Vietnam War, because a college deferment meant I could put off becoming a soldier, and then a high number in the draft lottery meant the Army wasn’t in my future. I thought about being a high school biology teacher. But during student teaching, I realized I didn’t like high schools and I was woefully unprepared for teaching. I wanted to leave New York, so, I decided to try graduate school at Northeastern University in Boston. The rest, as they say, is history.

In graduate school, the whole world opened, and I discovered things I had no idea existed. I was incredibly naïve as a graduate student. I didn’t have a clue what to work on, but my supervisor, Ernest Ruber, suggested salt marshes and estuaries, and a light bulb went on in my head because I had spent a lot of time surfing off beaches and fishing the bays with my father. But it never occurred to me that something that was fun would be something I could do for a living, and I have never worked outside of a university since. My thesis described succession of microbes and small invertebrates during *Spartina* decomposition (Montagna and Ruber 1980).

My first job was at Oregon State University where I was a research assistant for Andrew Carey, who exposed me to oceanography and benthic ecology as a discipline. I sorted sediment samples and identified benthic invertebrates from the oil producing areas of the Beaufort Sea (Montagna and Carey 1978, Carey and Montagna 1982). I learned taxonomy and described some new

species of Harpacticoida. But most importantly, I took an undergraduate English course for 7 semesters in a row. During my Master’s studies, I discovered that my language skills were poor. These courses, and the free time to read during long cruises and field campaigns, opened me to a new world of literature.

Newly literate and with enhanced lab skills, I was ready to tackle a doctoral program at the University of South Carolina. Bruce Coull was the perfect mentor to “polish me” and help me become a scientist in my own right. His focus on publishing encouraged my newfound love of writing. After every explanation, he would ask: “now explain it to me without jargon so I can explain it to my 10–year–old.” He taught me that I had been doing meiofaunal ecology all along. My dissertation was on meiofaunal–microbial trophic interactions (Montagna et al. 1983, Montagna 1984a, b). But there was one more lesson from my Master’s, which was that I had no idea what to do with data. So, I took 7 graduate level courses in math and statistics while a doctoral student. I graduated with 2 essential skills: I could analyze data, and I could write.

My final training stop was at the Lawrence Livermore National Laboratory, where I was a postdoc under Robert Spies. We studied meiofaunal–microbial relationships in the Santa Barbara oil seeps (Montagna et al. 1986, 1987, 1989, Bauer et al 1989). This job married all my previous experiences together and set me up as an expert on the effects of offshore hydrocarbon production, exploration, and accidents. But that is another story.

Throughout my career there has been a tension between 2 camps of ecologists: those who prefer an experimental or theoretical approach, and those who prefer an empirical approach. I was

most influenced by 19th century naturalists like Charles Darwin who spent 5 years aboard the *HMS Beagle*, or Louis Agassiz who founded one of the first marine labs in the US and exhorted “study nature, not the books.”

FRESHWATER INFLOW

My first faculty position was at a marine lab in 1986, and again, I was incredibly lucky. The Texas Legislature passed a law in May 1985 requiring any new water withdrawal permits would have to consider the effects on downstream bays and estuaries. By summer 1986, Gary Powell (then director of the Bay and Estuary Program, Texas Water Development Board, Austin, TX, USA) was charged with identifying how much fresh water had to flow to the coast to maintain productivity. He commissioned the faculty at the University of Texas Marine Science Institute to help answer the question. At the time, it appeared to be a simple question that would be easy to answer within 2 or 3 years by measuring processes along salinity gradients and comparing them to changes in flow rates over time. Looking back, it was a rather naïve assumption, and it actually took nearly 18 years to figure out how to ask the question in a way that it could be answered. It also provided me with a research question that would drive my entire career.

1990's: Environmental flows are the natural flows of water in the environment that create and modify habitats. There are 3 major types of environmental flows: 1) instream flows, i.e., flow within rivers, creeks, and streams; 2) inflow, i.e., flows from freshwater sources into coastal estuaries; and 3) outflow, i.e., flows from estuaries to the ocean or continental shelf (Montagna et al. 2013). The field of environmental flow research was still in its infancy in the 1980's and was primarily conducted in freshwater ecosystems, so early work in estuaries was strongly influenced by studies of rivers and streams. In rivers and streams, flow creates habitats (e.g., runs, riffles, and pools), thus directly influencing community structure. Early estuarine researchers developed a conceptual model that formed the basis of the State of Texas method to determine estuary inflow needs (Powell and Matsuoto 1994, Powell et al. 2002). These initial studies focused on managing 7 commercially and recreationally important fish and shellfish species (Figure 1), which were valued but subject to fishing pressure.

In contrast, benthic infauna (i.e., invertebrates > 0.5 mm in length) are excellent bioindicators of sediment quality and estuarine health, because they are relatively long-lived, fixed in place, integrate variations in the overlying water column over time, and are forage for commercial and recreational fish species (Dauer 1993). Benthos must respond to ephemeral changes in the overlying water column because they don't move as much as nekton, therefore we have used benthic organisms as bioindicators of freshwater inflow effects on bays and estuaries since the 1990's. Initially, community metrics were correlated with inflow (Kalke and Montagna 1991) or lags in inflow (Montagna and Kalke 1992). Mollusks, especially filter-feeding bivalves, were identified as the best bioindicators of inflow effects (Montagna and Kalke 1995, Montagna et al. 2008). Bivalves depend on microalgal pro-

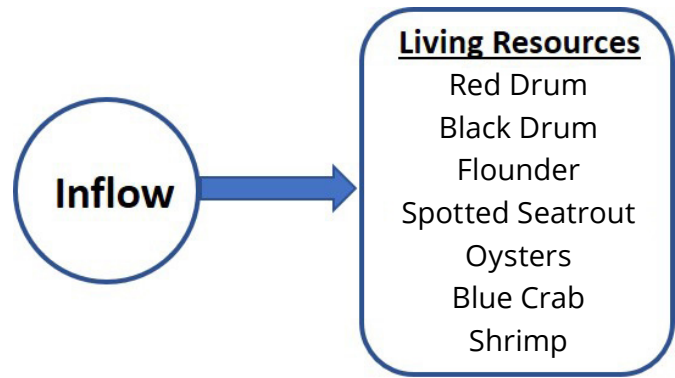


FIGURE 1. The 20th Century conceptual model of direct effects of inflow in estuaries.

duction, which depended on nutrients carried into the estuary by river flow. My early studies were criticized over a concern that sediment and inflow might be confounded. It is well known that sediment composition (i.e., sand versus mud) controls benthic populations (Gray 1981). However, Texas bays are broad, open, shallow lagoons that are dominated by muddy bottoms (Montagna et al. 2007, 2011a,b). Studies demonstrated that infauna in these lagoon-estuaries were responding to salinity and not sediment type, likely because the habitats are similar throughout the coast (Mannino and Montagna 1996, 1997).

Another concern was whether other anthropogenic stressors could be confounding the biotic signals related to inflow. Hypoxia was found in Corpus Christi Bay during the first summer sampling trip in 1987 (Montagna and Kalke 1992). Because the hypoxia is seasonal, the bay is hot and at times hypersaline (Applebaum et al. 2005). The combination of high temperature, high salinity, and low dissolved oxygen (DO) caused benthos metrics to decline when DO was ≤ 3 mg/L (Ritter and Montagna 1999), compared to most other areas where hypoxia effects are present at DO ≤ 2 mg/L (Dauer et al. 1992, Diaz and Rosenberg 1995). The hypoxic community is a subset of the normoxic community for both infauna and epifauna, indicating that stress is affecting taxa intolerant of low oxygen conditions (Montagna and Froeschke 2009). Corpus Christi Bay is hydrologically neutral, meaning inflow is about equal to evaporation and diversions (Montagna et al. 2007, 2011a,b). The high salinities occur over the southeastern part of the bay, which is furthest from the Nueces River input, is caused primarily by evaporation (Cooper-smith et al. 2011). The solubility of oxygen in water decreases with higher temperatures and salinity, so hypoxia occurs in the same region as the high salinities. Another problem is the locations of storm-water outfalls which surround Corpus Christi Bay (Carr et al. 2000). There are higher levels of xenobiotic contaminants near outfalls, but there is no correlation between benthic metrics and sediment chemistry (Carr et al. 2000, Burgess et al. 2005).

We knew that commercial fisheries harvest was correlated to lower salinity and higher nutrient loading rates, which were driven by increasing freshwater inflow (Armstrong 1982). That

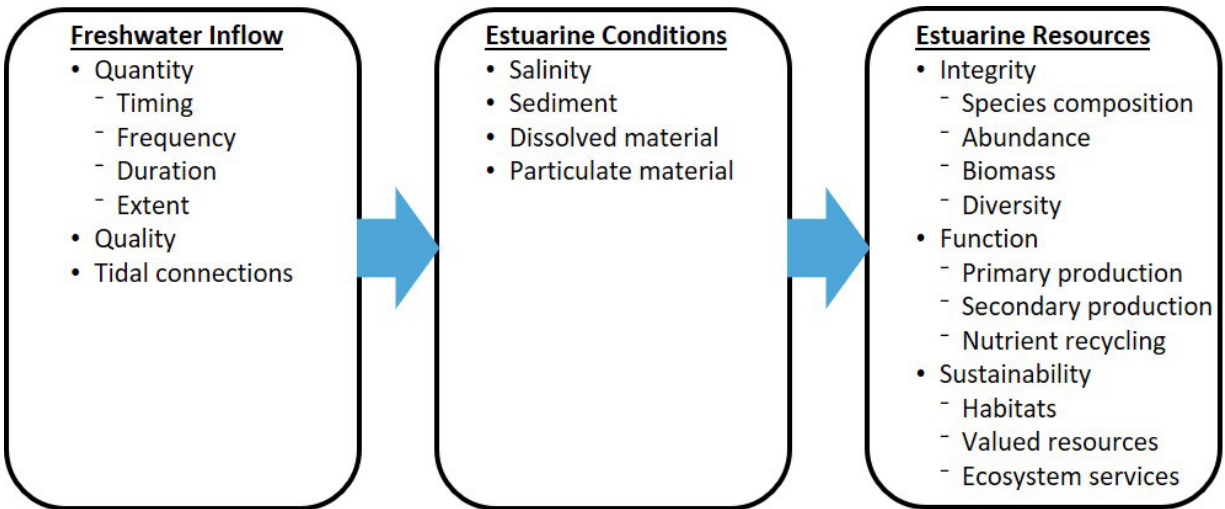


FIGURE 2. The 21st Century conceptual model of inflow as an indirect effect in estuaries, i.e., the domino theory as discussed in Palmer et al. (2011) and Montagna et al. (2013). (Modified from Alber 2002).

led to the idea that organic matter loading could stimulate bacterial metabolism and production, which could in turn stimulate benthic consumption of microbes (Montagna and Yoon 1991). It was shown that carbon derived from inflow was also stimulating shrimp movement and utilization of nursery habitats (Riera et al. 2000). Organic matter loading from rivers is deposited on the bottom and thus is a major control of benthic nutrient fluxes (Hargrave 1973, Nixon et al. 1976), which varies along salinity gradients (Boynton and Kemp 1985) and inflow gradients (Twilley et al. 1999, Russell and Montagna 2007).

2000's: The recognition that inflow was mainly creating habitat rather than defining it required a major rethinking of the conceptual model. It was clear that inflow was driving estuary conditions (i.e., salinity, nutrients, and sediments) that define salinity zone habitats, and that biological resources were responding to the habitat conditions (Figure 2). While this was implied in many earlier studies, I believe the first publication of this concept as an explicit conceptual model was by Alber (2002). The original conception was modified in 2 important ways: 1) adding the concept of an inflow regime in the context of disturbance theory (i.e., timing, frequency, duration, and extent) that is interacting with tidal connections, and 2) redefining the ecological components of structure and function into the ecological health context (i.e., integrity, function, and sustainability; Palmer et al. 2011, Montagna et al. 2013). The transformation to a “health” context was adopted from the U.S. Environmental Protection Agency methodologies and it was important for the resource management community because it meant there could be assessment of inflow needs and standards developed for managing inflow (Montagna et al. 2002a).

Defining ecological health is vexing. Consider the analogy with human health. Scientists know that the normal human body temperature range is 36–38°C. If a person's body temperature is above this range, then they have a fever and are likely

sick. This example illustrates several important principles about human health as it relates to defining ecological health and how the definition has evolved for water quality assessment (Montagna et al. 2002a, 2009, 2013). It is easy to integrate the conceptual model of inflow effects and the risk assessment paradigm to provide a general reference frame to define “ecological health”. Indicators of health must be identified, and the indicators must be within an acceptable range (which is large because of spatial and temporal variability). Ecological indicators include function, integrity, and sustainability. But in the end, the most important indicator is likely ecological sustainability. Sustainability is the ultimate definition of ecological health because sustainable is healthy in the strict sense (Montagna et al. 2013).

Because inflow is driving inorganic and organic nutrient loading (Nixon 1981, Arismendez et al. 2009, Shank et al. 2009), it is also driving metabolism (Russell et al. 2006, Russell and Montagna 2007). The inflow quantity and distance from the source constrains the dependence of metabolism on inflow. Metabolism is variable over time but during high flow periods metabolism accurately predicts shifts from balanced to heterotrophic conditions (Russell et al. 2006). The mechanistic relationship between inflow and inorganic and organic matter loading was used to create a modeling system to estimate benthic productivity for grazers and detritivores (Figure 3, Montagna and Li 2010). Community structure is controlled by inflow, with more suspension feeders in high inflow estuaries and more deposit feeders in low inflow estuaries. Higher inflow translates into higher benthic productivity. The production to biomass ratio (P/B, units/y) increased with proximity to the freshwater source in 4 estuaries, and increased with water residence time (i.e., inflow volume adjusted by the estuary volume, units/y). Simulations indicate decreasing nutrients, primary production, and benthic secondary production during droughts, and increasing during floods (Kim and Montagna 2009). Along the climatic gradient

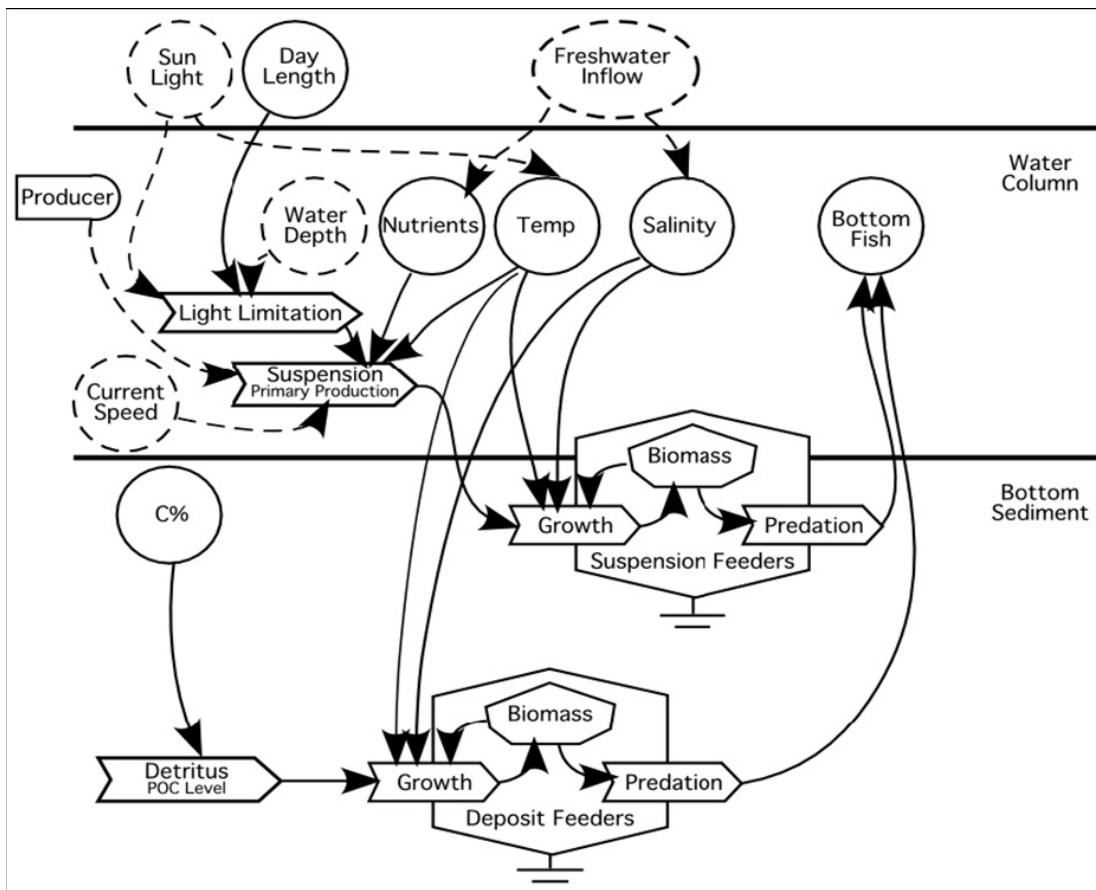


FIGURE 3. Structure of the benthic macrofaunal biomass model driven by freshwater inflow (from Montagna and Li 2010). Copyright 2010 from *Coastal Lagoons: Critical Habitats of Environmental Change* by M.J. Kennish and H. Paerl, eds. Reproduced by permission of Taylor and Francis Group LLC, a division of Informa plc.

in Texas, estuaries with increased salinity (and thus decreased inflow) benefited deposit feeders, while suspension feeders were reduced; this leads to a decrease in functional diversity when salinity is increased because of loss of a trophic guild (Kim and Montagna 2012). Within estuaries, the upstream benthic community is reduced by reduced inflow, whereas the downstream community increases with reduced inflow and higher salinities. This is because lower salinity regimes are required to support food production for suspension feeders, and polyhaline deposit feeding species increase during marine conditions.

After it was well-established that freshwater inflow was important to maintain estuary health (Palmer et al. 2011, Montagna et al. 2011b, 2013), there was great interest in hydrological restoration to benefit the environment (Montagna et al. 2002a). There was a focus on the Nueces Estuary because construction of the Choke Canyon Reservoir in 1982 reduced the Nueces River freshwater inflows to the estuary by about 48% (Asquith et al. 1997). Consequently, the annual mean net inflow balance in Nueces Bay decreased from slightly positive to negative, transforming the Nueces Delta, Marsh, and Estuary into a negative estuary with higher salinity upstream near the river mouth than downstream near the tidal inlet with the Gulf of Mexico (Montagna et al. 2009). An experimental river diversion was created to increase the opportunities for marsh enhancement (Ward et al. 2002). Two overflow channels were constructed to increase flooding from the Nueces River to the upper delta. The total volume of freshwater inflow into the upper Nueces Delta was

increased about 7-fold over what would have occurred without the project, but historical volumes were not restored. Macrofauna responded to inflow events with increased abundances, biomass, and diversity but decreased during hypersaline conditions (Montagna et al. 2002b). The diversion restored normal salinity patterns in the upper reaches (<14 km) of Rincon Bayou and freshwater pulses ($> 10^6 \text{ m}^3$) in fall increased benthic productivity indicating ecological functions were restored as well (Palmer et al. 2002). However, the salinity-stressed estuary of Rincon Bayou appears to be in a constant state of early and intermediate succession because of frequent salinity-related disturbances (Ritter et al. 2005). The long-term prognostication is not good as the marsh continues to suffer periods of hypersalinity (Del Rosario and Montagna 2018). To improve the marsh, salinity should be maintained between 6 and 18, minimum water depth should be between 0.2–0.3 m, and to improve ecological stability inflows should be continuous, not a pulsed flood (Montagna et al. 2018a). But this is not likely to occur, and under current climate and water management conditions, the marsh will degrade further (Montagna et al. 2017).

Management of freshwater inflow in the late 2000's changed based on the scientific advances in the 1990's, which demonstrates the broader impacts of the earlier studies. The adaptive management approach established for hydrological regimes in the Nueces Estuary (Montagna et al. 2009) was adopted state-wide in Texas with passing of new legislation in 2007 (SAC 2009). The State also expanded the definition of protected re-

sources from 7 commercial and recreational species (Figure 1) to “maintain the productivity, extent, and persistence of key aquatic habitats in and along the affected water bodies” (Senate Bill 3, 2007; Texas Water Code 11.002(16)). Thus, the scientific focus moved from a species-based approach to an ecosystem-based approach using the domino theory (Figure 2). The ecosystem-based approach required a multivariate assessment tool. We created a Freshwater Inflow Biotic Index (FIBI) to determine how changes in freshwater inflow affect benthic populations, which in turn reflect the ecological condition of an estuary (Pollack et al. 2009). The FIBI was based on benthic succession theory (Person and Rosenberg 1978, Rhoads et al. 1978) and biotic metrics that characterized benthic community structure in response to inflow regimes. The metrics were ranked and then reduced to one variable using principal component analysis (PCA) to form the index. Thus, if inflow is reduced (i.e., salinity increased), it will cause upstream communities to take on characteristics of downstream communities (Pollack et al. 2009). This same approach was also applied to identifying inflow needs for estuaries on the west and east coasts of Florida (Montagna et al. 2008, Mattson et al. 2012).

Water has value in its many different uses, such as drinking, irrigation, cooling, etc. So, what is the value of water when it is not used at all, but remains in what is referred to as “environmental flow”? A “willingness-to-pay” contingent valuation survey was conducted among the general public and 64% were willing to make a one-time donation to a ‘water trust’ and make a donation averaging \$129/person to maintain environmental flows (Yoskowitz and Montagna 2009). Again, this demonstrates the broader impact of research on environmental flows.

2010’s: The first 20 years of studies provided sufficient long-term data to demonstrate that long-term hydrological cycles affect freshwater inflow and water quality (Paudel and Montagna 2014, Paudel et al. 2015), which in turn regulates benthic abundance, productivity, diversity, and community structure (Palmer et al. 2011, Kim and Montagna 2012). Thus, these hydrological cycles were driven by long-term climate cycles and change, which ultimately control salinity, temperature and DO in estuaries. There are 3 emergent themes described below: 1) importance of climatic gradients and climate change, 2) hydrological control of biogeochemistry of estuaries, and 3) environmental drivers of infauna ecosystem function, community structure, and diversity patterns.

CLIMATE

There is a climatic gradient along the Texas coast where mean rainfall decreases from 142 cm/y at the northeast border with Louisiana to 69 cm/y at the southwest border with Mexico (Montagna et al. 2013). Consequently, the 7 major estuarine systems along the 600 km coastline have decreasing freshwater inflow and increasing salinities along the gradient (Figure 4; Longley 1994, Montagna et al. 2007, 2011b, Montagna et al. 2013). The estuaries with higher inflow and lower

salinity have greater nutrient and sediment loading (Pollack et al. 2011b, Paudel and Montagna 2014, Paudel et al. 2015, 2017, 2019), and consequently higher primary production (Turner et al. 2014), which leads to higher secondary production of benthic and pelagic consumers (Kim and Montagna 2012).

The hydrological spatial gradient is analogous to change over time because if the climate is drier, then in the future estuaries will resemble the estuaries further southwest today. In contrast, if the climate is wetter in the future, then the estuaries will change to resemble estuaries in the northeastern range today. This is important for 2 reasons: 1) the hydrologic cycle controls the dynamics of freshwater delivery to coastal ecosystems and that cycle is likely to change under a changing climate (Scavia et al. 2002) and 2) the southwest of the United States will be hotter and drier (Seager et al. 2007, Wentz et al. 2007), and this will compound water deficits leading to unprecedented drought challenges (Nielsen-Gammon et al. 2020).

Hydrological events, such as floods and droughts, are another proxy for climate change effects. Droughts effect estuary water column conditions with decreases in turbidity, nutrient concentrations, chlorophyll concentrations, and epibenthos (Palmer and Montagna 2015). During droughts, there were decreases in white shrimp (*Penaeus setiferus*) and blue crab (*Callinectes sapidus*). In contrast, infauna abundance and diversity increased during droughts with a dominance of marine fauna in

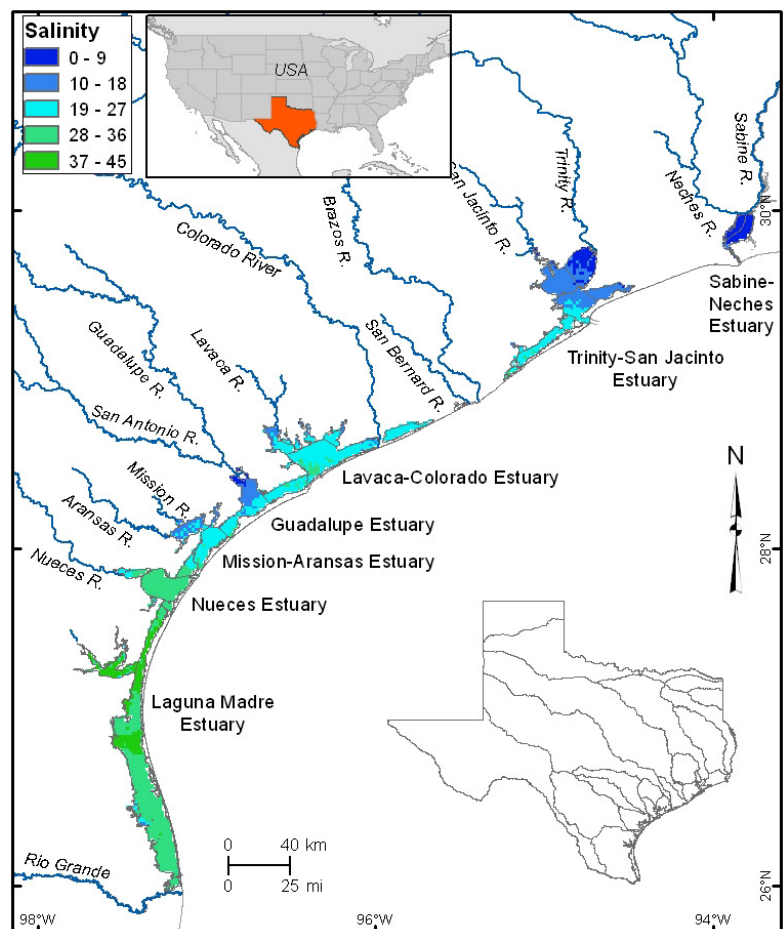


FIGURE 4. Long-term mean salinities in Texas estuaries.

the estuary. Oysters (*Crassostrea virginica*) can be harmed by large flood events when salinities become too low and stress oyster physiology (Turner 2006). Floods in Texas bays caused temporary reductions in salinity, oyster abundance, spat settlement, disease levels, and filtration rates (Beseres–Pollack et al. 2012). Oyster populations recovered rapidly to pre–flood levels because freshwater pulses maintain low salinities that are unfavorable for predators and disease. Thus, episodic flood events appear to play a critical role in maintaining oyster populations. Hurricanes are storm surge, wind, and flood events. After Hurricane Harvey (25 August 2017), large volumes of freshwater run–off reduced the abundance of riverine fauna and caused hypoxic and hyposaline conditions in the estuaries for over a week (Patrick et al. 2020, Walker et al. 2020). In the estuary, infauna diversity and abundance decreased, but mobile fauna such as estuarine fishes did not change. Although hydrographic and biogeochemical components were highly perturbed, they returned to baseline conditions within days. In contrast, biotic components demonstrated lower magnitude changes, but some of these organisms, particularly the sedentary flora and fauna, required weeks to months to return to pre–storm conditions, and some did not recover within the 6 months reported in the study (Patrick et al. 2020).

There are also long–term trends, which are linked to global climate cycles, such as the El Niño–Southern Oscillation (ENSO). ENSO is a fluctuation between warmer (El Niño) and cooler (La Niña) conditions in the tropical Pacific. While its influence on the Earth system is broad, many intertwined issues regarding ENSO dynamics, impacts, forecasting, and applications remain unresolved (McPhaden et al. 2006). ENSO variability is likely to increase under global warming (Cai et al. 2018). However, we do know that during the El Niño phase of ENSO there is flooding in the southwest region of the United States. The higher rain and river discharge extend across the Gulf of Mexico reaching Florida (Schmidt et al. 2001). The increased rain and river discharge during the warm phase of ENSO leads to lower salinities in all Texas bays (Tolan 2007) and Florida bays bordering the Gulf of Mexico (Schmidt et al. 2002). Benthic macrofaunal abundance was significantly correlated with salinity, the ENSO index and the North Atlantic Oscillation index, indicating that global climate variability and the resulting effects on local salinity patterns are important factors shaping Texas benthic macrofaunal communities (Pollack et al. 2011b). El Niño enhanced macrofauna metrics off Chile by increasing bottom water DO in areas that experience periodic hypoxia and anoxia (Gutiérrez et al. 2000). Both ENSO and the Pacific Decadal Oscillation (PDO) influence the long–term variability of benthic community structure in estuaries of southern Brazil (Francisco and Netto 2020). However, there are multiple interacting drivers of benthic macrofauna that control the degree of interaction between broad–scale climatic factors (e.g., ENSO) with smaller scale variability, and this will determine the consistency of responses over large spatial scales (Hewitt and Thrush 2009).

Temperatures have been rising across the globe since the late 19th century (IPCC 2014). This has led to a concordant rise in seawater temperatures. Since 1977, there has been a linear increase in water temperature in all Texas estuaries averaging 0.0428

°C/y, which translates into an increase of 1°C every 23 years (or 1°F every 13 years; Montagna et al. 2011a). The solubility of DO is temperature dependent, so a direct result of the increased temperatures is a decrease in DO concentration. Over the same period, DO has decreased linearly at a rate of 0.0532 mg/L/y, which translates into an increase of about 0.7%/y (Montagna et al. 2011a). If the current trend continues, surface water DO will not meet exceptional aquatic life standards (≤ 5 mg/L) by 2032 (Applebaum et al. 2005).

There has also been a long–term decrease in alkalinity and increase in acidification in all Texas estuaries (Hu et al. 2015). From 1960 to 2010, alkalinity decreased at a rate of 3.0–21.6 $\mu\text{M}/\text{y}$, and pH decreased at a rate of 0.0014–0.0180/y. The alkalinity decrease is thought to be related to reduced inflow from precipitation decline under drought conditions and freshwater diversion for human consumption, as well as calcification in the bays.

Overall, the effects of climate variability and climate change are changing estuarine habitats in the northwest Gulf of Mexico because higher temperatures and lower DO concentrations are stressing organisms (Ritter and Montagna 1999, Montagna and Froeschke 2009, Montagna and Ritter 2006), floods are lowering salinities to stressful levels (Palmer and Montagna 2015), and acidification may have negative impacts on shellfish production in these waters (Buskey et al. 1997, Pollack et al. 2011a). It does appear that consequences of these changes are being seen because benthos appear to be disappearing. A 20–year (1988–2008) study in the Lavaca–Colorado Estuary found that benthic abundance, biomass, and diversity declined at log–scale rates (Pollack et al. 2011a). This has dire implications for coastal ecosystems because benthos are important food sources for many commercial and recreational fish, leading to the question: Are fish running out of food? In fact, a black drum starvation event has already been recorded in Baffin Bay, Texas (Olsen 2016). The benthos decline in Lavaca and Matagorda Bays raises several serious questions: Is this happening elsewhere in Texas? Is it continuing? What is driving the trend?

BIOGEOCHEMISTRY

Another emerging theme is the importance of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) loading with flooding (Shank et al. 2009, Kim and Montagna 2012, Kim et al. 2014, Hu et al. 2015). But there has always been a paradox because Baffin Bay and Laguna Madre, the Texas estuaries with the least amount of freshwater inflow, have the highest concentrations of salinity as well as DOC and DON (Wetz et al. 2017), and are known for persistent brown tide blooms (Buskey and Hyatt 1995) and high mean chlorophyll concentrations (Wetz et al. 2017). The brown tide blooms have been explained by 2 main mechanisms: 1) a disruption of planktonic and benthic grazer control that resulted in failure to control phytoplankton growth (Buskey et al. 1997); and 2) the inability of the algae to use nitrate and a preference for ammonium (DeYoe and Suttle 1994). Today we also know the brown tide algae thrives where DON is high (Wetz et al. 2017). The answer to the paradox lies in oxidation–reduction reactions. Nutrients and chlorophyll patterns

illustrated an emerging paradigm where phytoplankton biomass in positive estuaries (with high inflow) is supported by “new” nitrogen from riverine input that is oxidized (e.g., nitrate and nitrite), while high concentrations of “old” reduced nitrogen (DON and ammonium) allow for high chlorophyll in the negative estuary (with low inflow; Montagna et al. 2018b). Inflow also plays a role in estuarine acidification because alkalinity decreases when weathering products were diluted during high–flow conditions, resulting in carbonate undersaturation (for aragonite) and decreases in pH (Figure 5, Montagna et al. 2018b).

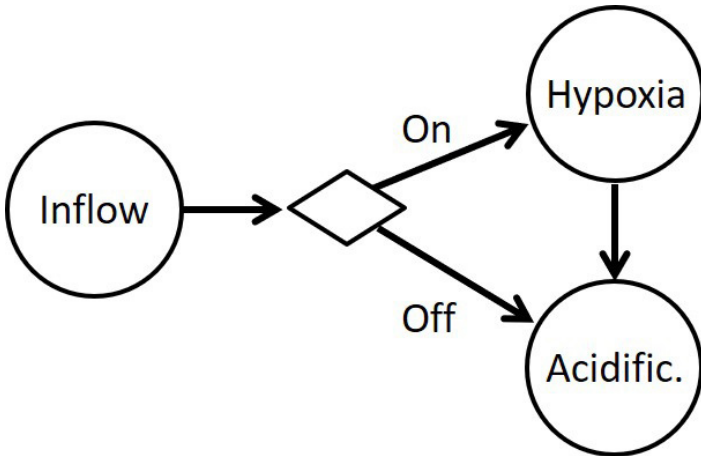


FIGURE 5. Hydrological switch hypothesis.

DIVERSITY

Initially, it was discovered that mean salinity was important for controlling infauna diversity (Kalke and Montagna 1991, Montagna and Kalke 1992, 1995, Palmer et al. 2002, Montagna et al. 2002b). Diversity always increases with increasing salinity temporally during droughts or spatially over the climatic gradient in estuaries with higher salinities. Recently it was discovered that it was the variance of salinity, not the mean, that was controlling diversity, and high variance leads to very low biodiversity in Texas bays (Van Diggelen and Montagna 2016). This response was

observed after Hurricane Harvey, which caused steep declines in benthos diversity when salinity in San Antonio Bay dropped from a salinity of 10 to 0 (Patrick et al. 2020).

The other trait of infauna diversity in Texas bays is that it is characterized by dominance. Dominance alone does not explain infauna community structure because diversity is made up of rare species. In all past studies (Montagna and Kalke 1995, Pollock et al. 2009, 2011b, Palmer et al. 2011, Van Diggelen and Montagna 2016), usually 10–15 species compose 80–90% of all individuals from a total of 110–220 species. This means diversity is driven by the unusual occurrence of different rare species over time. Dominance in estuaries is not unusual, and current approaches condense abundance and richness data into one of many single metric or index values (e.g., Shannon’s diversity measure). The problem is that the typical diversity index simplifies and ignores which species makes up diversity. Ignoring rare species amplifies uncertainty when it comes to understanding ecosystem tipping points.

THE FUTURE

It is now clear that there is one more indirect driver to estuary structure and function, and that is climate because climate variability and change is driving hydrology (Figure 6). Thus, it is hypothesized that there is a series of indirect drivers that control estuary structure and function, i.e., there is one more domino than we thought. Climate variability occurs on multiple scales ranging from daily to seasonal to annual to decadal. Climate variability alters the timing and amount of freshwater, nutrients, and sediment delivery, and this will drive estuarine productivity. This will intensify other ecosystem stresses (i.e., pollution, harvesting, habitat destruction, invasive species, land and resource use, extreme natural events, etc.), which may lead to more significant consequences (Scavia et al. 2002).

Some ecological questions cannot be answered with short-term studies, and this is particularly true for questions about the effects of freshwater inflow because there is large year-to-year variability in climate and weather, which leads to periods of floods and droughts. Ecological relationships can be obscured in short term studies by common features such as time lags, natural variability, nonlinear relationships, interactive drivers, or rela-

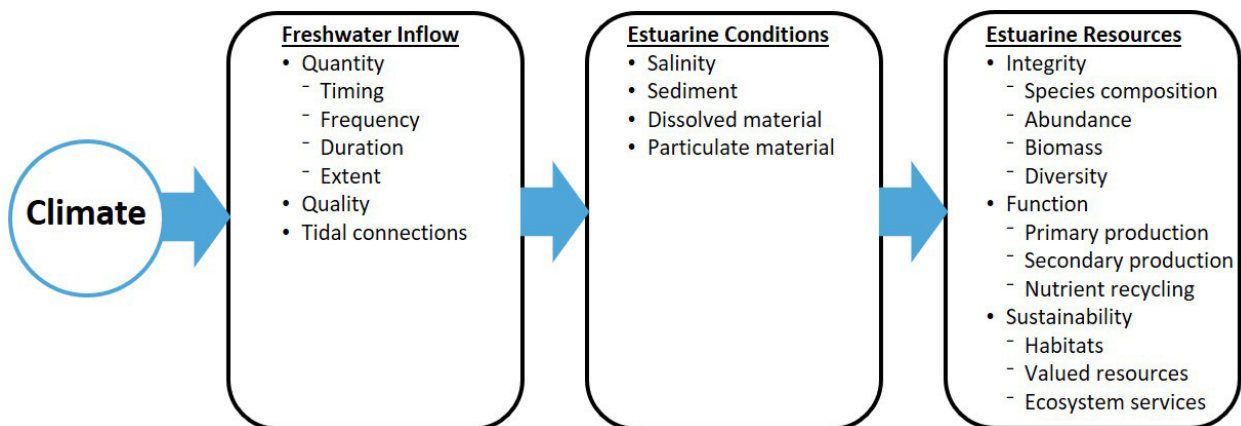


FIGURE 6. Proposed conceptual model, the “domino theory” for freshwater inflow effects on estuaries.

tively slow processes (Hampton et al. 2019). Thus, much more long-term research is needed to provide perspectives on environmental processes, dynamics of populations and communities of organisms.

MANAGEMENT IMPACTS

The results of the studies described here have been used to create methods for science-based inflow standards for estuaries in Florida (Mattson et al. 2012, Palmer et al. 2016) and Texas (SAC 2009), and recommend hydrological restoration strategies (Montagna et al. 2009, 2018a, Del Rosario and Montagna 2018, Middleton and Montagna 2018). Managing environmental flows to the coast is difficult because bays and estuaries are open to ocean connections, and there are gradients from the river to the sea. I believe there are only 3 states in the U.S. that have environmental flow requirements for estuaries: California, Florida, and Texas. The problem to solve is balancing the environmental needs with human needs for fresh water for cities, farms, and industry. The first step is for stakeholders and resource managers to understand the importance of inflow to estuaries. The research described here contributes to that need. The second step is to have laws and regulations that require withdrawal permits to consider downstream effects. In the U.S., this has to happen

state-by-state. The third step is to create methods that can be used as tools to identify freshwater inflow needs. A major goal of the studies discussed here has been to identify general principals, so that they will have applicability world-wide.

EPILOGUE

My work has been remarkably diverse, from microbes to birds, hydrology to biogeochemistry, rivers to the bottom of the deepest parts of the oceans, and in every part of the globe from the coast of Africa to Asia and from the Arctic to Antarctica. But a focus on benthic processes has been a constant, and estuaries have always been dearest to my heart. Estuaries in the coastal zone make up only 5% of the world's ocean areas, but account for 95% of the world's marine productivity, and provide a nursery ground for estuarine-dependent species. For people, estuaries provide recreational opportunities, natural buffers protecting the land and built environments during storms, and will naturally clean pollution from the water. These free benefits to people are called ecosystem services and provide a great way to integrate social and natural science. So, even though I have traveled the world's oceans, I always come back to the bay in my backyard. Overall, I have been pretty lucky (see Box).

FREE ADVICE TO GRADUATE STUDENTS

Free advice is worth what you pay for it, which is nothing. However, experience is a teacher, and maybe some experiences are worth mentioning. Here are a few.

In the book *Outliers*, Malcom Gladwell (2008) argues that successful people have three common factors in their background: 1) they are smart enough with above average intelligence, but not necessarily genius, 2) they work about 10,000 hours (5 years at 2000 h/y) to build sufficient skills to succeed, and 3) they had a lucky break or fortuitous circumstance. This argument resonated with me because my motto had always been, "I'd rather be lucky than smart" and at every key turning point in my life, I was presented with a great opportunity at just the right time. Isn't that luck? Sure, as my uncle Pat used to say, "you make your own luck" with preparation and hard work. For me, there were decisions that were made out of curiosity and luck more than prescience. When I was in middle school, I took a typing class rather than the printshop class all the other boys were taking. So, when the computer revolution came along, I already had keyboarding skills. Luck!

Most people learn the wrong lessons from sports. They think sports are important because it teaches teamwork and winning. That's wrong. The important lessons from sports come from losing. In baseball, if you strike out, it's not because the pitcher doesn't like you, it's because you need more skill. You don't give up, and you don't sulk, you get up early the next morning and take extra batting practice. The lesson is that science is hard, and success depends on maturity. Take constructive criticism for what it is, "it's business, not personal," and improve your skills.

One more sports analogy. If the pitcher knows you can't hit a curve ball, that is all you will see. So, make your weakness your strength. Image the pitcher's surprise when you hit the next curve ball over the fence. My Masters research taught me that I was weak at two basic skills: writing and statistics. So, I made these 2 weaknesses my strengths, and this has been critical to my career.

FREE ADVICE TO ASSISTANT PROFESSORS

The experiences recounted above forms the basis for how I recruit and train graduate students. I sometimes call this Paul's triplet code.

Anticipate, Act, Adapt = Rule for work life, perhaps life in general, classic adaptive management paradigm.

Didactic, Diagnostic, Discriminatory = Rule for making exams or tests. Exams should not be punishment. They should be opportunities for learning, discovering what needs more work, but also to decide passing and failing.

Mind, Maturity, Motivation = Rule for screening applications (for graduate school or a job). It is easy to obtain data on the mind, such as grades or scores on standardized exams. But how we deal with adversity matters. The immature person looks for someone else to blame, while the mature person realizes "I just have to work a little harder." Graduate school and creating something new is really hard, and that is where motivation comes in. You have to really want to do this, you have to have some "fire in the belly," or as they say in Spanish "ganas."

This business is hard, but it does get easier over time. After a while it's no longer work. Be confident, don't quit!

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More than 100 people contributed to the work described here. But a few deserve special mention. Richard D. Kalke, known as Rick, has been a steady contributor since 1986, and without his leadership in the laboratory, we would know much less about benthos of Texas and inflow effects in particular. Larry J. Hyde has worked side-by-side with Rick since 2000, and together they are responsible for most of the data described here. Terence A. Palmer contributed Figure 4. Terry started as an undergraduate in 2000, finished a Master's degree in 2006, and worked in the benthic lab until 2018.

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