Title

Comparative physiological selectivity of Pennsylvanian to Jurassic extinction in bony fish, sharks and invertebrates

Author

Vazquez, Priscilla Rose

Publication Date

2015

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

COMPARATIVE PHYSIOLOGICAL SELECTIVITY OF PENNSYLVANIAN TO JURASSIC EXTINCTION IN BONY FISH, SHARKS AND INVERTEBRATES

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF SCIENCE

in

EARTH SCIENCE

by

Priscilla Rose Vázquez

March 2015

The thesis of Priscilla Rose Vázquez is approved:

Professor Matthew Clapham

Professor Paul Koch

Professor George Somero

Tyrus Miller
Vice Provost and Dean of Graduate Studies

Table of Contents

Priscilla Vázquez

Comparative physiological selectivity of Pennsylvanian to Jurassic extinction in bony fish, sharks and invertebrates

Abstract

The end-Permian and end-Triassic extinctions coincided with flood basalt eruptions that would have released large quantities of CO_2 into the atmosphere, leading to ocean warming, anoxia, and perhaps acidification. Multiple stresses present during these extinction events provide analogues for anthropogenic CO_2 emissions and can help us understand which taxonomic groups will be threatened by ocean acidification and warming. Bony fish and sharks (Actinoptyergii and Chondrichthyes) have cellular mechanisms to buffer extracellular pH changes from exercise-induced metabolic CO_2 production, which also prove advantageous in buffering against changes in seawater pH. Assessing the extinction of fish during CO_2-driven extinctions will test the hypothesis that active fish are less vulnerable than sessile marine invertebrates. We compiled a database of fossil fish and shark occurrences from the Pennsylvanian to the Middle Jurassic, using the Paleobiology Database, to quantify extinction rates during background and mass extinctions. We used maximum likelihood estimation to compare models using separate extinction rates for vertebrates and invertebrates to models with one extinction rate for all groups. We also reviewed photographs of shark teeth from primary sources in order to classify them based on morphology and interpret changes in feeding mode and activity level through the interval of study. Our results show that sharks suffered less extinction than marine invertebrates during the end-Permian crisis. During the end-Triassic extinction, both sharks and bony fish suffered extinction comparable to that of marine invertebrates. Our results show that sharks and fish are adaptable groups that may have survived extinction through their adaptations for an active life habit, and may be more likely than marine invertebrates to survive extinction in modern global change scenarios.

Acknowledgements

I would like to thank the following people:

Matthew Clapham, my advisor, for this opportunity and his continued help and dedication.

George Somero for letting me sit in on his class on the physiology of global change, and for being on my committee.

Paul Koch, for agreeing to be on my committee even though he’s busy at the ‘deanery’ these days.

the UCSC Earth & Planetary Sciences department, where I learned so much.

the many Paleobiology Database contributors and data enterers.

my husband, Thomas Marlette, for being the most supportive and for providing all the llamas necessary for this study.

and my mother, Susan Vázquez, for being my best friend and for saying “you should move to California!”

Introduction

Since the industrial revolution, carbon dioxide (CO_2) emissions have continued to rise drastically as a result of burning fossil fuels. The addition of CO_2 into the atmosphere is associated with increasing temperature, known as the greenhouse effect. Anthropogenic CO_2 emissions have been released over a short timescale, and the IPCC "business as usual" projection predicts a continual increase of CO_2 in the atmosphere, resulting in further global change (Greene et al. 2012, IPCC 2013, Zeebe et al. 2008).

CO_2 emitted to the atmosphere rapidly is readily absorbed by the ocean and lowers the pH of surface waters. Ocean acidification can occur when a quantity of CO_2 is released over a time period that is too short to allow adequate buffering from adjustment of the carbonate compensation depth, causing dissolution of deep sea carbonates and decreased ocean pH (Zeebe et al. 2008). The biological consequences of a lower pH ocean varies between groups. Marine invertebrates with calcified hard parts would experience difficulty maintaining their skeletons (Gazeau et al. 2010). Metabolic processes are pH sensitive and CO_2 can diffuse easily into organisms (Hochachka & Somero 2002).

The end-Permian and end-Triassic mass extinctions were associated with large releases of CO_2 as a result of volcanic eruptions occurring over short periods of time, making them viable analogues for the short term emissions of CO_2 associated with modern global change (Blackburn et al. 2013, Reichow et al. 2008). These extinctions had devastating effects on marine ecosystems, especially coral reefs (Anlauf et al. 2010). Many biological studies predict that ocean acidification will negatively affect ecosystems in shallow seas and coral reefs (Kroeker et al. 2010). Deep time extinctions provide an opportunity to analyze survival of organisms in their natural environment, rather than in controlled experiments (Greene et al. 2012). CO_2-driven mass extinctions in deep time can provide valuable information on which groups of marine life may suffer extinction as a result of anthropogenic CO_2 emissions.

The time period of study is the Pennsylvanian to the Jurassic, from approximately 318mya to 170mya, which spans both the end-Permian and end-Triassic mass extinction events. Studies of the end-Permian and end-Triassic mass extinctions have linked these events to physiological stress related to large influxes of CO_2 into the environment (Kiessling & Simpson 2011). Knoll et al. (2007) utilized data on marine invertebrate and conodont extinction to interpret the end-Permian mass extinction as a physiologically driven crisis as a result of multiple stresses induced by global change. Using occurrence data from the Paleobiology Database (PaleoBioDb), Clapham & Payne (2011) further proved that the end-Permian mass extinction was physiologically selective for unbuffered, sessile groups of marine invertebrates such as brachiopods and corals. However, these studies focused on marine invertebrates, and do not include marine vertebrates, with the exception of conodonts.

There has been little detailed work focused on the response of active marine vertebrate groups to these mass extinction events (Friedmann & Sallan 2012). Fish and sharks must regularly utilize acid-base regulation to accommodate exercise-induced increases in CO_2, therefore they might be better adapted to environmental increases in CO_2 during times of acidification and warming (Pörtner & Langenbuch 2005). Although some marine invertebrate groups are more active than others, comparing fish and sharks to marine invertebrates provides a greater contrast between activity levels.

We analyze the extinction rate of marine bony fish (Actinopterygii) and sharks (Chondrichthyes) in comparison to that of marine invertebrates through CO_2-driven extinctions from the Pennsylvanian to the Jurassic (Bashkirian-Bajocian) using occurrences of fossil taxa from the PaleobioDB. We are testing the hypothesis that active fish are less vulnerable than sessile marine invertebrates to CO_2-driven extinctions. We expect fish and sharks to suffer less extinction because of their better adapted respiratory physiology. The results will provide information on advantageous physiological adaptations during times of CO_2-driven warming and ocean acidification.

In order to further understand the nature of shark faunal change through period of study, we used occurrence data from shark teeth to interpret abundance changes or extinction within different groups of sharks. Tooth types can indicate different modes of carnivory, and can thus be related to activity level as carnivory requires active pursuit of prey. Using tooth morphology from our occurrence data, we are able to classify genera based on tooth types and interpret changes within families over our time period of study. This can provide insight into activity levels and feeding mode of surviving genera.

End-Permian Mass Extinction

The end-Permian mass extinction is known for its severity as a major biodiversity crisis, and changed the ecological structure of marine ecosystems (Payne & Clapham 2012). The extinction coincided with eruptions of the Siberian traps, one of the largest flood basalts of the Phanerozoic (approximately 5 million km^2). Radiometric dating of flood basalts supports intermittent eruptions spanning a 5 to 10 million period, with the main period of activity coincident with the beginning of the end-Permian extinction (Reichow et al. 2009).

The eruption of the Siberian traps would have released large amounts of volatiles into the atmosphere, perturbing the global carbon cycle and disrupting atmospheric and ocean chemistry. Calculations by Svenson et al. (2009) estimate that the Siberian traps could have released over 30,000 GT of carbon into the atmosphere. A $\delta^{13}C$ excursion observed in marine carbonates at more than 100 localities supports global carbon cycle disruption (Payne et al. 2004). The rapid release of large quantities of volatiles into the atmosphere may have reduced ocean pH in the surface oceans, implied by a negative shift in calcium isotopes suggestive of limestone dissolution (Payne et al., 2010). Permian oceans lacked deep-sea carbonate sediment to buffer this change in pH (Archer et al. 1997, Payne et al. 2004, Payne et al. 2010).

The increase in atmospheric CO_2 levels would have caused warming in addition to reduction of ocean pH. At the Permo-Triassic boundary a large decrease in $\delta^{18}O$ values has been interpreted to represent a global temperature increase of approximately 10-14°C, with sea surface temperatures possibly reaching 40ºC (Sun et al. 2012). This warming may have reduced the amount of dissolved oxygen in the ocean and slowed ocean circulation (Kidder & Worsley 2004). Laminated sedimentary deposits with small pyrite framboids indicate euxinia and further support anoxia in shallow seas. (Bond & Wignall 2010, Wignall & Twitchett 1996).

The combined stresses of ocean acidification, global warming, and periodic anoxia resulted in the decimation of many Paleozoic fauna; there were few areas of refuge for marine invertebrates, resulting in widespread extinction of many groups. Trilobites, goniatite ammonoids, blastoids, fenestrate bryozoans, strophomenate and spiriferid brachiopods all occur for the last time in Changhsingian strata (Payne & Clapham 2012). The end-Permian is associated with a large turnover among crinoids and severe extinction of calcified foraminifera, especially fusulinids. Reef ecosystems were particularly affected; tabulate and rugose corals went extinct, as well as approximately 70% of sponge genera (Payne & Clapham 2012). Reef ecosystems collapsed abruptly at the end-Permian, leading to the early Triassic replacement of traditional reef structures with microbialite reefs (Bond & Wignall 2009, Clapham & Payne 2012, Payne & Clapham 2011, Pruss & Bottjer 2004, Weidlich 2002).

End-Triassic Mass Extinction

The end-Triassic mass extinction also severely affected marine invertebrates and reef ecosystems, and did not spare the modern fauna (mollusks) that dominated these ecosystems in the recovery following the end-Permian. The end-Triassic extinction coincided with the eruption of the Central Atlantic Magmatic Province (CAMP), 10 million km^2 of flood basalts associated with the breakup of the Pangea supercontinent. (Blackburn et al. 2013). Volcanic activity consisted of 3-5 pulses over a period of less than 2 million years (Greene et al. 2012, Hautmann 2004, Pálfy 2003).

As a result of CAMP volcanic activity, large amounts of ^{13}C-depleted CO_2 and other greenhouse gases were released into the atmosphere. Negative carbon excursions in marine sediments, leaf wax lipids, and wood have been demonstrated as evidence of a perturbation of the global carbon cycle (Pálfy 2003, Whiteside 2010). Analysis of plant stomata from Greenland and Europe support pCO_2 rising from approximately 800-1000ppm at the end of the Rhaetian to 1700-2500ppm at the beginning of the Hettangian (McElwain et al. 1999). Studies of paleosols have estimated even higher CO_2 concentrations (Hautman et al. 2008). The CO_2 and other volatiles released in the eruptions led to an approximated 3-4°C global temperature increase. Palynological data also support warming across the extinction event (Greene et al. 2012, Ruhl et al. 2011).

The magnitude of emissions associated with CAMP volcanic event along with their short timeframe are sufficient to cause acidification in end-Triassic oceans (Kiessling & Simpson 2011, Greene et al. 2012). Correlation of sections across Europe and the Americas shows a reduction in limestone deposition across the boundary that may have been caused by ocean acidification and reduced carbonate saturation (Hautmann 2004).

The combined stresses of warming and ocean acidification proved catastrophic for Triassic marine invertebrates, including the modern fauna. Reef organisms were most severely affected, including families of bivalves, brachiopods, sponges and corals. The end-Triassic also exhibits a large turnover of foraminifera, dinoflagellates and radiolarians (Hallam 2002). Pelagic fauna such as ceratite ammonoids and conodonts also went extinct. Recently, studies involving the PaleobioDB further elucidated the severity of the extinction, demonstrating that 41% of benthic Rhaetian genera did not survive to the beginning of the Hettangian (Kiessling et al. 2007). In bivalves, infaunal lifestyle and aragonite and high magnesium calcite skeletal mineralogy were selected against (Hautmann 2004, Kiessling et al. 2007). Ammonoids were the most severely affected aragonite mollusks and all but one superfamily may have gone extinct (Hautmann 2004). Study of the PaleobioDB shows that extinction was also related to habitat preference; inshore reef fauna were more affected than offshore fauna (Greene et al. 2012, Kiessling et al. 2007).

The end-Triassic extinction may have been as brief as 50kya, but diversity did not recover for millions of years (Hautmann 2004). The brief timeframe of the end-Triassic extinction indicates that short term periods of ocean acidification may have detrimental effects on organisms and long term effects on ecosystems (Marzoli et al. 2004). The coupled stresses of warming and ocean acidification proved especially detrimental to end-Traissic fauna incapable of adapted to harsh environmental changes within short periods of time.

Physiological Selectivity of Extinctions

Further study of the end-Permian and end-Triassic extinctions have led to the conclusion that these extinctions were physically selective. Knoll et al. (2007) analyzed the extinction of marine invertebrates through the end-Permian extinction event using Sepkoski's compendium and proposed that survival of the combined stresses of warming and acidification selected against clades with weakly buffered respiratory and skeletal physiology. Particular groups of marine invertebrates, such as calcified and sessile organisms, suffered more severe extinction as a result of high atmospheric carbon dioxide levels, ocean acidification and anoxia in shallow seas (Knoll et al. 2007, Payne & Clapham 2012).

Studies using the PaleoBioDb confirm the importance of respiratory physiology and shell mineralogy in determining which species survived CO_2 driven extinctions like the end-Permian and end-Triassic. Clapham & Payne's study (2011) of nearly 50,000 marine invertebrate fossil occurrences showed that taxa with non-calcareous shells were more likely to survive. The importance of shell mineralogy to survival indicates ocean acidification was a major stress in the end-Permian extinction. Marine organisms with limited ability to buffer themselves against changes in pCO_2, temperature, pH and oxygen concentration were selected against. The Permian fauna was more susceptible to these stresses as it was dominated by low-metabolism, physiologically unbuffered Paleozoic marine invertebrates, which have largely been replaced by mollusks in modern day ecosystems (Clapham & Payne 2011). The end-Triassic extinction was also CO_2-driven and studies using the PaleoBioDb show it was selective against calcified sponges and corals and physiologically unbuffered groups (Kiessling & Simpson 2011).

Global change and resulting physiological effects

The entry of CO_2 into the ocean causes a shift in the equilibrium of carbonate in the ocean, reducing the saturation state of calcite and aragonite and potentially leading to carbonate dissolution. Skeletal physiology is vulnerable to acid-base perturbations; during times of acidification, marine invertebrates with calcified shells have difficulty forming and maintaining their skeletons. Precipitation of calcite and aragonite requires acid-base regulation in ocean waters; this causes metabolic demand to be increasingly costly during times of low carbonate saturation (Pörtner 2008).

CO_2-driven warming can also negatively affect physiology in many different ways. Warming perturbs the structures of macromolecules, which in turn negatively affects the systems and functions they support. Most intracellular processes are temperature dependent and must be in steady state for optimal function. Biochemical reaction rates approximately double for every 10ºC increase in temperature; rates of metabolic reactions are temperature sensitive (Hochachka & Somero 2002).

Respiratory physiology is negatively affected during times of CO_2-induced warming because higher temperatures increase oxygen consumption in poikilothermic organisms like marine invertebrates and fish. High temperature extremes trigger loss of aerobic scope in an organism, caused by the limited capacity of effective oxygen supply through ventilation and/or circulation (Pörtner 2005). Marine invertebrates and fish exhibit an oxygen-limited thermal tolerance in which internal hypoxia modifies the constraints of the organisms' thermal tolerance (Pörtner 2005). Oxygen binding in blood is inhibited by high CO_2, limiting metabolic function; thus marine invertebrates may not be able to consume enough oxygen to reach their metabolic demands during times of CO_2 driven stress (Somero 2010). Hypoxic stress interacts with stresses from hypercapnia and high temperature to reduce metabolic function and growth (Payne & Clapham 2012, Pörtner 2005). The consequences of combined stresses are simultaneous; rising atmospheric CO_2 leads to falling pH, increase in temperature, and decreases in dissolved oxygen within the oceans.

Long term inadequate oxygen supply affects all higher functions of the organism including behavior, feeding, digestion, motor activity, growth and reproduction; this will affect species over longer timescales at the population, species and ecosystem levels (Pörtner 2005). Compression of habitat by depth range may also occur due to hot shallow seas and low oxygen at depths (Pörtner 2005).

Why we expect fish and sharks to be 'winners'

Modern marine invertebrates show limited adaptive capability when subjected to the stresses of CO_2-driven warming and acidification. A meta-analysis of 251 unique physiological experiments involving biological responses of marine organisms to ocean acidification shows that many groups exhibit negative effects on survival, growth, reproduction and calcification despite varying sensitivity between groups (Kroeker et al. 2010).

Organisms in the ocean depend heavily on ion exchange as a means of compensation for disruptions in pH or CO_2 (Pörtner 2005). CO_2 diffuses into organisms easily and oxygen uptake and metabolism are pH sensitive processes. For an organism to adapt to these disruptions, it must be able to reach an acid-base equilibrium at different values, which may limit processes such as growth and reproduction (Pörtner & Langenbuch 2005).

While invertebrates with high internal CO_2 suffer acidosis, fish are able to compensate for hypercapnic stress. Sharks and fish may be less sensitive to stresses of hypercapnia because of intracellular haemoglobin involved in oxygen transport as opposed to extracellular hemocyanin found in cephalopods (Pörtner & Langenbuch 2005). Hemocyanin relies on specific extracellular pH conditions in order to effectively transport oxygen; intracellular haemoglobin is advantageous in that it is less likely to be disrupted by changes in extracellular pH (Pörtner & Langenbuch

2005). Sharks and fish have higher regulatory capacities of ion exchange than invertebrates; they also have epithelia (ie. more advanced gills) which help to minimize diffusive ion losses (Pörtner & Langenbuch 2005).

Active species like sharks and bony fishes regularly experience high pCO_2 fluctuations during exercise. Increases in metabolic rate as a result of exercise require transepithelial ion regulatory mechanisms to counteract pH disruption as a result of high pCO_2 (Pörtner & Langenbuch 2005). Acid-base perturbations as a result of global change can be compared to continual circulatory acidosis as observed during strenuous exercise. The efficiency of acid-base compensation scales with metabolic rate; thus more active, high metabolism species have more tolerant CO_2 physiotypes and can better regulate their extracellular environment (Melzner et al. 2009, Pörtner & Langenbuch 2005).

Thermal stresses affect physiological mechanisms in a similar manner as CO_2 driven stresses. Size and activity level also affect thermal tolerance, with active species exhibiting higher heat tolerances than less active species (Peck et al. 2009). Since sharks and fish have higher metabolic rates they may have higher heat tolerances, and thermal stress may not be as detrimental. This advantageous adaptation indicates that sharks and fish are more likely to survive thermal stress as a result of CO_2-driven extinctions than marine invertebrates (Peck et al. 2009, Pörtner & Langenbuch 2005, Somero 2010).

Previous studies of the end-Permian extinction have found little loss in richness of species of fish and sharks (Blieck 2011, Mutter et al. 2007, Mutter & Neuman 2008, Schaeffer 1973). The effect of the end-Triassic extinction on fish and sharks remains unclear, with the exception of the well documented disappearance of conodonts (Friedman 2012). Analyzing the extinction of bony fish and sharks through the Mesozoic will provide insight into how these groups will be affected under modern CO_2-driven stress.

Methods

We are testing the hypothesis that active cartilaginous and bony fishes are less vulnerable than sessile marine invertebrates to CO_2-driven extinctions in the Mesozoic. We used data from marine invertebrate occurrences in the PaleoBioDB, and entered occurrences of marine fishes and sharks from the primary literature. Marine invertebrate occurrences include Bryozoa, Cnidaria, Porifera, Brachiopoda, Mollusca, Trilobita, Echinodermata, and Ostracoda. A total of 158601 occurrences from 3904 references were used. Shark occurrences consist of Chondrichthyes, excluding Xenacanthiformes, totaling 2391 occurrences from 360 references. Occurrences of bony fishes were from the group Actinopterygii, including 1693 occurrences from 273 references. Nonmarine collections from all groups were excluded. Xenacanthiformes were excluded because they may be euryhaline; they are primarily freshwater species but may be found washed into marine localities (Schutlze 1985).

Extinction rates of sharks, bony fishes and invertebrates were calculated at the Fossilworks site (www.fossilworks.org) using the boundary crosser method (Foote 2000) through ten million year bin time intervals (table 1) (Alroy 2010). We used maximum likelihood estimation to compare models using separate extinction rates for vertebrates and invertebrates to models with one extinction rate for all groups. Maximum likelihood estimation has been used previously to compare models of extinction selectivity of reef-builders to that of marine invertebrates (Kiessling & Simpson 2011). Following the methods of Kiessling & Simpson (2011), we then used Akaike's modified information criterion (AIC) to measure the support for preselected models. A model is supported if it receives an AIC weight greater than 0.89 (Kiessling & Simpson 2011).

To analyze shark ecology based on occurrences, we searched for articles within the primary shark literature in which teeth specimens were illustrated. Ciampaglio et al. (2005) observed several morphological characters of shark teeth and used principal component analysis (PCA) to map morphospace based on those characteristics. Ciampaglio et al. (2005) designated tooth types based on the different map regions; tooth types are clutching, piercing/gouge, crushing/grinding, slicing/gouge, grasp/crush/chop. We looked at as many morphological characteristics available in images that were visible in plates and diagrams. Many specimens were omitted due to pathology, poor preservation and/or poor scanned quality of diagrams and images. Characters observed included the number and configuration of cusps, width of cusps, presence of serrations and presence of lateral cusplets.

The clutching group is characterized by a generally homodont dentition, with prominent lateral cusplets used for holding onto prey. This tooth type is found mainly in small bottom feeding sharks. Specimens belonging to the slicing/gouge group have teeth that are wide and flat labiolingually, usually oriented as one row of blade with serrated cutting edges. These serrated edges may have been used to slice or gouge flesh of larger prey. The pierce/gouge group is characterized by teeth with narrow anterior cusps that are smooth and pointed. The teeth are usually arranged in many functional rows to facilitate piercing and grasping prey. Crushing/grinding dentitions are arranged in many files and rows with robust, bulging crowns. The teeth can have a smooth or pitted enamel surface; some may have a polygonal outline. This dentition enabled the specialization of smashing open prey with hard shells, enabling sharks to eat shellfish, small fish and cephalopods. The grasp/crush/chop dentition consists of rather simple, conical robust teeth used to puncture and restrain prey, and smash and chop bones (Cappetta 1987, Ciampaglio et al. 2005).

We used assigned tooth types to genera within the PaleobioDB, and counted the number of occurrences of each type in each ten million year bin. The Early Permian (Permian 1 and 2 bins), Early Triassic (Triassic 1 bin) and Jurassic bins were omitted because they had fewer than 20 occurrences. We then analyzed the proportion of occurrences of each tooth type per interval.

All calculations and data analyses were done using SciPy. Data sets were downloaded from Fossilworks on November 16, 2014.

Results

Actinopterygii and marine invertebrate extinction comparison

Marine invertebrate groups exhibit high extinction rates for both the end-Permian and end-Triassic (figure 3). Actinopterygian occurrences are so sparse that time periods Permian 1 - 3 have 0 value extinction rates. The end-Triassic extinction is well exhibited, and the peak in extinction rate value in the Triassic 4 period is similar to that of marine invertebrates.

In the Akaike weights of the maximum likelihood estimation results, NA values are present where there are not enough occurrences to perform maximum likelihood estimation on the raw boundary crosser extinction rate data (table 2). In all time periods, neither one rate nor two rate models of extinction are supported by an Akaike weight greater than 0.89. The one rate model during the Triassic 4 time period has nearly enough support, suggesting that Actinopterygii and invertebrates may have shared one extinction rate at the end-Triassic.

Unfortunately, end-Permian actinopterygian occurrences were too sparse to interpret boundary crosser extinction rates for the end-Permian mass extinction (figures 1 and 2).

Chondrichthyes and marine invertebrate comparison

The number of occurrences of Chondrichthyes per ten million year bin is less than that of marine invertebrates over the time period of study (figures 5 and 2).

Though the data are sparse, there are enough occurrences of Chondrichthyes to calculate extinction rates accurately using the boundary crosser method, as well as perform maximum likelihood analysis on the raw data.

In our comparison of chondrichthyan and marine invertebrate boundary crosser extinction rates, there is a peak in Chondrichthyes extinction rate prior to the end-Permian extinction (Permian 3 and 4 respectively, figure 5). This is followed by a peak in the Triassic 4, higher than that of marine invertebrates, within the end-Triassic extinction interval.

Akaike weights of the maximum likelihood results are used to compare one rate and two rate models of extinction for Chondrichthyes and marine invertebrates (table 3). NA values represent time periods where there are not enough occurrences to perform maximum likelihood estimation on raw boundary crosser extinction rate data. The only time period supporting separate extinction rates for Chondrichthyes and marine invertebrates is Carboniferous 5 (Akaike weight >.089, shown in bold print). For all other time periods, neither one rate nor two rate model received significant support. The Akaike result for the end-Permian extinction event is very close to supporting two separate extinction rates for Chondrichthyes and marine invertebrates. While the result does not meet the 0.89 threshold for Akaike weights, it likely is significant as the weights for most of the other intervals show more support for the one rate model.

Chondrichthyan tooth ecology

To compare tooth type data between time periods we used the proportion of each tooth type per time period (figure 6). Though we do have data from Permian 4, which ends in the end-Permian extinction, Triassic 1 does not have enough occurrences for analysis. The final bin in our data with sufficient occurrences is Triassic 4, the end-Triassic extinction interval, but we do not have enough occurrences in Jurassic 1 to include the interval in our study. Unfortunately due to this sparseness of data we cannot draw conclusions on these extinction events.

The proportion of occurrences of tooth type 1 (clutching) diminishes after Permian 3, with the exception of a small fraction of occurrences in intervals Triassic 2 and Triassic 4 (figure 6). Tooth type 2 (slicing/gouging) reaches its maximum proportion at Permian 4, and declines in Triassic 4. Tooth type 3 (piercing/gouging) decreases in proportion from Carboniferous 5 to Permian 4, and then increases in Triassic 2. Tooth type 4 (crushing/grinding) increases after Carboniferous 4 and maintains a steady proportion until it increases again in Triassic 2. Tooth type 5 (grasp/crush/chop) maintains a small proportion from Carboniferous 4 to Permian 3, then decreases significantly and does not return to its original proportion. Of all the tooth types, tooth type 5 has the least number of occurrences in the time period of study.

Carboniferous 4 (figures 6-7)

The Carboniferous 4 interval has a somewhat balanced proportion of all included tooth types, with tooth type 2 (slicing/gouge) containing the most occurrences. Occurrences of the families Edestidae and Siborhynchidae contribute to the high proportion of tooth type 2. Siborhynchidae occurrences also account for the majority of tooth type 5 occurrences within this stage. Tooth type 3 has few occurrences relative to the other types, most of which are contributed by the family Symmoridae. Tooth type 1 occurrences are almost entirely from the families Ctenacanthidae and Heslerodidae.

Carboniferous 5 (figures 6, 8)

In comparison to Carboniferous 4, the Carboniferous 5 interval exhibits a decrease in tooth types 1 through 3 (clutching, slicing/gouge, pierce/gouge respectively) and an increase in type 4 (crushing/grinding). The decrease in occurrences of tooth type 1 is likely due to the lower number of occurrences within the families Ctenacanthidae and Heslerodidae. The decrease of occurrences of tooth type 2 reflects the lower number of occurrences within the families Siborhynchidae, Janassidae, and Edestidae, all of which only have 1-2 occurrences of this type in this time period. The lower proportion of tooth type 3 occurrences is likely due to fewer occurrences within the Iniopterygidae and Ctenacanthidae families. The increase of tooth type 4 is reflected in a significant increase in the occurrences of Petalodontidae, a durophagous group. The slight increase of tooth type 5 occurrences is contributed by an increase in Iniopterygidae occurrences of this type; in Carboniferous 4 this family had a higher proportion of tooth type 3 occurrences relative to tooth type 5.

Permian 3 (figures 6, 9)

The earliest Permian interval present in our data is Permian 3. In Permian 3, the proportion of type 3 (pierce/gouge) occurrences decreased substantially compared to the Carboniferous 5. There is only 1 occurrence of tooth type 3 within this time period, contributed by an unclassified genus. There are occurrences of Ctenacanthidae in this time period, however none are classified as tooth type 3.

The proportion of occurrences of tooth type 4 is slightly less than that of Carboniferous 5, however the occurrences are contributed largely from unclassified families. Ctencanthidae occurrences provided a proportion of tooth type 4 occurrences in Carboniferous 5, however there is only 1 occurrence of tooth type 4 in this family in Permian 3. The proportion of tooth type 5 in Permian 3 is unchanged from Carboniferous 5, however the occurrences of tooth type 5 in this stage are mostly from unclassified genera.

Permian 4 (figures 6, 10)

Permian 4 shows a very different proportion of tooth types from Permian 3. Occurrences of tooth type 1 are absent from the Permian 4 interval. The largest proportion of occurrences in the Permian 4 interval is tooth type 2 (slicing/gouge). In our study tooth type 2 does not again reach this high proportion (figure 6). This trend is driven largely by the increase of occurrences within the family Janassidae. While there were no occurrences of Edestidae in Permian 3, in Permian 4 they contribute 2 occurrences of tooth type 2. Cochliodontidae, another family that contributed occurrences of tooth type 2 in Permian 3, has no occurrences in Permian 4. There are a few more occurrences of tooth type 2 within Agassizodontidae that also contribute to the high proportion of this tooth type. This concurs with shifts in tooth type proportions observed by Koot (2013), and supports the variable pattern of this tooth type through the Permian.

Tooth type 3 (pierce/gouge) increased slightly (by 3 occurrences) in Permian 4 relative to Permian 3. This is due to a small number of occurrences being contributed by Ctenacanthidae, and a larger number of occurrences contributed by unclassified genera.

Tooth type 4 (crushing/grinding) decreased slightly in Permian 4 relative to Permian 3. These findings agree with the results of Koot (2013). There are no occurrences tooth type 4 from unclassified genera in this time interval, unlike that of Permian 3. The family Ctenacnathidae contributes a significant number of these occurrences, as previously discussed, and a small number of occurrences are again contributed by occurrences of Edestidae. Other occurrences come from families not included in previous intervals: Caseodontidae, Hybodontidae, Pristodontidae, and Acrondontidae.

There are no occurrences of tooth type 5 in Permian 4. In our data this type does not reach its Carboniferous 4 and 5 proportions again.

Triassic 2 (figures 6, 11)

The next stage included in our study is Triassic 2, which is within the Middle Triassic. In our data tooth type 1 returns as a single occurrence within an unclassified genus, and tooth type 2 decreases back to near its Carboniferous 5 proportion (figure 6). In Triassic 2 there are no occurrences of Janassidae in our data; this family contributed a majority of tooth type 2 occurrences in Permian 4. Agassizodontidae and Edestidae also do not occur; the small number of occurrences within tooth type 2 are provided by the family Paleospinacidae, which has not occurred in previous stages for our data. Tooth type 3 increased significantly in proportion of occurrences, reaching its highest proportion since Carboniferous 4. A small number of occurrences are provided by unclassified genera. Hybodontidae contributes the majority of the tooth type 3 occurrences, and only 1 occurrence of tooth type 4.

Though Hybodontidae only has 1 occurrence of tooth type 4 in Triassic 2, tooth type 4 increased from its Permian 3 proportion. This is due to a larger number of occurrences, the majority of which are within Acrodontidae and Polyacrodontidae. A small number of occurrences are from unclassified genera, as well as the family Lonchidiidae, which has not been present in previous stages. In Triassic 2 there are no occurrences of tooth type 5 in our data.

Triassic 3 (figures 6, 12)

In the Triassic 3 interval, there are no occurrences of tooth types 1 and 5. The proportion of occurrences of tooth type 2 increased in Triassic 3. Paleospinacidae is the only family with occurrences of tooth type 2 in Triassic 3; Pseudodalitiidae provided occurrences of tooth type 2 in Triassic 2, however in Triassic 3 this family is no longer represented. Tooth type 3 decreased in proportion from its Triassic 2 condition. The remaining occurrences within tooth type 3 are from unclassified genera.

The proportion of occurrences of tooth type 4 is generally unchanged from Triassic 2. In Triassic 3 there are more occurrences of Acrodontidae, which is again the main contributing family. The other contributing families, Lonchidiidae and Polyacrodontidae, both decreased in number of occurrences.

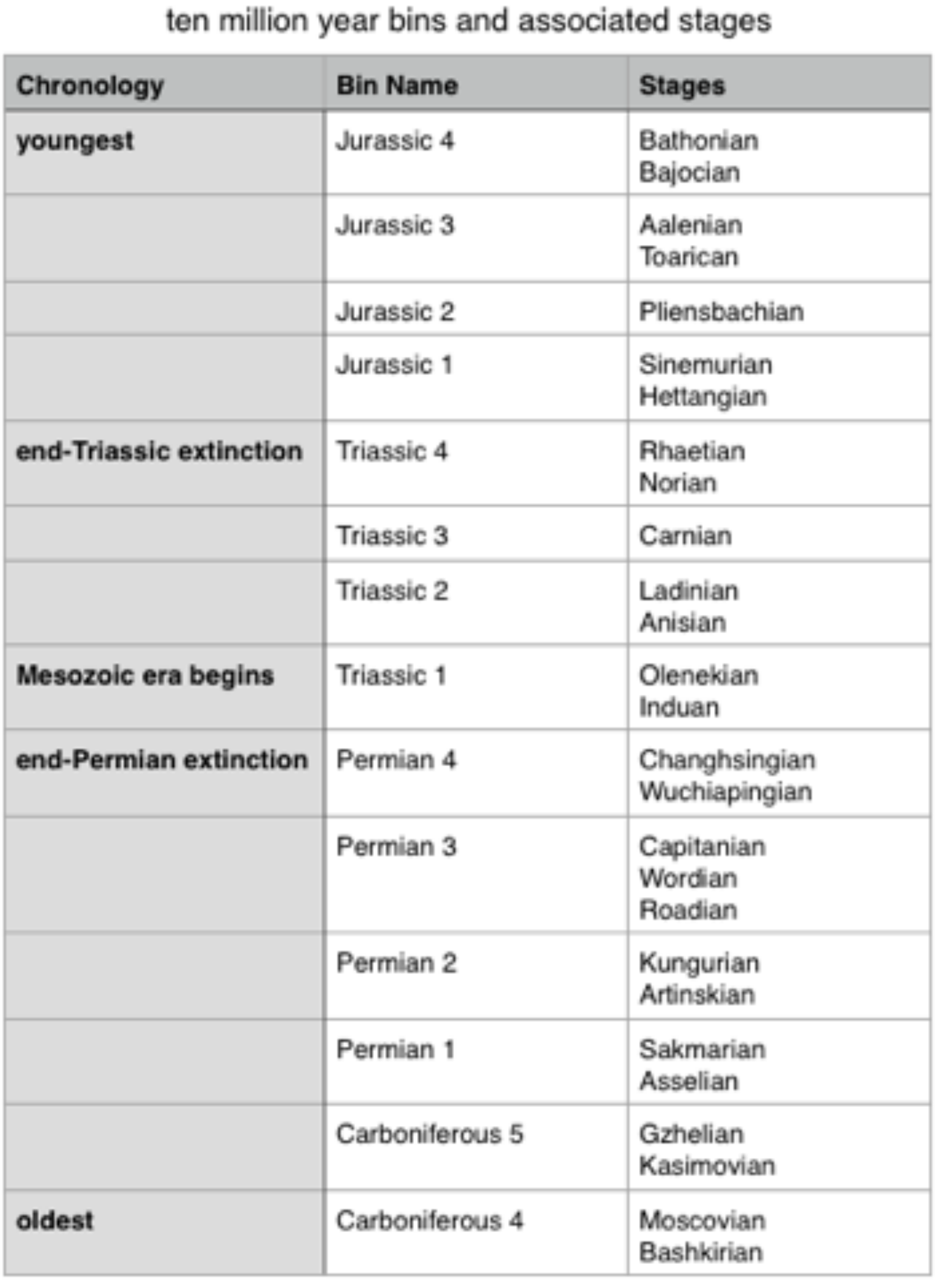
Triassic 4 (figures 6, 13)

The final stage included in our study of chondrichthyan tooth types is the Triassic 4, the final interval in the Triassic. In Triassic 4, tooth type 1 reappears with 3 occurrences contributed from unclassified genera. The proportion of tooth type 2 decreased from its Triassic 3 value. Though the family Pseudodalatiidae reappears as a contributor to this tooth type, there are far fewer occurrences of Paleospincidae, which likely accounts for this decrease. Cetorhinchidae appears for the first time in our data in Triassic 4 and contributes 3 occurrences to tooth type 2.

Tooth type 3 nearly doubles in proportion of occurrences in Triassic 4. This is likely influenced by an increase of occurrences in the family Hybodontidae, as well as from unclassified genera. Tooth type 4 remains stable in proportion of occurrences, however in Triassic 4 the family Acrodontidae has fewer occurrences. An increase in the occurrences of Lonchiidae and Polyacrodontidae contribute to the stable proportion of this tooth type. Tooth type 5 reappears in Triassic 4 with only 1 occurrence from an unclassified genus.

Figures

Table 1



ten million year bins and associated stages

Chronology	Bin Name	Stages
youngest	Jurassic 4	Bathonian Bajocian
	Jurassic 3	Aalenian Toarican
	Jurassic 2	Pliensbachian
	Jurassic 1	Sinemurian Hettangian
end-Triassic extinction	Triassic 4	Rhaetian Norian
	Triassic 3	Carnian
	Triassic 2	Ladinian Anisian
Mesozoic era begins	Triassic 1	Olenekian Induan
end-Permian extinction	Permian 4	Changhsingian Wuchiapingian
	Permian 3	Capitanian Wordian Roadian
	Permian 2	Kungurian Artinskian
	Permian 1	Sakmarian Asselian
	Carboniferous 5	Gzhelian Kasimovian
oldest	Carboniferous 4	Moscovian Bashkirian

Table 1: Ten million year bins in chronological order with stages included within each.

Figure 1

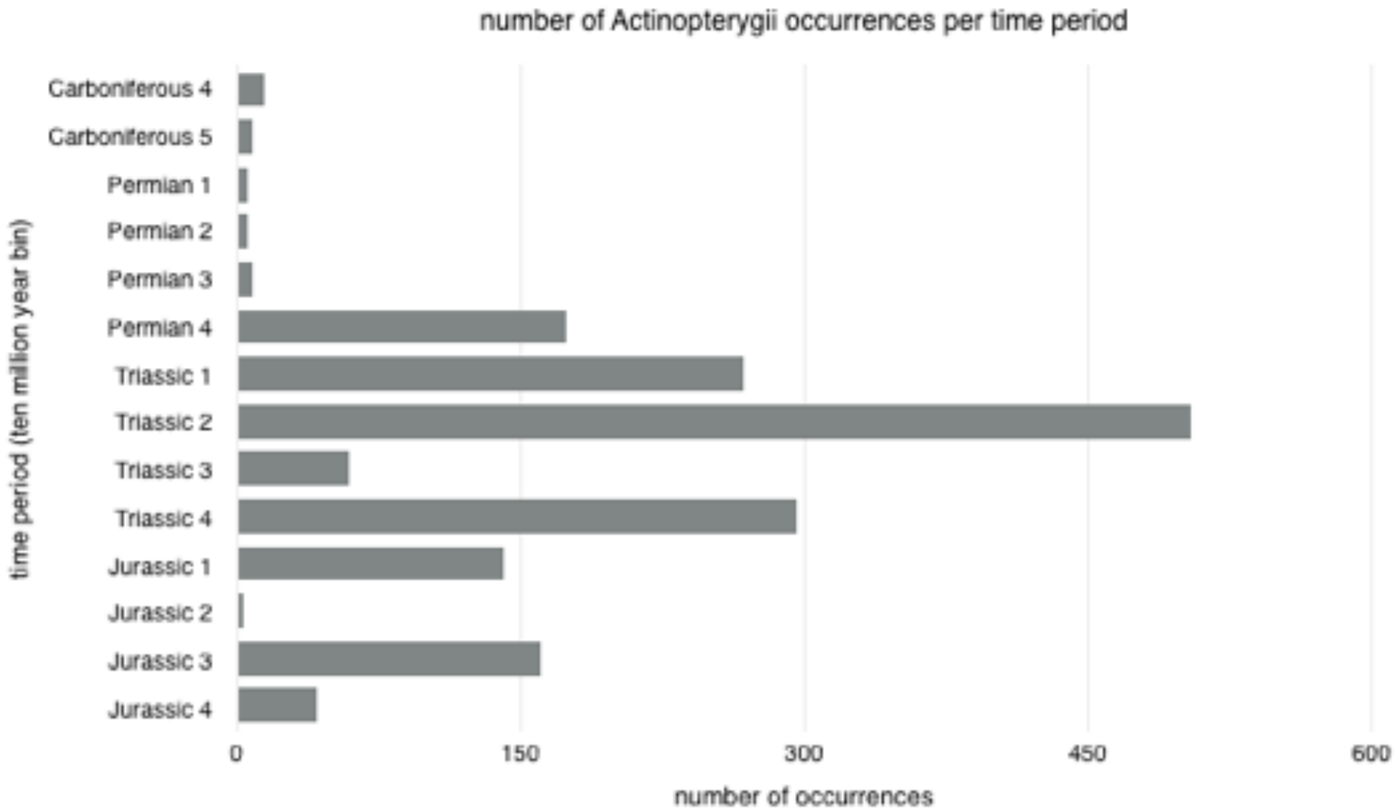


Figure 1: Number of actinopterygian occurrences in each ten million year bin included in this study.

Figure 2

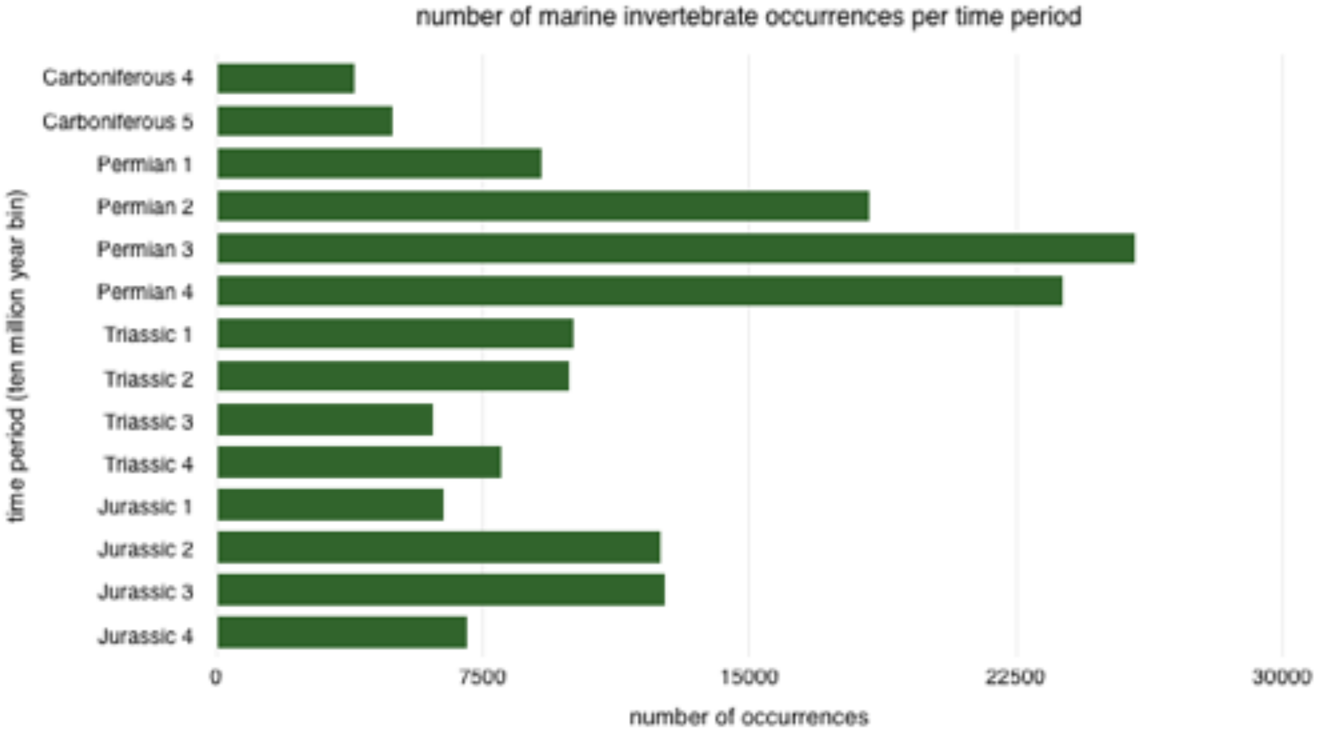
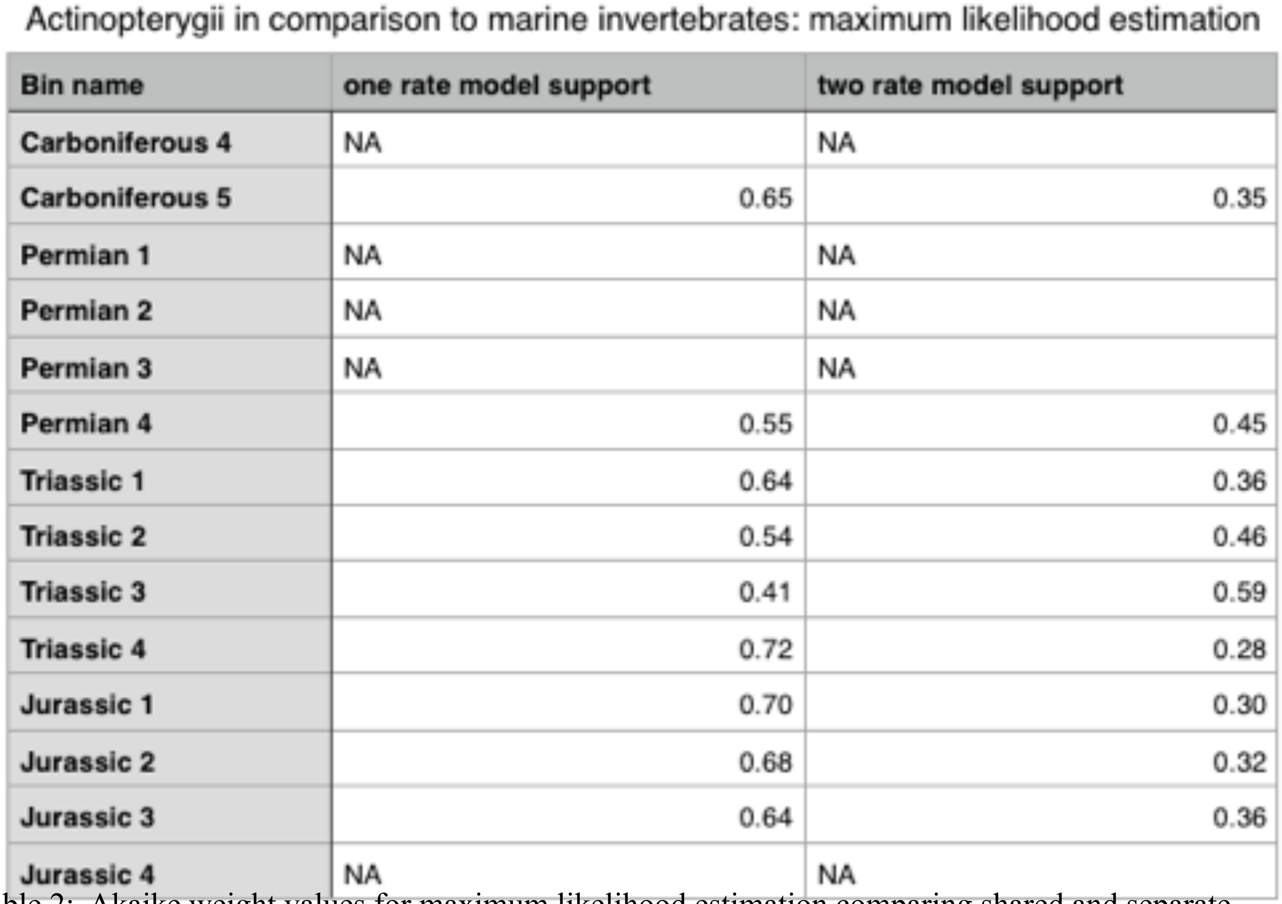


Figure 2: Number of marine invertebrate occurrences in each ten million year bin included in this study.

Table 2



Actinopterygii in comparison to marine invertebrates: maximum likelihood estimation

Bin name	one rate model support	two rate model support
Carboniferous 4	NA	NA
Carboniferous 5	0.65	0.35
Permian 1	NA	NA
Permian 2	NA	NA
Permian 3	NA	NA
Permian 4	0.55	0.45
Triassic 1	0.64	0.36
Triassic 2	0.54	0.46
Triassic 3	0.41	0.59
Triassic 4	0.72	0.28
Jurassic 1	0.70	0.30
Jurassic 2	0.68	0.32
Jurassic 3	0.64	0.36
Jurassic 4	NA	NA

Table 2: Akaike weight values for maximum likelihood estimation comparing shared and separate extinction rates for actinopterygians and marine invertebrates.

Figure 3

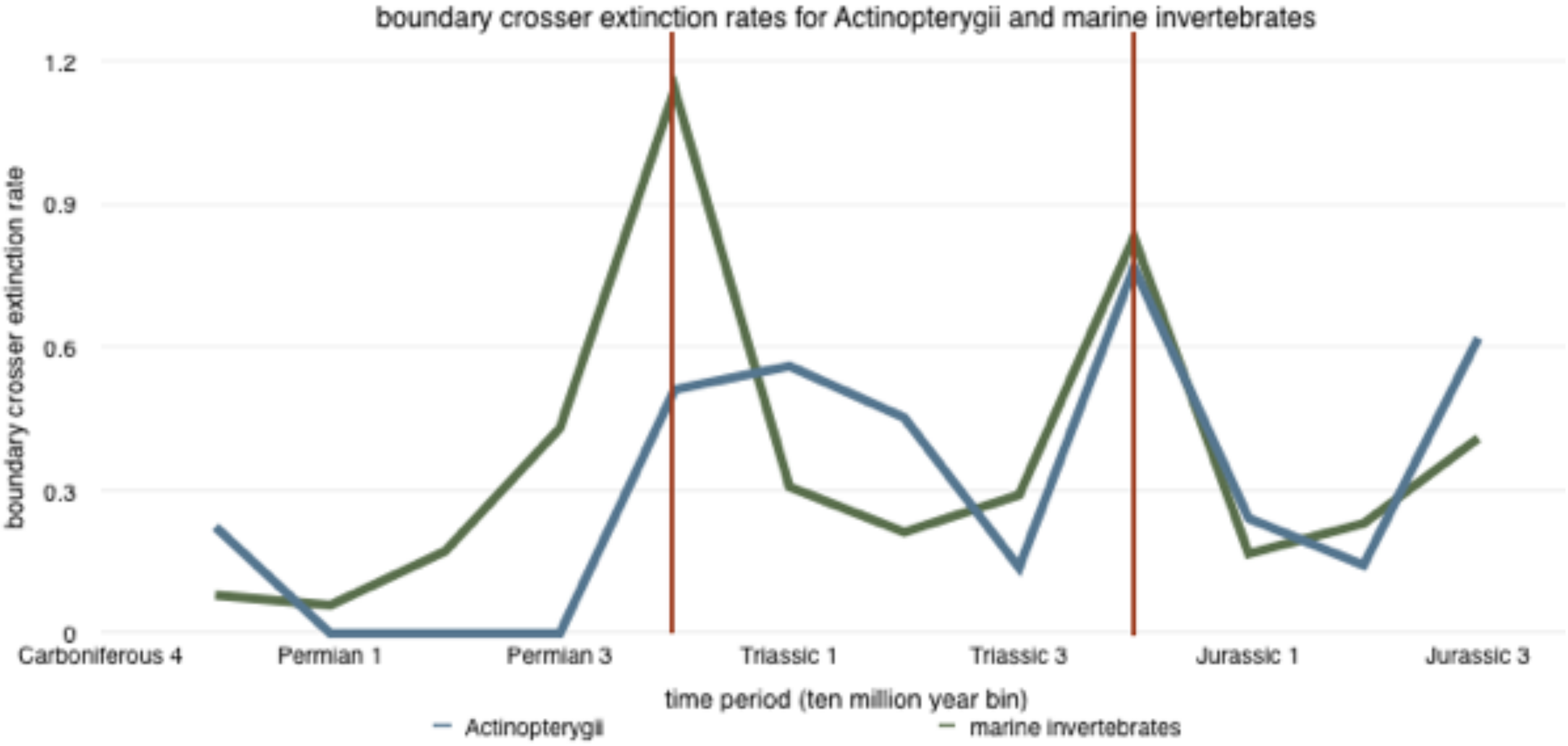


Figure 3: Raw boundary crosser extinction rates for actinopterygians and marine invertebrates. Calculated using FossilWorks. Vertical red lines indicate end-Permian and end-Triassic mass extinction events.

Figure 4

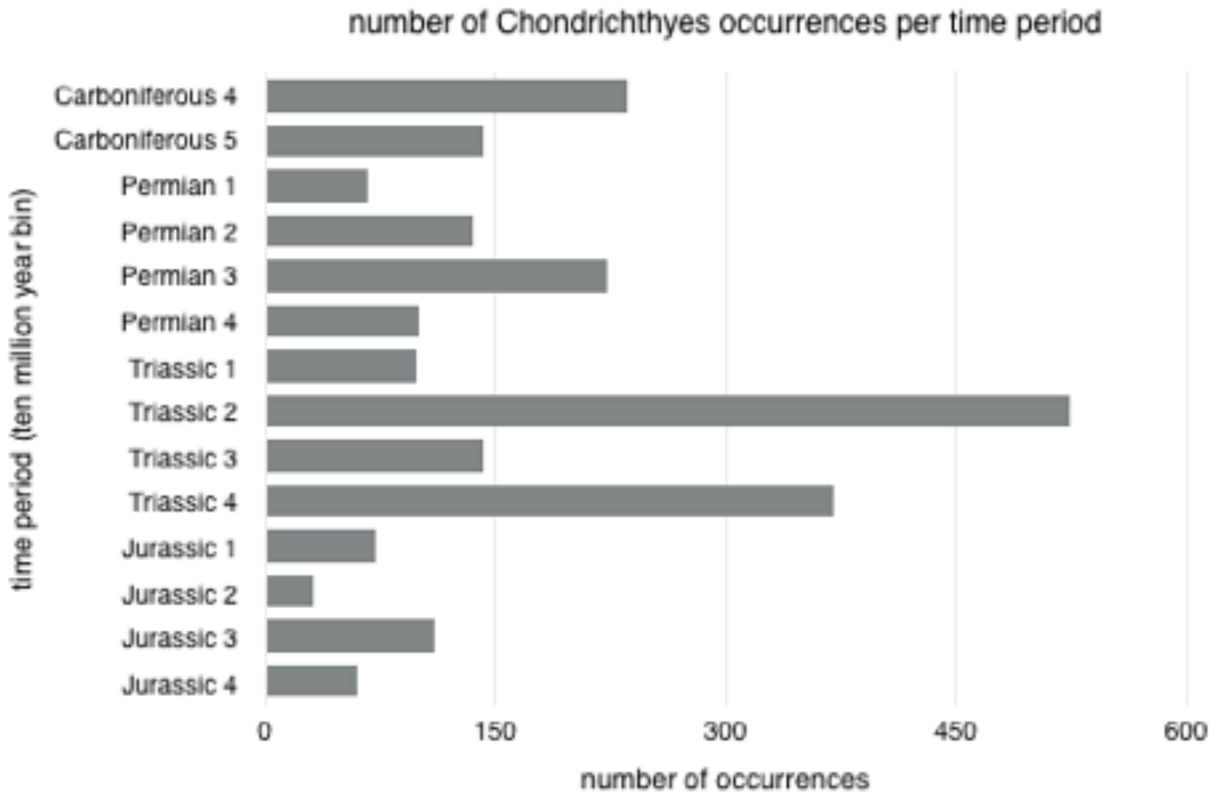


Figure 4: Number of occurrences of chondrichthyans per ten million year bin included in this study.

Figure 5

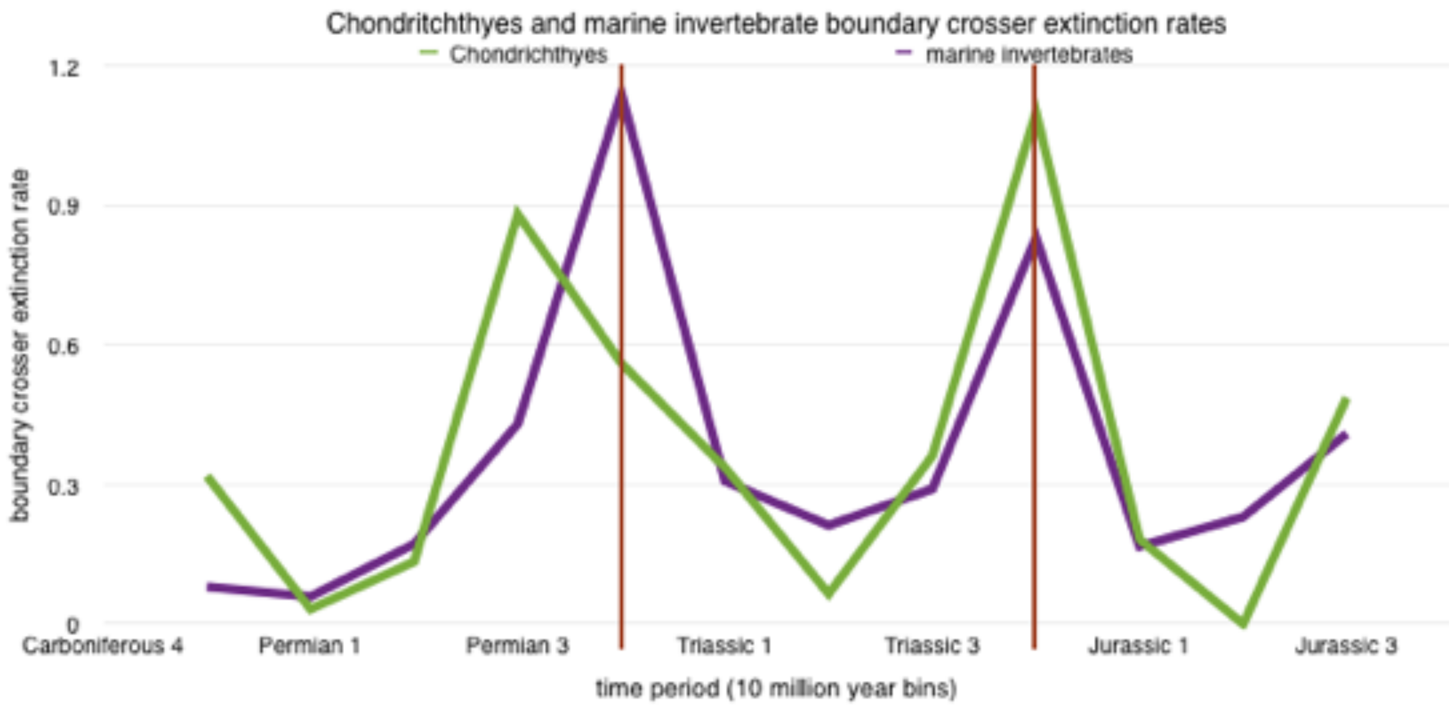
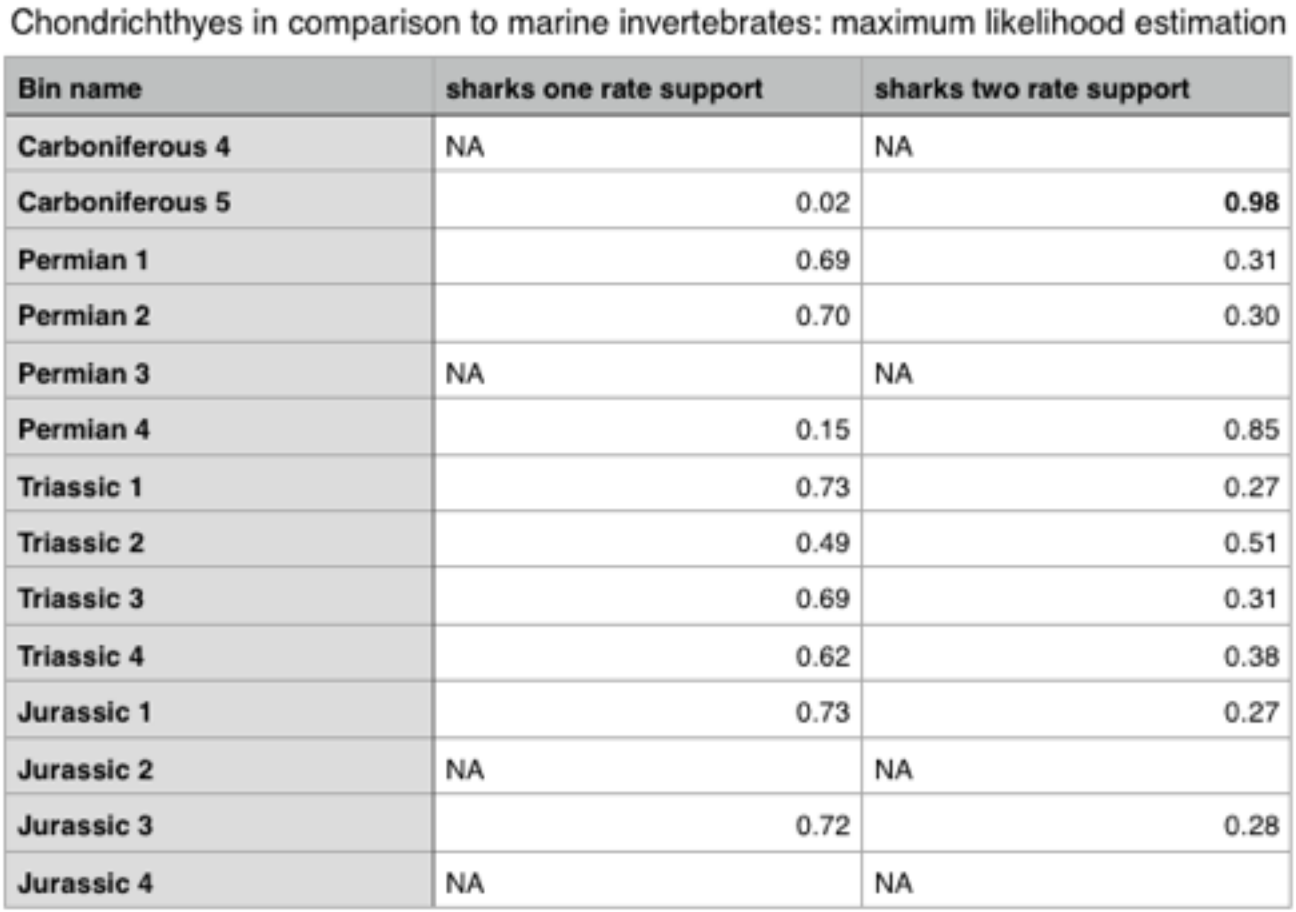


Figure 5: Raw boundary crosser extinction rates for chondrichthyes and marine invertebrates. Calculated using FossilWorks. Vertical red lines indicate end-Permian and end-Triassic mass extinction events.

Table 3



Chondrichthyes in comparison to marine invertebrates: maximum likelihood estimation

Bin name	sharks one rate support	sharks two rate support
Carboniferous 4	NA	NA
Carboniferous 5	0.02	**0.98**
Permian 1	0.69	0.31
Permian 2	0.70	0.30
Permian 3	NA	NA
Permian 4	0.15	0.85
Triassic 1	0.73	0.27
Triassic 2	0.49	0.51
Triassic 3	0.69	0.31
Triassic 4	0.62	0.38
Jurassic 1	0.73	0.27
Jurassic 2	NA	NA
Jurassic 3	0.72	0.28
Jurassic 4	NA	NA

Table 3: Akaike weight values for maximum likelihood estimation comparing shared and separate extinction rates for chondrichthyans and marine invertebrates.

Figure 6 : Proportion of tooth types per ten million year bins

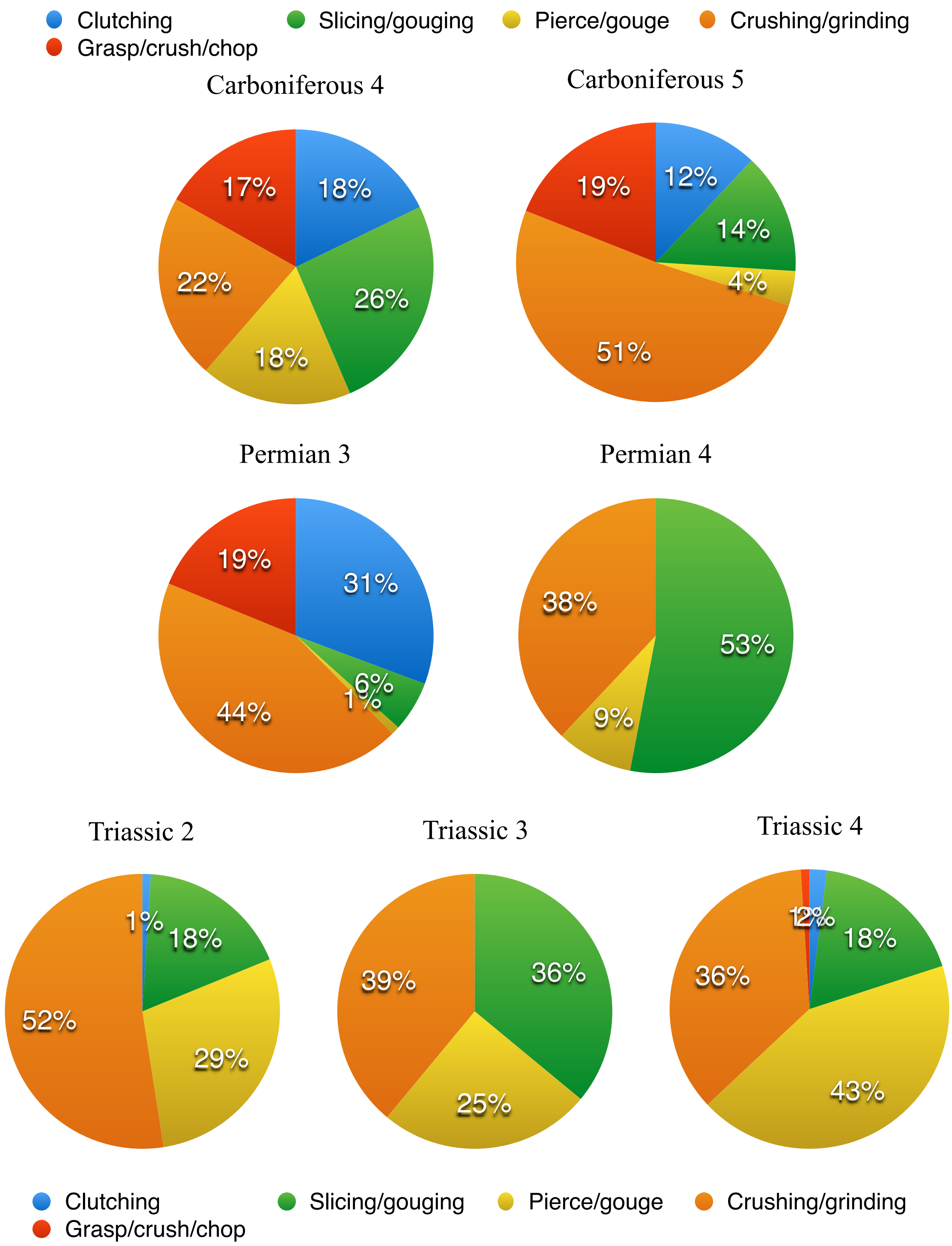


Figure 6: Proportion of chondrichthyan tooth types per ten million year bins. Ten million year bins not included did not have enough occurrences (<20).

Figure 8: Carboniferous 5 tooth type occurrences per

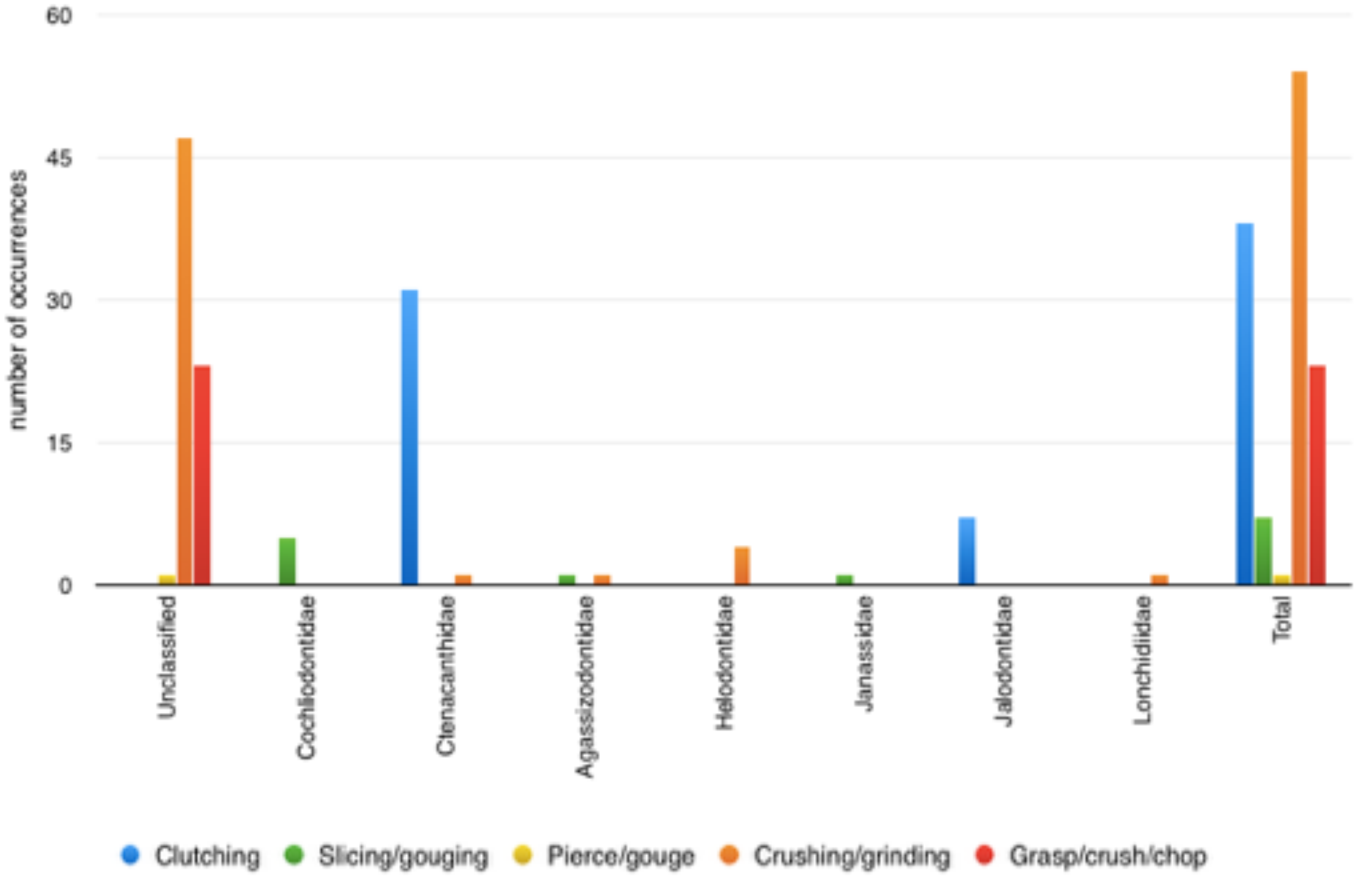


Figure 8: Number of occurrences within each family per tooth type within Carboniferous 5 data.

Figure 9: Permian 3 tooth type occurrences per family

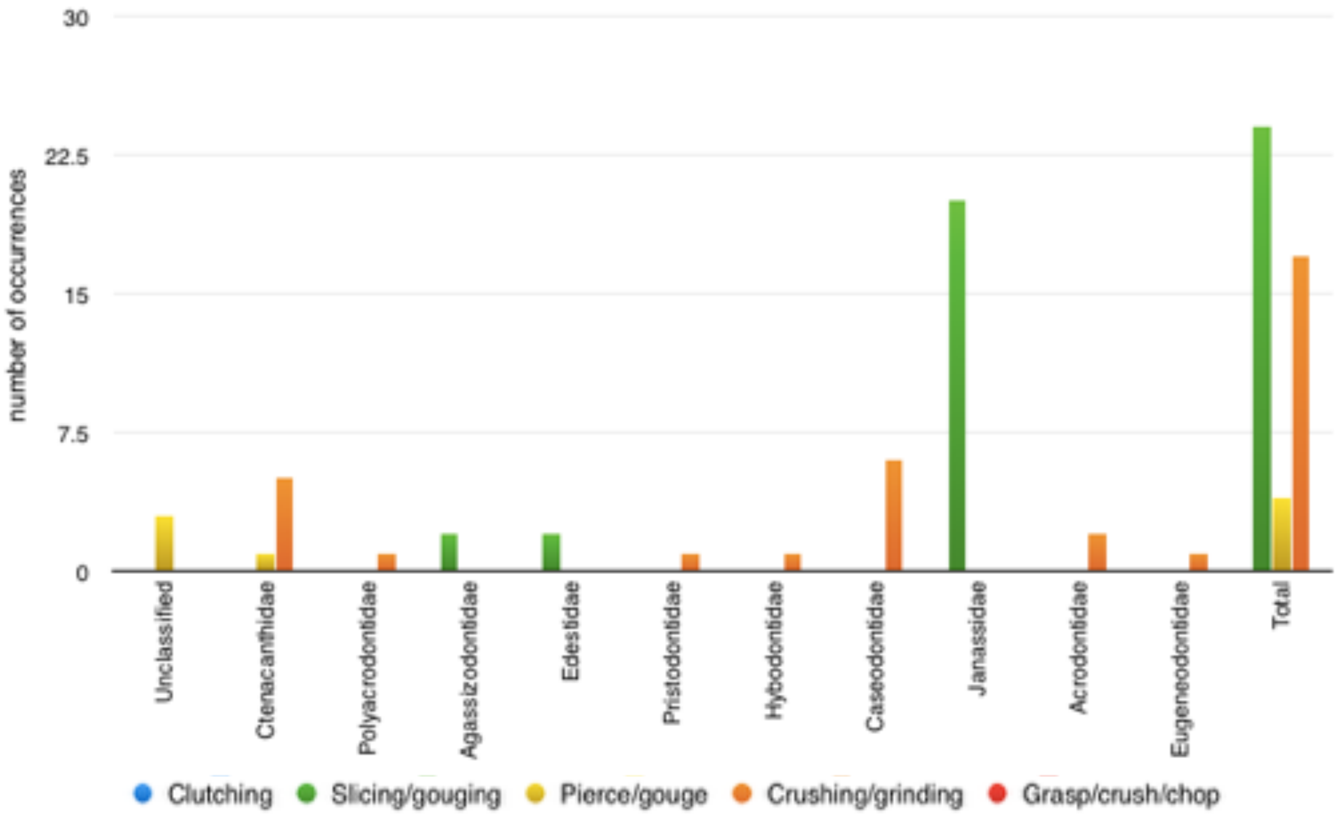


Figure 9: Number of occurrences within each family per tooth type within Permian 3 data.

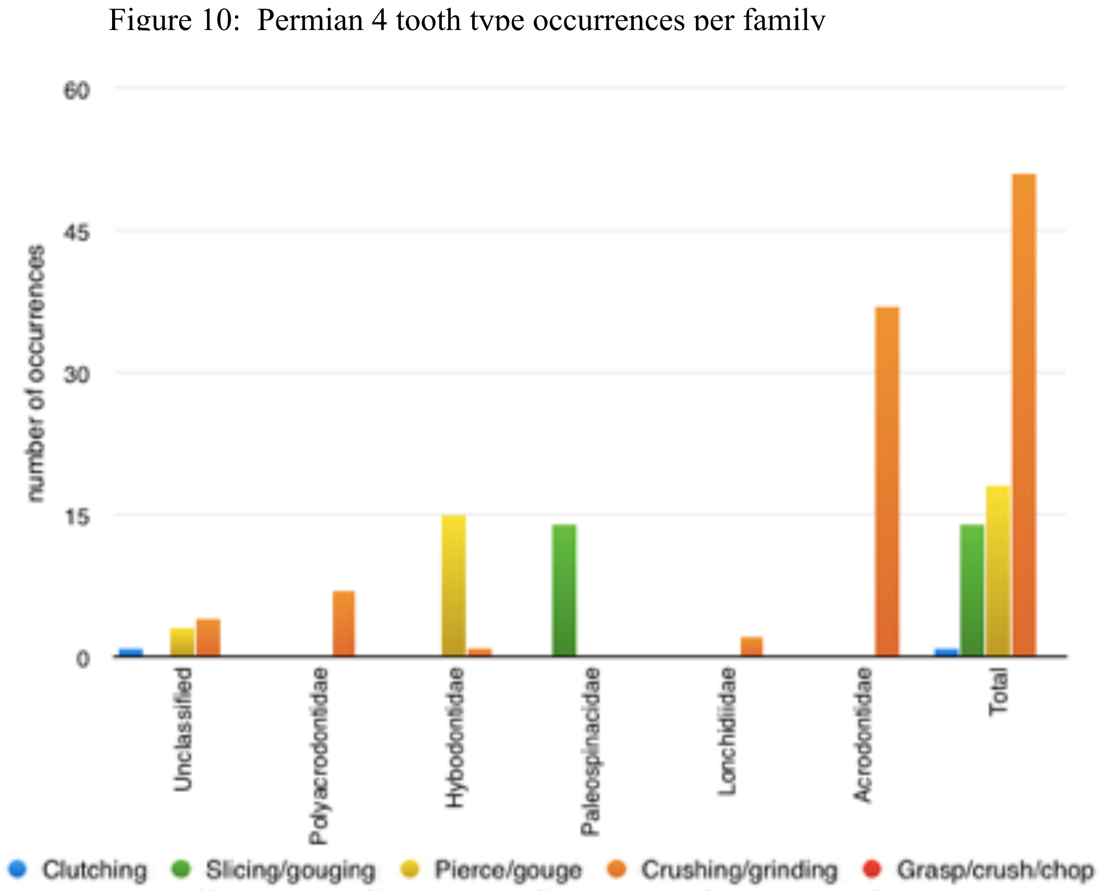


Figure 10: Number of occurrences within each family per tooth type within Permian 4 data.

Figure 11: Triassic 2 tooth type occurrences per family

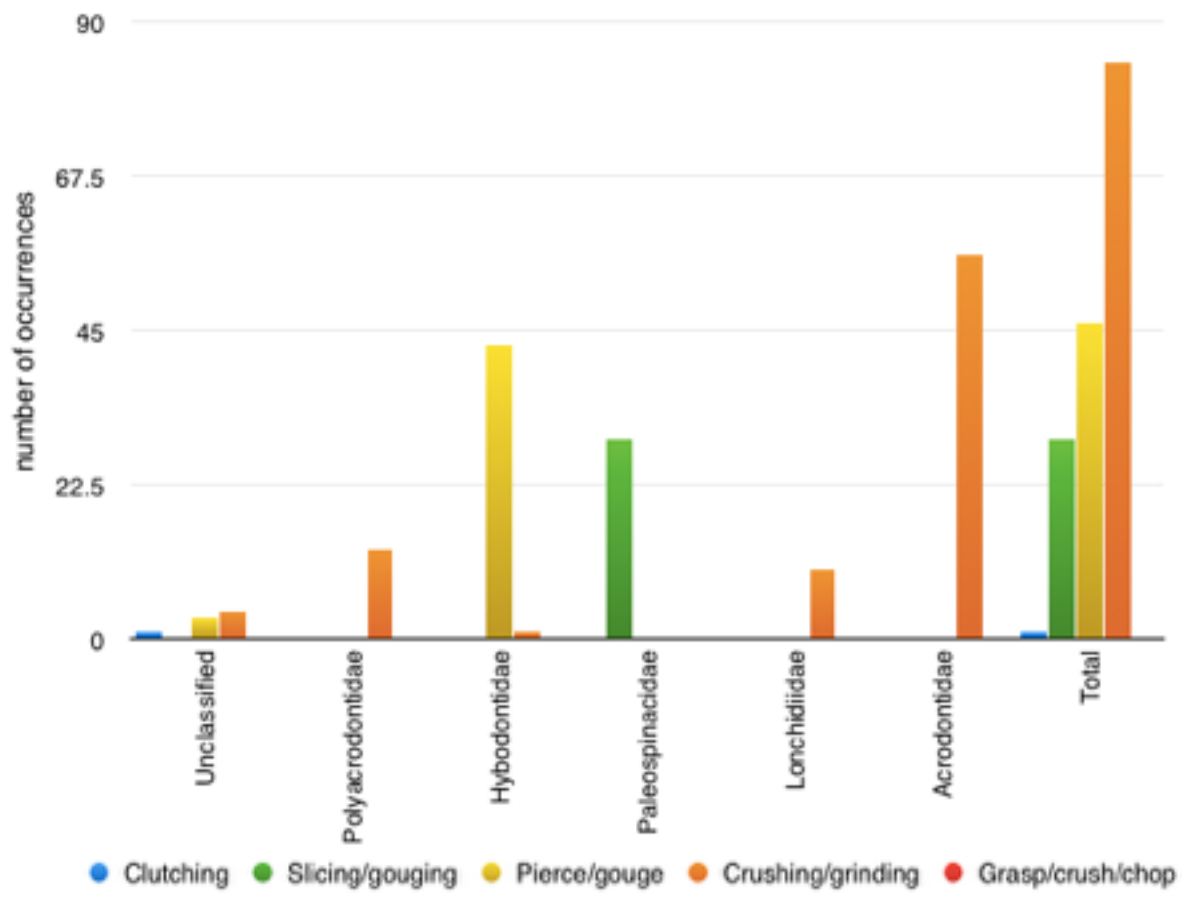


Figure11: Number of occurrences within each family per tooth type within Triassic 2 data.

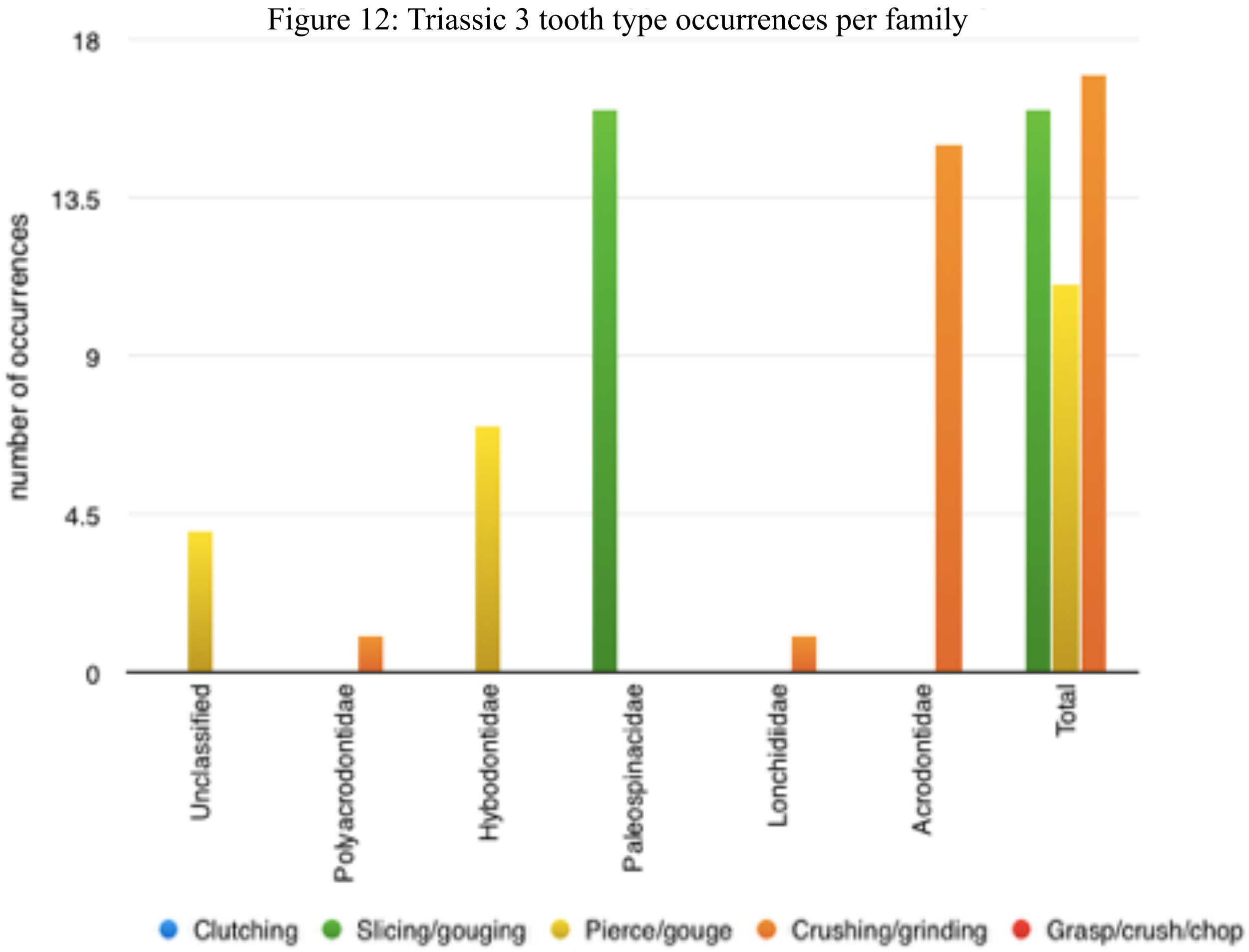


Figure 12: Triassic 3 tooth type occurrences per family

Figure 12: Number of occurrences within each family per tooth type within Triassic 3 data.

Figure 13: Triassic 4 tooth type occurrences per family

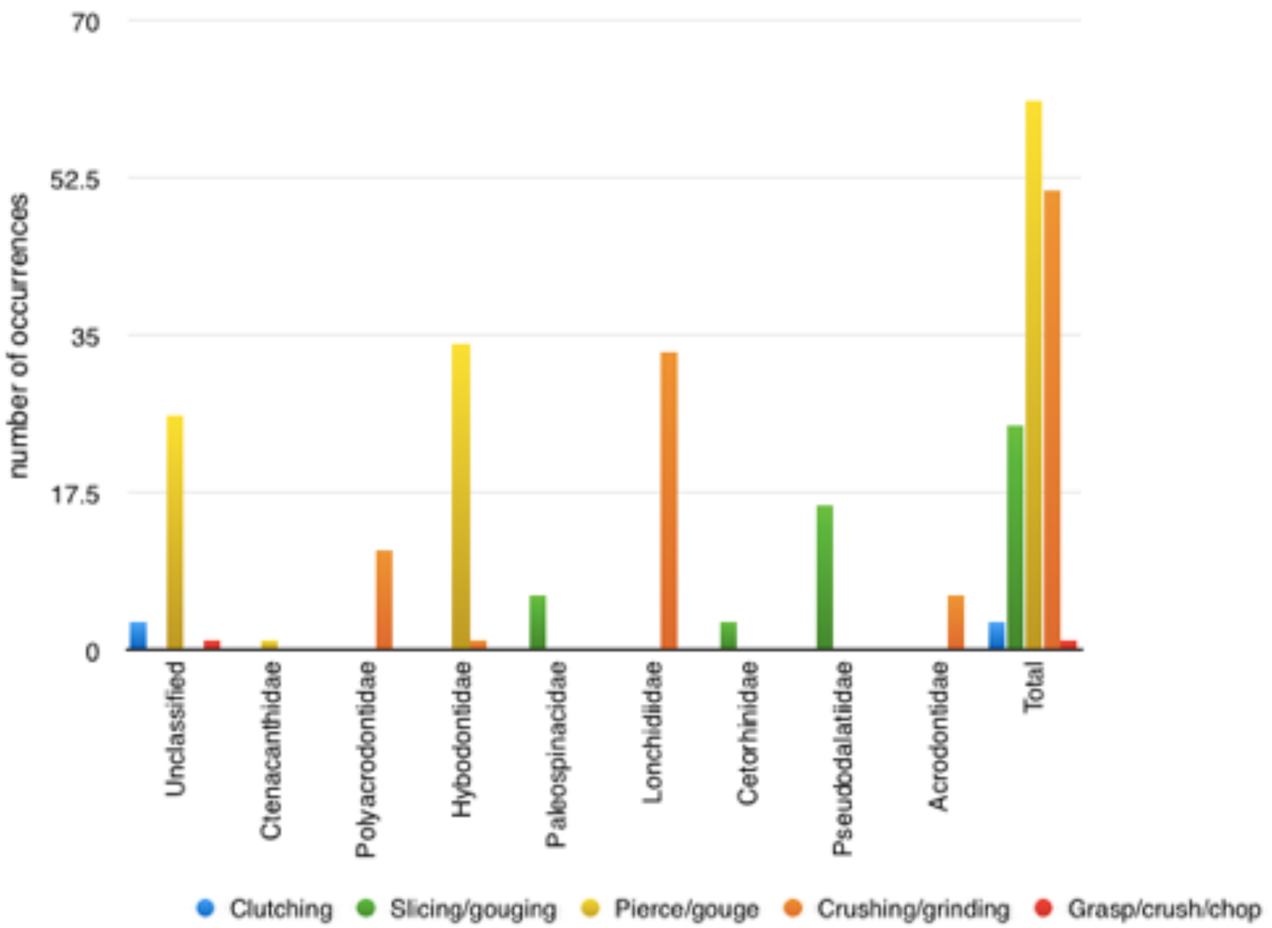


Figure 13: Number of occurrences within each family per tooth type within Triassic 4 data.

Discussion

Actinopterygii extinction rate in comparison to marine invertebrates

In our period of study, Carboniferous 4 through Permian 3, as well as Jurassic 2 are particularly sparse in occurrences (figure 1). Therefore, these intervals do not have valid results in our maximum likelihood estimation analysis.

The effect of the end-Permian extinction event on fish groups is not well understood (Friedmann & Sallan. 2012, Guinot et al. 2012). However, as shown in our data, actinopterygians are indeed within the four lineages of marine vertebrates to survive the Permo-Triassic boundary (Friedmann & Sallan 2012). A lack of signal for extinction of actinopterygians has been documented at the end-Permian extinction event (Friedman & Sallan 2012, Schaeffer 1973). Friedman & Sallan (2012) postulated that euryhaline actinopterygian lineages were largely unaffected during the end-Permian mass extinction. Our raw data support this conclusion; the actinopterygian boundary crosser extinction rate is much lower than that of marine invertebrates at the end-Permian extinction (figure 3). This result supports our hypothesis that the active lifestyle of actinopterygians is physiologically advantageous during ocean acidification and warming events.

The highest peak in boundary crosser extinction rates occurs at the end-Triassic extinction during the Triassic 4 interval (figure 3), where the actinopterygian extinction rate approaches that of marine invertebrates. In this interval, the Akaike weight for a shared extinction rate for marine invertebrates and actinopterygians is the highest compared to other intervals in our study. (table 2). This indicates that actinopterygians may have suffered extinction comparable to that of marine invertebrates at the end-Triassic.

The extinction of actinopterygians during the end-Triassic is not well understood. While the extinction of conodonts has been thoroughly documented, there is little documentation on the extinction of actinopterygians (Friedmann & Sallan 2012). While others have suggested a lack of extinction of fishes at the end-Triassic (Friedmann & Sallan 2012, Hautmann et al. 2008), our findings indicate there may have been an extinction event in actinopterygians similar in intensity to that of marine invertebrates.

Chondrichthyes extinction rate in comparison to marine invertebrates

The end-Permian extinction boundary crosser extinction rate of chondrichthyans is half that of marine invertebrates (figure 5). An Akaike weight of 0.85 suggests that chondrichthyans and marine invertebrates suffered two different models of extinction and the chondrichthyan boundary crosser extinction rate at the end-Permian is not much higher than background level. Therefore, chondrichthyans were not very threatened by the CO_2 driven stresses of the end-Permian mass extinction. Our data show that sharks were likely to survive the end-Permian, consistent with our hypothesis that sharks are better adapted to deal with the stresses of acid-base perturbations and are thus more likely to survive CO_2-driven extinction events.

The fossil record of early chondrichthyans shows that hybodonts, eugeneodontiformes and neoselachians were widespread and present in early Triassic assemblages, therefore they survived the end-Permian and adapted to CO_2 driven stresses and ocean acidification (Sheyer et al. 2014). However, all Symmoriiformes and many Paleozoic holocephalans went extinct. These groups were primarily marine, and likely not as euryhaline as surviving groups (Friedman & Sallan 2012, Koot 2013). Friedman and Sallan (2012) proposed that extinction of chondrichthyans selected against marine groups that were not euryhaline; euryhaline chondrichthyans (including freshwater xenacanths) and actinopterygians survived in ecosystems that were otherwise decimated.

At the end-Triassic extinction interval, chondrichthyans have a higher peak in boundary crosser extinction rate than marine invertebrates; the Akaike weight value for a one rate model during the Triassic 4 interval is much higher than the two rate model weight value (figure 5, table 3). Our findings indicate that some groups of chondrichthyans suffered extinction at the end-Triassic similar in severity to marine invertebrates. While both hybodonts and neoselachians were present in early Triassic assemblages, phylogenetic studies indicate that synechodontiformes were the only neoselachians present in the late Triassic (Kriwet et al. 2008, Sheyer et al. 2014). Therefore, many other groups of neoselachians may have been selected against during the end-Triassic mass extinction. Recently, early primitive shark groups have been discovered in Cretaceous deposits, indicating that some groups may have survived both the end-Permian and end-Triassic mass extinctions by seeking refuge in deep sea environments (Guinot et. al 2013).

Chondrichthyan tooth types

Carboniferous trends (figures 6-8)

In comparison to Carboniferous 4, Carboniferous 5 exhibits an increase of Petalodontidae occurrences, which is reflected in proportion of tooth type 4. This may be a result of an increase in available niches for benthic, shell crushing chondrichthyans.

Permian trends (figures 6, 9-10)

The decrease in the proportion of tooth type 3 in Permian 3 may indicate that this primitive tooth type became more specialized. In Permian 3 there are no occurrences of Iniopterygidae in our data, which contributed largely to the proportion of tooth type 3 previously. In our Carboniferous data, Ctenacanthidae contributed to the proportion of tooth type 3 and tooth type 4 occurrences. Ctenacanthidae occurrences in Permian 3 are mostly tooth type 1, which drives the increase of the proportion of tooth type 1 within this stage. This may reflect changing dietary adaptations within this family.

The lack of occurrences of tooth type 1 in the Permian 4 interval reflects a change in the tooth type of and number of occurrences within the family Ctenacanthidae. While Ctenacanthidae occurrences were dominated by tooth type 1 in Permian 3, in Permian 4 there are fewer occurrences, most of which are classified as tooth type 4 and none of which are classified as tooth type 1. This decrease from the Permian 3 proportion may reflect a slow decline in abundance within this tooth type through the Permian.

Though the proportion of tooth type 3 increased in Permian 4, this increase in proportion largely reflects the lower number of total occurrences in Permian 4 relative to Permian 3. Thus this increase may be a result of random noise.

Tooth type 5 decreased significantly following Permian 3. This is likely related to the disappearance of Inioptyergidae and Siborhynchidae in our data, both of which were previously contributing families.

While the data are sparse, there is little difference in tooth type proportion across the Permian-Triassic boundary. This supports our hypothesis and findings in the previous section; sharks active lifestyle and carnivorous life habit predisposes them toward survival of CO_2-driven extinction due to their more advanced acid-base regulation.

Triassic trends (figures 6, 11-13)

In Triassic 2, tooth type 2 returns near its Carboniferous proportion. This decline in proportion from its Permian 4 height might reflect an early Triassic decrease in abundance. Tooth type 3 increases in proportion of occurrences in Triassic 2, however the occurrences are from different families. The increase in proportions of tooth type 4 from Permian 4 to Triassic 2 may be a result of an increase in the total number occurrences (from 45 to 160, respectively), as the contributing families are the same. Triassic 2 is the best sampled interval included in our study, thus this proportion likely a more accurate reflection of the shark tooth ecology record. This increase in proportion of tooth type 4 is inferred as a shift in dietary mode and feeding habit from nektonic carnivory to durophagy.

Though lack of occurrences limits the time periods included in our study, our results indicate there were several significant changes in dentition and feeding habit in chondrichthyans. Changes in tooth morphology and feeding habit indicate changes in activity levels, as nektonic carnivory requires more constant swimming and agility than durophagy. While we cannot interpret tooth type trends through the end-Triassic extinction event, we can infer that some groups of chondrichthyans experienced changes in activity level, and perhaps respiratory physiology.

Conclusions

While our end-Permian actinopterygian data are too sparse to perform maximum likelihood analysis, our raw boundary crosser extinction rates indicate they may not have suffered much extinction. Our results show actinopterygians did suffer an end-Triassic extinction of comparable magnitude to marine invertebrates. This is interesting because fish, unlike marine invertebrates, have ion regulatory mechanisms to protect their extracellular pH against the stresses of warming and acidification. Maximum likelihood estimation did not support a separate or shared rate of end-Triassic extinction for actinopterygians and marine invertebrates; this indicates that there may be other factors to consider when comparing patterns of extinction.

Some taxa of chondrichthyans went extinct at end-Permian, but according to our data they did not suffer nearly as much extinction as marine invertebrates. Maximum likelihood analysis results nearly support two separate models of extinction for chondrichthyes and marine invertebrates at the end-Permian, with chondrichthyans affected less than marine invertebrates were. Permo-Triassic chondrichthyans may not have suffered because of their euryhaline life habit. Friedmann & Sallan (2012) proposed that Permian extinction of chondrichthyans selected against marine groups. Surviving genera were more tolerant of varying pH in seawater and could adapt to ocean acidification more easily. Our results support this, as many primitive chondrichthyans, such as euryhaline hybodonts, survived the end-Permian mass extinction.

Primitive chondrichthyans may have suffered an end-Triassic extinction similar to that of marine invertebrates. Maximum likelihood analysis does not support either a separate or shared extinction for marine invertebrates and chondrichthyes in this interval. While there is an extinction event at the end-Triassic, chondrichthyans as a whole continued to be successful through the Triassic and Jurassic. Our results show that chondrichthyans are a resilient, adaptable group that might have survived extinction events through their better adapted respiratory physiology.

Tooth type analysis shows that there were several changes in proportion of tooth types in chondrichthyans over time. This is related to the turnover of different families of chondrichthyans and their adaptive success. Many families contained genera of more than one tooth type, and the proportions of tooth types within families varied between stages. This indicates versatility within chondrichthyans, which is reflected in their opportunistic lifestyle and the adaptability of their feeding mode.

In conclusion, actinopterygians and chondrichthyans may have been more likely to survive CO_2-driven extinctions in deep time due to physiological adaptations associated with their active life habits. In comparison to marine invertebrates, actinopterygians and chondrichthyans have a better adapted respiratory physiology and more advanced acid-base regulation; these adaptations enable them to exercise and maintain prolonged activity, and may also enable them to more easily buffer changes in seawater pH. In the context of modern global change, our results indicate that the adaptations chondrichthyans and actinopterygians evolved to support their active lifestyle may provide physiological advantages during future times of CO_2-driven stresses.

References

Alroy, J. (2010). Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. The Paleontological Society Papers 16: 55-80.

Anlauf, H., D'Croz, L. & A. O'Dea (2010). A corrosive concoction: the combined effects of ocean warming and acidification on the early growth of a stony coral are multiplicative. Journal of Experimental Marine Biology and Ecology 397: 13-20.

Archer, D., Kheshgi, H. & E. Maier-Reimer (1997). Multiple timescales for neutralization of fossil fuel CO_2. Geophysical Research Letters 24: 405-408.

Blackburn, T.J., Olsen, P.E., Bowring, S.A., McLean, N.M., Kent, D.V., Puffer, J., McHone, G., Rasbury, E.T., & M. Et-Touhami (2013). Zircon U-Pb geochronology links the end-Triassic extinction with the Central Atlantic Magmatic Province. Science 340: 941-945.

Blieck, A. (2011). From adaptive radiations to biotic crises in Palaeozoic vertebrates: a geobiological approach. Geologica Belgica 14: 203-227.

Bond, D.P.G., and Wignall, P.B., (2009). Latitudinal selectivity of foraminifer extinctions during the late Guadalupian crisis: Paleobiology, v. 35, p. 465–483, doi:10.1666/0094-8373-35.4.465.

Bond, D.P.G. & P.B. Wignall (2010). Pyrite framboid study of marine Permian-Triassic boundary sections: A complex anoxic event and its relationship to contemporaneous extinction. Geological Society of America Bulletin 122: 1265-1279.

Cappetta, H. (1987). Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii. Handbook of Paleoichthyology 3B.

Carlson, J.K. & G.R. Parsons (2001). The effects of hype on three sympatric shark species: physiological and behavioral responses. Experimental Biology of Fishes 61: 427-433.

Ciampaglio, C. N., Wray, G. A., & B. H. Corliss (2005). A toothy tale of evolution: convergence in tooth morphology among marine Mesozoic - Cenozoic sharks, reptiles, and mammals. The Sedimentary Record 3: 4-8.

Clapham, M.E. & J.L. Payne (2011). Acidification, anoxia, and extinction: A multiple logistic regression analysis of extinction selectivity during the Middle and Late Permian. Geology 39: 1059-1062.

Clapham, M. E., W. Kiessling, M. Aberhan, D. J. Bottjer, A. I. Miller, F. T. Fursich, J. Alroy, Józ. Pálfy, T. D. Olszewski, A. J. McGowan, L. Villier, and P. J. Wagner. 2014. Taxonomic occurrences of Bashkirian to Bathonian Bryozoa, Porifera, Brachiopoda, Mollusca, Trilobita, Echinodermata, and Ostracoda recorded in Fossilworks, the Evolution of Terrestrial Ecosystems database, the

Paleobiology Database, and the Paleogeographic Atlas Project database. Fossilworks. http://fossilworks.org.

Foote, M. (2000). Origination and extinction components of Taxonomic diversity: general problems. Paleobiology 26: 74-102.

Friedman, M. & L.C. Sallan (2012). Five hundred million years of extinction and recovery: A Phanerozoic survey of large-scale diversity patterns in fishes. Palaeontology 55: 707-742.

Gazeau, F., Gattuso, J.-P., Dawber, C., Pronker, A. E., Peene, F., Peene, J., Heip, C. H. R., & J. J. Middelburg (2010). Effect of ocean acidification on on the early life stages of the blue mussel Mytilus edulis. Biogeosciences 7: 2051 - 2060.

Greene, S.E., R.C. Martindale, K.A. Ritterbush, D.J. Bottjer, F.A. Corsettie & W.M. Berelson (2012) Recognising ocean acidification in deep time: An evaluation of acidifcation across the Triassic-Jurassic boundary. Earth Science Reviews 113: 72-93.

Guinot, G., Adnet, S., & H. Cappetta (2012). An Analytical Approach for Estimating Fossil Record and Diversification Events in Sharks, Skates and Rays. PLoS ONE 7(9): e44632. doi:10.1371/journal.pone.0044632

Guinot, G. Adnet, S., Cavin, L., & H. Cappetta (2013). Cretaceous stem chondrichthyans survived the end-Permian mass extinction. Nature communications 4: DOI: 10.1038/ncomms3669

Hallam, A. (2002). How catastrophic was the end-Triassic mass extinction? Lethaia 35: 147-157.

Hautmann, M., Benton, M. J. & A. Tomašovych (2008). Catastrophic ocean acidification at the Triassic-Jurassic boundary. – N. Jb. Geol. Paläont. Abh., 249: 119 – 127; Stuttgart.

Hautmann, M. (2004). Effect of end-Triassic CO_2 maximum on carbonate sedimentation and marine mass extinction. Facies 50: 257-261.

Hochachka, P.W. & G.N. Somero (2002). Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, Inc. New York, New York 10016.

IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp, doi:10.1017/CBO9781107415324.

Kidder, D.L. & T. R. Worsley (2004). Causes and consequences of extreme Permo-Triassic warming to globally equable climate and relation to the Permo-Triassic extinction and recovery. Palaeogeography, Palaeoclimatology, Paleoecology 203: 207-237.

Kiessling, W., Aberhan, M., Brenneis, J. & P.J. Wagner (2007). Extinction trajectories of benthic organisms across the Triassic-Jurassic boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 204: 201-222.

Kiessling, W. & C. Simpson (2011). On the potential for ocean acidification to be a general cause of ancient reef crises. Global Change Biology 17: 56-67.

Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S. & W.W. Fischer (2007). Paleophysiology and end-Permian mass extinction. Earth and Planetary Science Letters 256: 295-313.

Koot, M. B. (2013). Effects of the Late Permian mass extinction on chondrichthyan palaeobiodiversity and distribution patterns.

Kroeker, K.J., Kordas, R.L. & G.G. Singh (2010). Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters 13: 1419-1434.

Kriwet, J., Kiessling, W., & S. Klug (2008). Diversification trajectories and evolutionary life-history traits in early sharks and batoids. Proc. R. Soc. B. 276: 945-951.

Marzoli, A., Bertrand, H., Knight, K.B., Cirilli, S., Buratti, N., Vérati, C., Nomade, S., Renne, P.R., Youbi, N., Martini, R., Allenbach, K., Neuwerth, R., Rapaille, C., Zaninetti, L., & G. Bellieni (2004). Synchrony of the Central Atlantic magmatic province and the Triassic-Jurassic boundary climatic and biotic crisis. Geology 32: 973-976. doi: 10.1130/G20652.1

McElwain, J.C., Beerling, D.J., & F.I. Woodward (1999). Fossil plants and global warming at the Triassic-Jurassic boundary. Science 285: 1386-1390.

Melzner, F., Gutowska, M. A., Langenbuch, M., Dupont, S., Lucassen, M., Thorndyke, M.C., Bliech, M. & H.-O. Pörtner (2009). Physiological basis for high CO_2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? Biogeosciences 6: 2313-2331.

Melzner, F., Stange, P., Trübenbach, K., Thomsen, J., Casties, I., Panknin, U., Gorb, S.N., & A.M. Gutowska (2011). Food supply and seawater pCO2 impact calcification and internal shell dissolution in the Blue Mussel Mytilus edulis. PLoS ONE 6(9): e24223. doi:10.1371/journal.pone.0024223

Meyer, K.M., Kump, L.R. & A. Ridgwell (2008). Biogeochemical controls on photic-zone euxinia during the end-Permian mass extinction. Geology 36: 747-750.

Mutter, R.J, De Blanger, K. & A.G. Neuman (2007). Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zoological Journal of the Linnean Society 149: 309-337.

Mutter, R. J. & A.G. Neuman (2008). Jaws and dentition in an early Triassic, 3-dimensionally preserved eugeneodontid skull (Chondricthyes). Act Geologica Polonica 58: 223-227.

Payne, J.L. & M.E. Clapham (2012). End-Permian mass extinction in the oceans: An ancient analog for the twenty-first century? Annu. Rev. Earth Planet. Sci 40: 89-111.

Payne, J.L., Lehrmann, D. J., Wei, J., Orchard, M. J., Schrag, D. P., & A. H. Knoll (2004) Large Perturbations of the carbon cycle during recovery from the end-Permian extinction. Science 305: 506-509

Payne, J.L., Turchyn, A.V., Paytan, A., DePaolo, D.J., Lehrmann, D.J., Yu, M., Wei, J., & A.H. Knoll (2010). Calcium isotope constraints on the end-Permian mass extinction. P. Natl. Acad. Sci. USA 107: 8543-8548.

Pálfy, J. (2003). Volcanism of the Central Atlantic Magmatic Province as a potential deriving force in the end-Triassic mass extinction. The Central Atlantic Magmatic Province: Insights from fragments of Pangea Geophysical Monograph 136: 255-267.

Peck, L.S., Clark, M.S., Morley, S.A., Massey, A. & H. Rossetti (2009). Animal temperature limits and ecological relevance: effects of size, activity and rates of change. Functional Ecology 23: 248-256.

Pörtner, H.-O. & M. Langenbuch (2005). Synergistic effects of temperature extremes, hypoxia, and increased CO_2 on marine animals: From Earth history to global change. Journal of Geophysical Research 110: 1-15.

Pörtner, H.-O. (2008). Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. Mar. Ecol. Prog. Ser. 373: 203-217.

Pruss, S.B. & D.J. Bottjer (2004). Late Early Triassic microbial reefs of the western United States: a description and model for their deposition in the aftermath of the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Paleoecology 211: 127-137.

Reichow M.K., Pringle, M.S., Al'Mukhamedov, A.I., Allen, M.B., Andreichev, V.L., Buslov, M.M., Davies, C.E., Fedoseev, G.S, Fitton, J.G., Inger, S., Medvedev, A.Ya., Mitchell, C., Puchkov, V.N., Safonova, I.Yu., Scott, R.A., & A.D. Saunders (2009). The timing and extent of the eruption of the Siberian Traps large igneous province: Implications for the end-Permian environmental crisis. Earth and Planetary Science Letters 277: 9-20.

Rosa, R. & B.A. Seibel (2008). Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. Proc. Natl. Acad. Sci. 105: 20776-20780.

Ruhl, M., Bonis, N.R., Reichart, G.-J., Sinninghe Damsté, J.S., & W.M. Kürschner (2011). Atmospheric carbon injection linked to end-Triassic mass extinction. Science 333: 430-434.

Schaeffer, B. (1973). Fishes and the Permian-Triassic boundary. Permian Triassic Systems and their Mutual Boundary - Memoir 2: 493-497.

Schultze, H.-P. (1985). Marine to onshore vertebrates in the lower Permian of Kansas and their paleoenvironmental implications. The University of Kansas Paleontological Contributions 113: 1-18.

Somero, G.N. (2010). The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers.’ The Journal of Experimental Biology 213: 912-920.

Sheyer, T.M., Romano, C., Jenks, J., & H. Bucher (2014). Early Triassic marine biotic recovery: the predators’ perspective. PLoS ONE 9(3): e88987. doi: 10.1371/ journal.pone.0088987

Sun, Y., Joachimski, M.M., Wignall, P.B., Yan, C., Chen, Y., Jiang, H., Wang, L. & X. Lai (2012). Lethally hot temperatures during the early Triassic greenhouse. Science 338: 366-370.

Svensen H, Planke S, Polozov AG, Schmidbauer N, Corfu F. (2009). Siberian gas venting and the end-Permian environmental crisis. Earth Planet. Sci. Lett. 277:490–500.

Weidlich, O. (2002). Permian reefs re-examined: Extrinsic control mechanisms of gradual and abrupt changes during 40 my of reef evolution: Geobios, v. 35, Supplement 1, p. 287–294, doi:10.1016/S0016-6995(02)00066-9. PNAS 107: 6721-6725.

Whiteside, J.H., Olsen, P.E., Eglinton, T., Brookfield, M.E., & R.N. Sambrotto (2010). Compound-specific carbon isotopes from Earth’s largest flood basalt eruptions directly linked to the end-Triassic mass extinction.

Wignall, P.B & R.J. Twitchett (1996). Oceanic anoxia and the end-Permian mass extinction. Science 272: 1155-1158.

Zeebe, R.E., Zachos, J.C., Caldeira, K. & T. Tyrrell (2008). Carbon emissions and acidification. Science 32: 51-52.