Professor Martin Grosell and colleagues have made a fascinating discovery about the contribution of fish to the marine inorganic carbon cycle and the potential impact they may have on future ocean acidification.

First, can you outline what defines teleostei and explain the links you have made between this infraclass of fish and the oceanic inorganic carbon cycle? What are your main research objectives?

Teleosts (bony fishes) comprise the largest group of vertebrates. A consequence of the high salt content of seawater is that teleost fish suffer from continuous water loss. To offset this water loss marine teleost fish drink seawater and are able to absorb water across the intestine from this salty solution.

The processing of seawater by the marine teleost fish intestine includes high rates of base (bicarbonate) secretion into the intestinal fluids. The resulting high bicarbonate concentrations in the intestinal fluids combine with the calcium in the ingested seawater to form calcium carbonate crystals. This process is important for the salt and water balance of the marine teleost fish and leads to the excretion of calcium carbonate crystals to the surrounding water.

My overall research focus is to understand how organisms living in water cope with environmental stressors, manmade or natural. My research objectives are to understand how the intestine is capable of absorbing fluid from seawater, how other organs (gill and kidney) cope with the consequences of the intestinal water absorption, and finally the interactions among these physiological processes within the fish and the surrounding marine environment.

Can you highlight your key findings to date?

My research group, along with international collaborators, have demonstrated that the intestinal bicarbonate secretion is fundamental for water balance in marine teleosts. We have also demonstrated that the intestinal water absorption is associated with a significant salt gain and acidification of the blood. Our group identified several cellular components – in the form of specific transport proteins and enzymes – of the bicarbonate and acid transport by the intestinal tissue. Finally, we have estimated the global contribution of marine teleost fish to the production of calcium carbonate in the ocean surface waters.

What are the implications of these findings for global carbon cycling in a time of rapid climate change?

Understanding the bicarbonate buffer system of our oceans is critical for predictions of ocean acidification as environmental CO₂ levels rise. Our discoveries – which identify fish as important contributors to oceanic calcium carbonate production – aid in this understanding. While many calcifying organisms, including corals and microorganisms, will likely display decreased calcium carbonate production as the pH of ocean surface waters decrease, marine fish will likely secrete more bicarbonate and are likely to produce calcium carbonate at higher rates as ocean CO₂ levels rise. Our most recent findings have demonstrated that the fish produced calcium carbonate is more soluble than calcium carbonate from other sources and that it consequently is more likely to dissolve at shallower depths, thereby elevating pH in surface waters.

What ultimate impact do you hope your research will have? How might it impact the wider biological and environmental sciences?

Our findings of high intestinal bicarbonate secretion in marine fish and the role this process plays in salt and water balance for this
large group of vertebrates have impacted the field of fish physiology. The cellular processes unravelled by studies of the marine fish intestinal bicarbonate secretion may inform further studies of bicarbonate secretion by mammalian tissues like the pancreatic ducts and kidney tubules and thus have implications for studies of human health. However, the most significant potential impact lies in the realisation that fish are important contributors to the inorganic carbon cycle in our oceans.

You state that, in your calculations, you "adopted a conservative approach that, if anything, underestimates fish carbonate production". What is the reason for this?

We chose conservative estimates consistently to avoid overstating the significance of this recently realised contribution to the oceanic carbon cycle. Making the field aware of this contribution from fish was our primary objective. Ongoing and future studies aim to more accurately quantify this contribution.

Could you outline the most exciting aspects of your work at present?

We are very excited to initiate the studies of bicarbonate secretion and calcium carbonate excretion under future CO₂ scenarios. Elevated CO₂ causes disturbances of the internal pH balance. However, fish are well known for excellent control of body fluid pH and will be able to maintain normal pH even in presence of much elevated CO₂ levels. We are currently examining the potential tradeoffs or metabolic costs of maintaining pH despite elevated CO₂, with particular emphasis on the intestinal processes.

GLOBAL CO₂ EMISSIONS and temperature increases have ongoing consequences for the Earth and its oceans. The popular media frequently cover the issues of melting glaciers and the rising of sea levels. However, there are other effects in motion that are not so easily portrayed. Rising levels of CO₂ emissions lead to larger amounts of CO₂ being dissolved into the ocean, consequently producing carbonic acid. This lowers the Ocean’s pH level – making it more acidic – with adverse consequences for marine ecosystems. Recent findings have discovered something potentially pivotal in this field. Bony fish, or teleost fish, produce calcium carbonate, a substance that helps to maintain the oceans pH balance. Due to the high salt content of sea water, teleost fish process the seawater internally via the intestine, extracting the freshwater and forming calcium carbonate which dissolves at relatively shallow depths to make seawater more alkaline.

Professor Martin Grosell, along with his research group at the University of Miami and international collaborators, have been demonstrating since the late 90s that intestinal bicarbonate secretion is fundamental for water balance in teleosts. The research effort strives to bring better understanding to the physiology of the marine teleost fish to determine how water absorption from seawater is possible. Grosell is quick to highlight the benefits of an interdisciplinary approach: "Through the collaboration between fish physiologists, chemical oceanographers and fisheries biologists, this approach has revealed novel aspects of fish physiology and the impact of the environment on physiological processes". Grosell’s group, specifically studies how fish react in changing environments integrating a range of techniques and tools including biochemistry, molecular and cell biology.

Field work in marine biology presents a range of unique challenges, but much of the group’s work avoided such travails and Grosell is keen to emphasise the nature of his research: “Most of the activities have been laboratory based and have involved studies on intact marine teleost fish, isolated organs and tissues as well as individual genes and proteins”. In one experiment, X-ray photos were used to display how the teleost fish process seawater. Freshwater fish drink less water than seawater fish and do not form CaCO₃ precipitates in the intestine. An X-ray taken after unfed freshwater flounder showed no presence of CaCO₃ in the gut. However, after only three hours in seawater X-rays revealed accumulations of CaCO₃ in the intestine ready to be excreted. This gives a clear indication of the intense rate at which calcium carbonate is created.

In order to calculate the teleostean contribution of calcium carbonate to the ocean Grosell and his team had to consider the biomass of marine fish globally. This was done by using two independent models; one of which was a size based macro-ecological approach and the other model generated using ecopath software. The calculation was based on estimates generated for each size class of fish and the relevant average local sea temperature. This was then combined with individual fish carbonate excretion rates to predict the teleost fish’s calcium carbonate production on a global scale.

UNDERESTIMATING THE CONTRIBUTION

The published results state that fish could be responsible for 3–15 per cent of all ocean calcium carbonate production. Whilst Grosell and his team have adopted a conservative approach,
INTELLIGENCE

IMPACTS OF CO₂ ON ACID-BASE BALANCE, RECTAL BASE EXCRETION AND INTESTINAL CARBONATE FORMATION IN MARINE FISH

OBJECTIVES
To test if elevated oceanic CO₂ will result in increased CaCO₃ production by marine fish and determine the solubility of fish-produced CaCO₃.

KEY COLLABORATORS
Martin Tresguerres, Scripps Institute of Oceanography
Rod Wilson, Exeter University, UK
Frank Millero, RSMAS, University of Miami
Simon Jennings, University of East Anglia, UK
Yoshio Takei, University of Tokyo

FUNDING
U.S. National Science Foundation (NSF) – award no. 1146695

CONTACT
Martin Grosell
Professor and Associate Dean of Graduate Studies
Marine Biology and Fisheries
RSMAS, University of Miami
4600 Rickenbacker Causeway
33149–1098 Miami, Florida
USA
T +1 305 421 4623
E mgrosell@rsmas.miami.edu

PROFESSOR MARTIN GROSELL received his PhD from the August Krogh Institute, University of Copenhagen, Denmark in 1997. He is currently Professor at the Rosenstiel School of Marine and Atmospheric Science (RSMAS), University of Miami, USA. The research objectives of his lab are pursued through whole animal studies, biochemical and electrophysiological studies on isolated tissues and organs as well as molecular techniques.

the results still clearly show that fish are a major but previously unrecognised source of oceanic carbonate and contribute substantially to the marine inorganic carbon cycle. On commenting on the conservative estimate Grosell mentioned various factors that had to be taken into consideration, one being the size of the fish. “Conservative estimates of the influence of size were chosen, likely leading to an underestimate of the contribution of smaller fish”. This is an important factor to take into account as smaller fish, on a per mass basis, excrete more calcium carbonate than larger fish. Teleost fish also excrete more carbonate in warmer sea temperatures so it was important for Grosell’s team to include this in the estimation.

The surface water of the oceans often have a considerably higher alkalinity than would be expected from solubility of CaCO₃ produced by many marine organisms, an observation that has often been a cause of bewilderment for marine scientists. Marine life such as plankton also releases calcium carbonate, with coccolithophores being considered the main contributors to oceanic CaCO₃ production. However, the often observed higher alkalinity in surface waters is likely the result of teleost carbonate excretion. Calcium carbonate produced by fish dissolves much faster in shallower water than carbonates produced by plankton. This may be the answer to a phenomenon that has puzzled oceanographers for decades. Whilst carbonate produced by plankton is less soluble and often settles at the bottom, fish carbonates dissolve more rapidly to affect surface water pH.

COMPLEXITIES
An obvious reaction would be that more should be done to prevent overexploitation to marine life. Whilst over fishing will definitely influence the amount of fish in the ocean, it may not have such a severe negative effect on the amount of calcium carbonate being produced as one might suspect. Grosell explains: “Overexploitation, while reducing biomass, also decreases the average size of individual fish and results in a greater rate of calcium carbonate production per unit mass”. Smaller fish, which often occur in larger numbers as a result of exploitation, ingest more seawater and therefore excrete calcium carbonate at a higher rate. Grosell notes how this could be cause for further study: “The balance between the negative effect of reduced biomass and the positive effect of reduced average size on calcium carbonate excretion is unknown but likely depends on the degree of exploitation, the fish species in question and environmental parameters like temperature”. The combination of future increases in sea temperature and rising CO₂ will also affect teleost fish contribution to the marine inorganic carbon cycle. Planned and ongoing studies aim to test if increases in sea temperature and rising CO₂ cause fish to produce more calcium carbonate as the fishes metabolic rates increase.

FUTURE RESEARCH
Grosell is eager to take this research even further and investigate the relation between bicarbonate secretion and calcium carbonate formation, the main focus being on the intestinal processes of the fish, and how it will adapt as CO₂ creates changes in the ocean’s pH levels and the organisms inhabiting our oceans. Many challenges in this area remain to be addressed and understood, as Grosell indicates: “Intestinal bicarbonate secretion is apparently a tightly regulated process and we are hopeful that our planned studies will begin to reveal the mechanisms of its regulation”. A further reason for the continued studies in this area is that the research could have a beneficial effect outside of marine biology. The studies of intestinal transport processes in fish, including bicarbonate secretion could inform scientific investigation of process related to the function of the mammalian kidney and pancreas and therefore impact studies of human health. At the moment, however, focus remains firmly on fish physiology, climate change and ocean surface water pH changes.

Fish are responsible for 3-15 per cent of all ocean calcium carbonate production

Grosell notes how this could be cause for further study: “The balance between the negative effect of reduced biomass and the positive effect of reduced average size on calcium carbonate excretion is unknown but likely depends on the degree of exploitation, the fish species in question and environmental parameters like temperature”. The combination of future increases in sea temperature and rising CO₂ will also affect teleost fish contribution to the marine inorganic carbon cycle. Planned and ongoing studies aim to test if increases in sea temperature and rising CO₂ cause fish to produce more calcium carbonate as the fishes metabolic rates increase.

FUTURE RESEARCH
Grosell is eager to take this research even further and investigate the relation between bicarbonate secretion and calcium carbonate formation, the main focus being on the intestinal processes of the fish, and how it will adapt as CO₂ creates changes in the ocean’s pH levels and the organisms inhabiting our oceans. Many challenges in this area remain to be addressed and understood, as Grosell indicates: “Intestinal bicarbonate secretion is apparently a tightly regulated process and we are hopeful that our planned studies will begin to reveal the mechanisms of its regulation”. A further reason for the continued studies in this area is that the research could have a beneficial effect outside of marine biology. The studies of intestinal transport processes in fish, including bicarbonate secretion could inform scientific investigation of process related to the function of the mammalian kidney and pancreas and therefore impact studies of human health. At the moment, however, focus remains firmly on fish physiology, climate change and ocean surface water pH changes.

The surface water of the oceans often have a considerably higher alkalinity than would be expected from solubility of CaCO₃ produced by many marine organisms, an observation that has often been a cause of bewilderment for marine scientists. Marine life such as plankton also releases calcium carbonate, with coccolithophores being considered the main contributors to oceanic CaCO₃ production. However, the often observed higher alkalinity in surface waters is likely the result of teleost carbonate excretion. Calcium carbonate produced by fish dissolves much faster in shallower water than carbonates produced by plankton. This may be the answer to a phenomenon that has puzzled oceanographers for decades. Whilst carbonate produced by plankton is less soluble and often settles at the bottom, fish carbonates dissolve more rapidly to affect surface water pH.

COMPLEXITIES
An obvious reaction would be that more should be done to prevent overexploitation to marine life. Whilst over fishing will definitely influence the amount of fish in the ocean, it may not have such a severe negative effect on the amount of calcium carbonate being produced as one might suspect. Grosell explains: “Overexploitation, while reducing biomass, also decreases the average size of individual fish and results in a greater rate of calcium carbonate production per unit mass”. Smaller fish, which often occur in larger numbers as a result of exploitation, ingest more seawater and therefore excrete calcium carbonate at a higher rate. Grosell notes how this could be cause for further study: “The balance between the negative effect of reduced biomass and the positive effect of reduced average size on calcium carbonate excretion is unknown but likely depends on the degree of exploitation, the fish species in question and environmental parameters like temperature”. The combination of future increases in sea temperature and rising CO₂ will also affect teleost fish contribution to the marine inorganic carbon cycle. Planned and ongoing studies aim to test if increases in sea temperature and rising CO₂ cause fish to produce more calcium carbonate as the fishes metabolic rates increase.

FUTURE RESEARCH
Grosell is eager to take this research even further and investigate the relation between bicarbonate secretion and calcium carbonate formation, the main focus being on the intestinal processes of the fish, and how it will adapt as CO₂ creates changes in the ocean’s pH levels and the organisms inhabiting our oceans. Many challenges in this area remain to be addressed and understood, as Grosell indicates: “Intestinal bicarbonate secretion is apparently a tightly regulated process and we are hopeful that our planned studies will begin to reveal the mechanisms of its regulation”. A further reason for the continued studies in this area is that the research could have a beneficial effect outside of marine biology. The studies of intestinal transport processes in fish, including bicarbonate secretion could inform scientific investigation of process related to the function of the mammalian kidney and pancreas and therefore impact studies of human health. At the moment, however, focus remains firmly on fish physiology, climate change and ocean surface water pH changes.

Fish are responsible for 3-15 per cent of all ocean calcium carbonate production

CO₂ will also affect teleost fish contribution to the marine inorganic carbon cycle. Planned and ongoing studies aim to test if increases in sea temperature and rising CO₂ cause fish to produce more calcium carbonate as the fishes metabolic rates increase.

FUTURE RESEARCH
Grosell is eager to take this research even further and investigate the relation between bicarbonate secretion and calcium carbonate formation, the main focus being on the intestinal processes of the fish, and how it will adapt as CO₂ creates changes in the ocean’s pH levels and the organisms inhabiting our oceans. Many challenges in this area remain to be addressed and understood, as Grosell indicates: “Intestinal bicarbonate secretion is apparently a tightly regulated process and we are hopeful that our planned studies will begin to reveal the mechanisms of its regulation”. A further reason for the continued studies in this area is that the research could have a beneficial effect outside of marine biology. The studies of intestinal transport processes in fish, including bicarbonate secretion could inform scientific investigation of process related to the function of the mammalian kidney and pancreas and therefore impact studies of human health. At the moment, however, focus remains firmly on fish physiology, climate change and ocean surface water pH changes.