While the history of taxonomic diversification in open ocean lineages of ray-finned fish and elasmobranchs is increasingly known, the evolution of their roles within the open ocean ecosystem remains poorly understood. To assess the relative importance of these groups through time, we measured the accumulation rate of microfossil fish teeth and elasmobranch dermal denticles (ichthyoliths) in deep-sea sediment cores from the North and South Pacific gyres over the past 85 million years (Myr). We find three distinct and stable open ocean ecosystem structures, each defined by the relative and absolute abundance of elasmobranch and ray-finned fish remains. The Cretaceous Ocean (pre-66 Ma) was characterized by abundant elasmobranch denticles, but low abundances of fish teeth. The Palaeogene Ocean (66–20 Ma), initiated by the Cretaceous/Palaeogene mass extinction, had nearly four times the abundance of fish teeth compared with elasmobranch denticles. This Palaeogene Ocean structure remained stable during the Eocene greenhouse (50 Ma) and the Eocene–Oligocene glaciation (34 Ma), despite large changes in the overall accumulation of both groups during those intervals, suggesting that climate change is not a primary driver of ecosystem structure. Dermal denticles virtually disappeared from open ocean ichthyolith assemblages approximately 20 Ma, while fish tooth accumulation increased dramatically in variability, marking the beginning of the Modern Ocean. Together, these results suggest that open ocean fish community structure is stable on long timescales, independent of total production and climate change. The timing of the abrupt transitions between these states suggests that the transitions may be due to interactions with other, non-preserved pelagic consumer groups.

1. Introduction

Ray-finned fishes (Actinopterygii) are a ubiquitous part of nearly all modern marine ecosystems. Both molecular and fossil studies have shown that while the actinopterygian lineage originated over 400 Ma, the great diversity of modern ray-finned fish in marine environments developed relatively recently, during the past 100 million years (Myr) [1–3]. Shark diversity, conversely, developed much earlier, with the vast majority of family-level diversity established between 250 and 100 Ma [4–6]. Yet, the structure and function of pelagic ecosystems are not only defined solely by the taxonomic diversity of organisms present, but also involve the roles and relative abundance of these taxa within pelagic food webs. The abundance of top predators, including pelagic sharks, fish such as tunas and billfish, seabirds and marine mammals, depends upon an efficient food chain and enough primary productivity to support large biomass, high trophic-level organisms [7,8], as well as how that energy is distributed between competing taxa [9].

We assess the ecological importance of pelagic ray-finned fish and elasmobranchs (sharks, skates and rays), by using the microfossil record of ichthyoliths, the mineralized teeth and dermal scales (denticles) of ray-finned fish and
elasmobranchs, respectively (figure 1). Their calcium phosphate composition makes ichthyoliths highly resistant to dissolution; they are among the most robust fossils of any kind, and are often preserved even when all other microfossils are dissolved [10,11]. The history of open ocean fish and elasmobranch communities is recorded by ichthyoliths in deep-sea sediments at high temporal resolution, delivered to the seafloor either shed by live or dead individuals, or as indigestible elements in faecal matter. This allows for the study of fish production and community structure through geologic time [12,13]. Nearly, all teeth in our samples are small (less than 300 μm), and most lack the multiple cusps and serrations that would identify large teeth as those of sharks rather than ray-finned fish [13].

We evaluated the ichthyolith record for the last 85 Myr from two red-clay deep-sea sediment cores: Deep Sea Drilling Program (DSDP) Site 596 in the South Pacific gyre and Ocean Drilling Program (ODP) Site 886 in the North Pacific gyre. Both ocean basins exhibit the same three distinct, stable ecosystem states during this interval, each lasting tens of millions of years. Open ocean gyres are the largest habitats on the planet and have very low net primary production per unit area, yet they support complex and diverse food webs [14]. The characteristics of the Pacific Ocean gyres are governed by the global wind-field, making their geographical location and size relatively stable on geologic timescales, and ideal for studying millions of years of ecosystem evolution. While the exact locations of these sites have migrated with the Pacific Plate, both DSDP 596 and ODP 886 are pure pelagic red clay, and have remained well within the boundaries of the South and North Pacific gyres, sufficiently far from the land to have no terrigenous input beyond wind-blown dust, for the entirety of the 85 Myr record [15,16].

The absolute number of elasmobranch scales or fish teeth is not directly translatable to an absolute standing stock of individuals during a given time period, since ichthyolith numbers can be affected by changes in the sedimentation rate as well as changes in the biological community. We have accounted for variations in the sedimentation rate by calculating the flux of teeth and denticles (ichthyolith accumulation rate (IAR): ich cm⁻² Myr⁻¹, see the electronic supplementary material, methods and figures S1–S8) to the seafloor using independent timescales for each drill core [15,16]. IAR represents a metric of relative changes in biomass over a fixed time interval, which we call 'fish (or elasmobranch) production'. We acknowledge that variation in IAR may also reflect changes in the mix of species with different population turnover rates or tooth abundances, such as the relative abundance of long-lived species and short-lived 'forage fish'. This same caveat also applies to the comparison of tooth accumulation rate (AR) to dentine AR where the relative fluxes are probably only meaningful as a general indication of the relative abundance and importance of ray-finned fish and elasmobranchs within the pelagic ecosystem. In the present day ocean, primary production in the North Pacific Gyre is somewhat higher than that of the South Pacific gyre, perhaps due to iron or nitrogen limitation in the South Pacific basin [17]. The absolute value of North Pacific IAR is significantly higher than that in the South Pacific throughout our record, suggesting that IAR may be related to productivity, and if so, that the North Pacific has been a more biologically productive region of the ocean than the South Pacific for at least 75 Myr.

2. Cretaceous Ocean

During the Cretaceous, ichthyolith assemblages in both the North and South Pacific gyres were dominated by denticles. Elasmobranch denticles are approximately 1.4 times as abundant as fish teeth (0.06 standard error of the mean (s.e.m.)) in

![Figure 1. Eighty-five million year accumulation records from (a) DSDP Site 596 in the South Pacific and (b) ODP Site 886 in the North Pacific, showing total ichthyolith accumulation (black filled squares) split into tooth accumulation (blue open squares) and dentine accumulation (red plus signs). The three ocean ecosystem states are indicated by shaded boxes (Cretaceous is blue, Palaeogene is green and Modern is orange). Note the peak in ichthyolith accumulation in the Early Eocene, and the high variability of the Modern Ocean. Images are of representative Eocene-age fish teeth and elasmobranch denticles. Scale bar, 500 μm.](http://rspb.royalsocietypublishing.org/Downloaded from http://rspb.royalsocietypublishing.org/)
the North Pacific and 1.5 times more abundant (0.10 s.e.m.) in
the South Pacific. During the oldest part of our records,
before 75 Ma, ichthyoliths of all kinds are rare in both the
North and South Pacific gyres, suggesting that both elasmo-
branchs and ray-finned fish were uncommon in the
Cretaceous open ocean gyre habitat. IAR in the North Pacific
was \(21.5 \pm 14.6 \text{ ich cm}^{-2} \text{ Myr}^{-1}\), while IAR in the South Paci-
fic was \(23.0 \pm 9.2 \text{ ich cm}^{-2} \text{ Myr}^{-1}\) (figures 1 and 2
a). The
Pacific open ocean gyres became significantly more favour-
able to both elasmobranchs and ray-finned fish by
approximately 75 Ma (figures 1 and 2
a), when IAR increased
to \(97.5 \pm 30.4 \text{ ich cm}^{-2} \text{ Myr}^{-1}\) in the North Pacific, and
\(34.6 \pm 9.1 \text{ ich cm}^{-2} \text{ Myr}^{-1}\) in the South Pacific, both signifi-
cantly different from the pre-75 Ma values (two-sided \(t\)-test,
\(\mu_1 \neq \mu_2, p < 10^{-16}\) for North Pacific, \(p = 0.003\) for South
Pacific). Despite the increase in the overall IAR, the relative
abundance of denticles to teeth remained unchanged until
the end of the Cretaceous (two-sided \(t\)-test, \(\mu_1 = \mu_2, p > 0.5\)
for both North and South Pacific) [13].

3. Palaeogene Ocean

The Cretaceous/Palaeogene extinction (K/Pg, 66 Ma) ended
the over 10-million year period of stable pelagic ecosystem
structure of the Late Cretaceous [13]. The relative abundance
elasmobranchs to ray-finned fish fossils fell to 0.63 denticles
for every tooth in the Palaeocene in both the North and
South Pacific gyres (figure 3), reflecting a dramatic post-
extinction change in ecological importance of elasmobranchs
compared with ray-finned fish [13]. Additionally, both fossil
and molecular studies suggest that pelagic lineages of
ray-finned fishes diversified following the extinction [2,18,19] while no such pelagic radiation is evident in shark molecular phylogenies [5], and an analysis of fossil shark diversity does not show increased origination following the extinction [6]. Ray-finned fish appear to have been ecologically released by the extinction of competitors or predators, possibly including ammonites and marine reptiles like mosasaurs and plesiosaurs [12,13]. Elasmobranchs, on the other hand, did not increase in relative or absolute abundance following the extinction event, suggesting that they either did not see the extinction of competitors, or that most of the newly available resources were subsumed by the ray-finned fishes. The ratio of elasmobranch fossils to fish fossils decreased through the Palaeocene, as the new pelagic ecosystem state developed, but remained relatively stable at approximately one denticle for every four teeth, from 56 Ma to approximately 20 Ma (North Pacific: 0.29 ± 0.11 s.d., South Pacific: 0.27 ± 0.10 s.d.).

Extreme climate change during the Palaeogene did not affect the ecosystem structure. However, absolute abundance of both elasmobranchs and ray-finned fish increased to the highest values in our 85-million record between 53 and 50 Ma (figure 1), at the peak of the Early Eocene Climate Optimum (EECO). Fish accumulation began an exponential increase approximately 58 Ma, reaching peak levels of 285 ich cm⁻² Myr⁻¹ at 52 Ma in the South Pacific gyre, a fivefold increase from the maximum Palaeocene values (41.45 ± 19.2 ich cm⁻² Myr⁻¹), and indeed nearly twice the maximum accumulation in the South Pacific of any other time in the past 85 Myr. Dentine AR displays a nearly identical fivefold increase during this time, albeit from a much lower baseline than fish, from 14.5 ± 5.9 denticles cm⁻² Myr⁻¹ in the later Palaeocene to nearly 71 denticles cm⁻² Myr⁻¹ in the Early Eocene (figures 1 and 3).

Some fishes are known to increase their tooth production in under differing environmental conditions [20,21], so it is possible that individual fish may have increased their rates of tooth production during the EECO. However, as both ray-finned fish teeth and elasmobranch denticles increase and decrease synchronously, it is unlikely that this mechanism explains the patterns observed. Alternatively, it is possible that the nearly identical rate of increase across elasmobranchs and fish reflects an increase in overall primary productivity or ecosystem efficiency in the warm Early Eocene ocean, as an increase in fish abundance may represent an increase in elasmobranch prey. Finally, changes in ichthyolith accumulation could reflect a variation in turnover rate of populations, and therefore more generations and biomass present over a fixed interval of time. For example, the warmer waters of the EECO may have increased metabolic rates, and thus shortened generation time, driving an increase in IAR.

Models of fish production in a warmer future ocean predict that the gyres will become more oligotrophic and less productive of fish and elasmobranchs as thermal stratification shifts primary production fully into long, bacterioplankton-based food chains [22]. Our results, in contrast, suggest that fish production in the gyres was much more efficient during the Early Eocene ‘Greenhouse’ than during cooler climates of the Palaeocene or later Cenozoic. Eocene fish and elasmobranch production was apparently supported by more efficient and/or shorter food chains, possibly because an overall warmer ocean may efficiently recycle organic matter and return nutrients to surface primary producers [23,24].

Coincident with the establishment of a permanent Antarctic icecap 34 Ma, South Pacific tooth accumulation fell by nearly 40%, from the Middle to Late Eocene value of 87.8 ± 20.6 to 52.6 ± 6.1 teeth cm⁻² Myr⁻¹ ($\mu_1 \neq \mu_2$, $p = 0.003$). Dentine accumulation also showed a decrease, from 16.1 ± 6.0 denticles cm⁻² Myr⁻¹ in the ice-free Eocene to 6.5 ± 3.1 denticles cm⁻² Myr⁻¹ in the Oligocene South Pacific; however, this decrease is not significant ($p = 0.058$), possibly due to lower abundances of denticles in the samples. The North Pacific IAR is 152 ± 60.4 ich cm⁻² Myr⁻¹ in the Early Oligocene, approximately double the contemporary values of the South Pacific, and slightly lower than those of the Palaeocene North Pacific (177.3 ± 21.5 ich cm⁻² Myr⁻¹; $\mu_1 \neq \mu_2$, $p = 0.006$), mirroring the observed difference in fish production between the Early Palaeogene and the Oligocene observed in the South Pacific (figure 2b). The Eocene–Oligocene transition is a time of increased diatom production in the Southern Ocean, which is thought to have driven an increase in food web efficiency, small forage fish abundance and the diversification of marine mammals and seabirds [25–29], which would prey on the small pelagic fish represented in our ichthyolith records. However, it appears that increased production of large phytoplankton at high latitudes did not drive an increase in ray-finned fish and elasmobranch production in the gyres, as the beginning of ‘Icehouse Earth’ was associated with a decrease in both fish and elasmobranch production.

### 4. Modern Ocean

At 20 Ma, both the relative and absolute abundance of pelagic elasmobranch fossils declined dramatically and suddenly, to one denticle for every 50 or more teeth (North Pacific: 0.013 ± 0.03 denticles per tooth; South Pacific: 0.033 ± 0.05 denticles per tooth), marking the beginning of the Modern Ocean ecosystem state (figure 3). The decline in the ratio of elasmobranch AR to fish AR between the Palaeogene and Modern Ocean states is highly significant (two-sided t-test, $\mu_1 \neq \mu_2$, $p < 10^{-10}$ for both gyres). In the Palaeogene Ocean, dentine accumulation was approximately 24.3 ± 12.4 denticles cm⁻² Myr⁻¹ in the South Pacific and 32.8 ± 12.9 denticles cm⁻² Myr⁻¹ in the North Pacific. The Modern Ocean saw an abrupt decrease in these ARs, which we interpret as a decline in the abundance of elasmobranchs, rather than a change in ecosystem states. The decline in elasmobranch production and abundance when compared with ray-finned fish reflects a dramatic difference in the ecological roles of elasmobranchs between the Palaeogene and Modern ecosystem states.

The exact timing of the decline in elasmobranch abundance is not pinpointed in our record due to sedimentary gaps in both gyres, but is constrained to fall between 19 and 21 Ma. There is no apparent climate or biotic event around 20 Ma which could have driven this abrupt shift [30]. The loss of denticles from the record means that nearly all the IAR signal is driven by ray-finned fish production. South Pacific tooth IAR is highly variable on short timescales in the Neogene when compared with the Palaeogene, with a mean IAR value of 58.4 ± 43.8 ich cm⁻² Myr⁻¹, but has a range of
3.7–185 ich cm⁻² Myr⁻¹ with rapid oscillations between these extremes. In the North Pacific, where a hiatus prevented observation of the basal Miocene there is a dramatic decline in ichthyolith accumulation between 11.6 and 11 Ma from 550 to 41 ich cm⁻² Myr⁻¹, immediately preceding a rise in diatom accumulation at the site (figure 2c). The South Pacific record shows a simultaneous, short-lived drop in ichthyolith abundance, falling from 130.8 ich cm⁻² Myr⁻¹ at 12 Ma to 41.1 ich cm⁻² Myr⁻¹ at 11 Ma (figure 2c), suggesting that the increased variability observed in the South Pacific may be an aliased record of real, basin-wide cycles of fish production such as the one observed at high resolution in the North Pacific. Both our North Pacific Gyre record and equatorial Pacific cores show a major increase in opal production and organic matter export peaking between 10.2 and 11.3 Ma [31], suggesting that gyre fish production was inversely correlated with major bloom periods in diatoms for at least some of their history. This drop in fish tooth flux is somewhat counter-intuitive, as most modern diatom-dominated modern ecosystems have a high abundance of fish due to the more efficient food web based on the large phytoplankton.

Notably, the Early Miocene coincides with the radiations of baleen whales [25,29,32], large pelagic ray-finned fish like tunas [33], and many sea birds [26], all of which may have been competitors for resources with elasmobranchs, either directly by targeting common prey, or indirectly by targeting lower trophic levels like krill and forage fish. Pelagic elasmobranchs obviously did not become extinct, indeed, there are numerous notable pelagic shark species, including *Megalodon*, that have a prominent fossil record during the Neogene [34]. We speculate that the rise of other pelagic vertebrate competitors alongside increased variability in fish production, may have driven decreased elasmobranch production, or favoured the rise of migratory super-predators in the clade. Abundance-based evaluations of marine tetrapods during these intervals, alongside evaluations of taxonomic richness, could help to address the role of environment versus ecology in these ecosystem structural changes [35,36].

Furthermore, although we might expect increased ichthyolith accumulation towards the recent due to better preservation, the most recent 3 Myr of ichthyolith accumulation in the South Pacific fluctuate between 25 and 75 ich cm⁻² Myr⁻¹, a mere fraction of the ichthyolith accumulation of the 10 Myr prior, and indeed for most of the Cenozoic. These low but variable levels of ichthyolith accumulation suggest that fish production in general may be depressed in modern gyres, perhaps due to focusing of nutrient supply to coastal and equatorial upwelling centres or nutrient trapping in the Southern Ocean [25,29]. Indeed, it has been proposed that radiations of large whales are in response to increasingly distributed centres of productivity, requiring long distance migration [25]. Seabirds may also be part of this trend, since many coastal and pelagic species have very long foraging flight distances [27]. As modern pelagic sharks undertake large migrations across ocean basins [37], it is possible that the observed decline in denticles in our Modern Ocean system represents not a decrease in elasmobranch biomass throughout the world’s oceans, but a rather decrease in the proportion of time spent in the gyre habitat, and thus in the flux of denticles to the deep ocean seafloor.

**5. Conclusion**

Over the past 85 Myr, there have been three distinct pelagic ecosystem structures in the Pacific Ocean gyres, defined by their relative and absolute abundances of elasmobranchs and ray-finned fish (figure 4). Abrupt transitions between the three ocean ecosystem states occur approximately simultaneously in both ocean basins, and are unrelated to major climate events during the interval. The shift from the Cretaceous Ocean to the Palaeogene Ocean was triggered by the K/Pg mass extinction [13]. The resulting Palaeocene Ocean system had remarkable stability in the relative balance of ray-finned fish and elasmobranchs, despite large changes in absolute abundance, and the imposition of numerous dramatic climate perturbations, including extreme greenhouse and hyperthermal events during the Palaeocene and Eocene [38] and the transition from a greenhouse to icehouse planet with permanent polar icecaps [39]. There is no apparent climatic or biotic driver for the transition from Palaeogene to Modern Ocean [36], since polar glaciation began more than 10 Myr prior, and there are no obvious perturbations to carbon or oxygen isotopes [30]. However, the basal Neogene is coincident with the rise and diversification of many other pelagic
groups, including radiations of pelagic diatoms [40], zooplankton [41] and pelagic vertebrates [28,32]. Hence, it is likely that the open ocean ecosystem structures of the past 85 Myr are driven by ecological thresholds triggered by changes in the pelagic resource base and dynamics of competition among pelagic consumers in the open ocean [36].

6. Methods

(a) Sampling protocol for ichthyolith extraction

Red-clay samples (5–15 g) were taken at 5 cm intervals throughout the two deep-sea sediment cores, effectively providing a continuous record downcore. For ODP Site 886, samples were 2–3 cm in length, taken at 5 cm intervals (approx. 30–50 kyr resolution). For DSDP Site 596, samples were taken at 5 cm intervals (approx. 200 kyr resolution) for the interval of 85–42 Ma, and approximately 20–25 cm intervals (approx. 1 Myr resolution) for the interval from 42 Ma to present. All samples were dried to a constant weight at 50°C, sometimes taking months to remove all water. Once dry, samples were weighed and disaggregated in 50–100 ml de-ionized water. Additionally, approximately 10–20 ml of 5% acetic acid were added to the samples to remove any residual carbonate. Samples were wet-sieved over a 38 μm sieve, and dried overnight at 50°C. All ichthyoliths more than 106 μm were picked out of the residue using a dissection microscope and very fine paintbrush, and classified as either a tooth or a denticle. They were mounted on cardboard micropalaeontological slides using gum tragacanth. Samples were processed in random order, rather than stratigraphic order, to avoid additional bias. IARs were calculated from established age models for the sites [15,16].

(b) Calculation of ichthyolith accumulation rates

While the community metric we report, the ratio of elasmobranchs to benthic foraminifers, is independent of timescale, the reported IARs and our interpretation of ‘how many’ fish or elasmobranchs is dependent on the accuracy of age models and sedimentation rates of each core. Red clays are traditionally very difficult to date, as they are lacking in traditional microfossil groups for biostratigraphy, and accumulate too slowly for magnetostratigraphy. We used independently developed geochemical-based age models well established in the literature, to calculate IAR for each site. For DSDP Site 596, we employ the sedimentological framework of Zhou & Kyte [16], which is based on an inverse-AR model using cobalt concentrations in the sediments. For ODP Site 886, we work within the framework compiled by Snoeckx et al. [15] which includes strontium isotope stratigraphy for the oldest samples, and magnetostratigraphy, and radiolarian biostratigraphy for the youngest. ODP Site 886 has two hiatuses in the record. In addition, ODP Site 886 had several intervals in the Late Cretaceous which included manganese oxides formed around ichthyoliths, making the determination of total ichthyoliths impossible. Both sites have a prominent iridium anomaly at the Cretaceous–Palaeogene boundary [15,16,42], providing an additional tie-point for the age models. Further discussion of the age models is provided in the electronic supplementary material.

Data accessibility. All data generated in this study have been archived in the Pangea Data Repository (doi:10.1594/PANGAEA.859876) and the Dryad data repository (doi:10.5061/dryad.38537).

Authors’ contributions. E.S. and R.N. designed the study. E.S. generated DSDP 596 dataset and 886 Cretaceous–Palaeocene. L.G. generated 886 Oligocene and J.C. generated 886 Miocene datasets. E.S. and R.N. wrote the paper with input from J.C. and L.G.

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