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A Pleistocene record of global fish production and implications for sustainability of polar fisheries

Author

Werner, Leah Kimberly

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A Pleistocene record of global fish production and implications for sustainability of polar fisheries

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in

Oceanography

by

Leah Kimberly Werner

Committee in charge:

Professor Richard D. Norris, Chair
Professor David M. Checkley
Professor Phillip A. Hastings

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University of California San Diego

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DEDICATION

To my family and friends, thank you for your endless support.

TABLE OF CONTENTS

LIST OF SUPPLEMENTAL FILES

Excel File 1 (Sample and Age Model Data for ODP 664, 677, 704, 982, 1123, and IODP U1313)

LIST OF FIGURES

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ABSTRACT OF THE THESIS

A Pleistocene record of global fish production and implications for sustainability of polar fisheries

by

Leah Kimberly Werner

Master of Science in Oceanography

University of California San Diego, 2019

Professor Richard D. Norris, Chair

Richly productive polar marine ecosystems are hypothesized to have evolved within the last ~30 million years through the rise of diatoms to ecological dominance and diversification of distinctive polar fish, sea birds, seals and whales. Today, short diatom-based food chains support substantial fish biomass, but whether polar fish production is high enough to sustain current industrial fishing is unknown. To this end, we compared ichthyolith accumulation rates (IAR), a proxy for fish production, across ocean ecosystems to trace the development of global fisheries stocks over the past 1.8 million years. We find that the magnitude of polar fish production, based on the flux of fish teeth to deep-sea sediments, is an order of magnitude lower than seen in subtropical and tropical sites. We suggest that polar fish production is systematically suppressed by extreme seasonality, phenological mismatch, low functional redundancy, and extreme glacial-interglacial climatic variability in the high latitude oceans. Comparisons of our Pleistocene data to similar records from the Eocene and Oligocene oceans (~42-28 Ma) show that fish production in high latitudes has been consistently low for the last 30-40 Ma relative to most of the tropical and subtropical locations. We conclude that the stock crashes observed in the polar regions over the past several decades reflect overexploitation of ecosystems that have had low fish production for tens of millions of years.

INTRODUCTION

Modern polar marine ecosystems have long been posited as highly productive regions because of the enormous spring and summer productivity pulses of plankton communities (1–3), efficient trophic transfers owed to the dominance of large diatoms within phytoplankton blooms (4), low-diversity food webs (5–8), and the ample supply of surface macronutrients during polar springtime. Phylogenetic diversity of planktonic communities and pulsed diatom production has been suggested to play a crucial role in supporting high trophic levels, including fish populations (9–11).

The evolution and biogeography of the polar regions also support the hypothesis that these ecosystems have high productivity, particularly in the Southern Ocean. The coincident development of the Antarctic Circumpolar Current (ACC), Subantarctic Front (SAF) and Antarctic Polar Front (APF) near the Eocene-Oligocene (EO) boundary (~34 Ma) (12) created nutrient-rich upwelling of deep waters and diatom-dominated food chains in the Southern Ocean (13). Nutrient trapping in the Circumpolar Current built silica inventories in the Middle Miocene that resulted in the radiation of diatoms over the last 15 Myr (14, 15). The rise of diatoms to ecological dominance is thought to have increased food web efficiency and supported the canonical diatom-krill-predator ecosystems of the Southern Ocean (9, 16). Indeed, molecular clock studies reveal important evolutionary radiations at higher trophic levels in the Southern Ocean since the Mid-Miocene ~15 Ma, including Antarctic krill (17), whales (18), penguins (19), seals (20), and fishes (21, 22). Taxonomic diversification of marine mammals, fish, and birds continued through the Pleistocene*,* perhaps because of the fragmentation of oceanic populations during glacial and interglacial periods, supporting cryptic speciation (23–25). For example, the shelf waters of the Antarctic and Sub-Antarctic are occupied by highly distinctive and endemic (c. 88%) fish fauna (26).

The biogeography of the Arctic Ocean, in contrast, is at most several million years old (27) and is characterized by relatively young, non-endemic marine benthic fauna (28, 29). During the late Cretaceous and early Paleogene, the embryonic Arctic Ocean was generally isolated from the rest of the world (30) albeit with a limited connection between the Atlantic and primeval Arctic Ocean (29). Proxy records indicate that sea ice and sea-ice dependent diatoms became a feature in the Arctic by 47 Ma, synchronous with glaciation in Antarctica, and then became consistently ice-covered for at least the last 13-14 Myr (31–33). The opening of the Bering Strait at approximately 3.5 Ma allowed for unrestricted biotic exchange between the North Pacific and Arctic-Atlantic basins, with far more taxa moving from the Pacific to the Atlantic than in the reverse direction (34). The periodic alternations between colder glacial and warmer interglacial climates drove extensive changes in Arctic species diversity, primary productivity, species' geographic range shifts in and out of the Arctic, and community restructuring (35). The Arctic Ocean has large inputs of organic material and secondary production, including zooplankton, which support a high proportion of top predators (e.g., seals, sea birds, narwhals, belugas, and polar bears) that depend on ice-associated marine fish species (36–38).

Despite seasonally highly productive regimes in the polar oceans, serial depletions of certain fish stocks have been documented in these regions within the last several decades. Since the finfishing industry ventured into the Southern Ocean in the late 1960s (39, 40), large-scale and unregulated industrial fishing moved from one stock and geographical area to the next triggering reductions of various stocks by 90-95% (41, 42). Similarly in the subarctic, crashes reduced some of the largest fisheries in the world to less than 10% of their original stock size, including the Atlantic cod (43) and capelin (44, 45). Biomass of high-trophic level fish species in the North Atlantic has declined by two-thirds during the second half of the 20th century (46).

Existing literature concerning global fish production is largely based on stock assessments and fish landing records and these typically only date to the start of industrial fishing approximately 60 years ago, barely long enough for informative statistical analysis (41). Further, most literature reviewing prehistoric trends in fish productivity highlights short-term to decadal-scale changes. While informative, relying on such studies may support fundamentally flawed management schemes as they may not capture processes influencing fish productivity that can only be understood through large-scale datasets. For example, Sakshaug (47) suggested that fish biomasses and productivities in the Barents Sea have always experienced pronounced annualized variation that sound management can diminish but never eradicate;

however, this conclusion was based on a 5-year dataset and is unequipped for basin-wide interpretations. The short period of fisheries observations suggests that longer baselines of fish production are fundamental to assess overall fish production in polar waters. Additionally, there is a paucity of production data based on remote sensing from the high-latitude regions. During the winter, the solar zenith angle is often larger than the maximum for which atmospheric correction algorithms have been developed (generally 70°), and consequently a large fraction of the polar ocean surface is undocumented for satellite-derived production estimates (48).

Our limited understanding of naturally occurring fish production in the polar regions leads us to speculate on their role in the Arctic and Southern Ocean food webs. Oceanographer Alfred Bigelow once opined, "all fish is diatoms," (49) in that diatom blooms fuel the growth of herbivorous zooplankton, and the zooplankton in turn are prey for fish and invertebrates such as krill. In following this logic, we speculate whether the diatom-dominated food chains that support large populations of higher trophic level species in polar ecosystems can dually support high baseline fish production. Are the polar stock crashes observed over the last half century a mere artifact of overfishing – one that a seemingly productive system can sustain?

To assess baseline production in mid- and upper-trophic level fish we collected a high-resolution time series of ichthyolith production (flux of microfossil fish teeth and shark denticles), in a global array of sedimentary cores spanning the past ~1.8 Myr. Ichthyoliths preserved in the deep-sea sedimentary record, provide an extensive and temporally continuous fossil record that can be used to estimate the production of teeth by fishes. Teeth and denticles are delivered to the seafloor by either live or dead individuals or as indigestible elements in fecal matter. Unlike most microfossils, ichthyoliths are composed of calcium phosphate which make them among the most dissolution resistant of any fossil remains (50). Overall, the abundance, preservation, and ubiquity of ichthyoliths in marine sediments make them an effective proxy to overall fish production through time.

We selected six sites from a global array of deep-sea sediment cores with astronomically-tuned chronologies. Ichthyolith abundances were quantified and converted to ichthyolith accumulation rates

(IAR; eq. 1), a method used to estimate changes in fish production independent of changes in sedimentation rate, sediment composition, and sediment density. We further compare our findings to a global record of pelagic fish tooth production through the middle Eocene and early Oligocene (23-41.8 Ma) (51) to assess how mid-level consumers responded to long-term oceanic and climatic changes through the last ~42 million years.

METHODS

Site Selection

We use ichthyoliths preserved in deep-sea sediment cores from six open ocean sites in the Atlantic and Pacific Oceans and representing different latitudinal and oceanographic regimes (Fig. 1). We compared our Pleistocene data with ichthyolith data derived from an additional seven sites of Eocene and Oligocene age that have been previously documented in an unpublished dataset (51). Site selection was determined by sample availability, geographic location, suitability, resolution of the Pleistocene section in each core, and the existence of robust age models. Thirty-cc sediment samples were obtained from the International Ocean Discovery Program (IODP) at a spacing of ~67,000 years in each site in the Pleistocene and ~139,000 years in the Eocene and Oligocene.

All sites were selected to cover the major ocean ecosystems in the global ocean. Our Pleistocene sites include Ocean Drilling Program (ODP) 704, 982, 664, 677, 1123 and IODP U1313. ODP Site 704 is located in the eastern South Atlantic within Subantarctic Surface Water (SSW) that is entrained within the ACC (52). ODP Site 982 is located in drift sediments on Rockall Plateau in the North Atlantic and is nannofossil ooze alternating with nannofossil clays and silty clays (53). ODP Site 664 is located in the central equatorial Atlantic and is clayey calcareous nannofossil ooze (54). ODP Site 677 is located in the equatorial Pacific and is siliceous-nannofossil and nannofossil-radiolarian oozes (55). ODP Site 1123 lies beneath the southwest Pacific deep western boundary current (DWBC) and is clayey nannofossil ooze (56). IODP Site U1313 is located on the upper-western flank of the Mid-Atlantic Ridge, northwest of the

Azores and under the influence of the North Atlantic Deep Water (NADW) circulation, and predominantly consists of calcareous biogenic oozes (57).

Samples processed through the Pleistocene were compared with a high-resolution time series of ichthyolith abundance through the middle Eocene and Oligocene (51). This record spans ~42-23 Ma, with resolutions of 3.6 to 17.8 samples/million years of pelagic tooth abundance in the South Atlantic (Deep Sea Drilling Project [DSDP] Site 522), North Atlantic (IODP U1406), South Pacific (DSDP Site 596), Equatorial Pacific (ODP Site 1217), subpolar North Pacific (ODP Site 886), and two Southern Ocean sites, Maud Rise, South Atlantic (ODP Site 689) and Kerguelen Plateau, Indian Ocean (ODP Site 748). The EO record was produced using comparable sampling and analytical methodologies to our Pleistocene record.

Sample Processing

Samples were dried at 50°C to a constant mass and weighed to enable the calculation of the IAR. Carbonates were dissolved in 5-15% acetic acid. The amount of acid varied per site and ranged from 400 mL to 1,000 mL acid per 30-g sample. Samples were left in acid until they stopped reacting (between 2-24 hours), and then washed over a 63-μm sieve using de-ionized water to remove the acid and concentrate the ichthyoliths.

Once re-dried in a 50°C oven, heavy liquids were deployed to remove most of the low-density siliceous sediment relative to ichthyoliths. A heavy liquid "LST" (heteropolytungstate) was diluted to a density of 2.4 g/cm^3 to separate low-density siliceous sediment (specific gravity ~2.0 g/cm^3) relative to ichthyoliths with a density of ~3.4 g/cm^3 (58). The sample residue and heavy liquid were mixed in a 25-50 mL tube to completely wet the sample grains. The tube was subsequently capped and centrifuged for approximately 10 minutes at 1000-1500 rpm to separate the ichthyoliths at the bottom of the tube from the light fraction that floated to the top. The light fraction was then poured off the top of the tube into filter paper in a funnel, concentrating the ichthyoliths in the bottom of the tube, which were poured into a separate filter paper in a funnel. Both the light and heavy fractions were separately rinsed with de-ionized water to recover the dilute heavy liquids solution, and then dried in a 50°C oven. The dilute heavy liquids solution was additionally placed in a 50°C oven to evaporate the rinse water and restore its density.

ODP Site 982 was especially heavy in residual sediment grains following carbonate dissolution and heavy liquids separation of biogenic silica. Consequently, samples from ODP 982 were stained with Alizarin Red S ($C_{14}H_7NaO_7S$), a calcium-specific dye that selectively colors calcium phosphate pink, to improve visual contrast of ichthyoliths against background detrital clay and silt. This protocol has been previously documented to stain fish bones (59) and ichthyoliths (58, 60). The stain is made with distilled water, 1% potassium hydroxide (KOH) solution, and enough Alizarin to turn the solution a deep purple. Following acid dissolution, washing, and employment of heavy liquids, a few drops of the Alizarin Red S solution were added to dried sample residue until the sample was completely wet. This was left for 24-48 hours, and then washed over a 63-µm sieve, transferred to filter paper in a funnel, and dried in a 50°C oven.

Dry sample residues were transferred to storage vials and later counted under a stereo binocular microscope, manually picked out of residue with a very fine paint brush and placed on cardboard micropaleontological slides. Only whole and intact teeth and denticles were counted towards ichthyolith totals (i.e., omitting fragments). Samples were processed in random order to minimize potential bias.

Data Preparation

We converted the raw ichthyolith counts into a comparable metric of ichthyolith flux or ichthyoliths falling to a fixed area of the seafloor over a fixed time interval. IAR is calculated as:

$$\textbf{Ichthyolith Accumulation Rate = Abundance * Dry Bulk Density * Sedimentation Rates}$$

$$\left(\frac{\textbf{Ichthyoliths}}{\textbf{cm}^2 * \textbf{myr}}\right) = \left(\frac{\textbf{Ichthyoliths}}{\textbf{grams}}\right) * \left(\frac{\textbf{grams}}{\textbf{cm}^3}\right) * \left(\frac{\textbf{cm}}{\textbf{myr}}\right)$$

The IAR calculation corrects for changes in sedimentation rate or sediment density and approximates the relative biomass of fish in the overlying water column over a fixed time interval, a proxy for overall fish production. Importantly, IAR enables the comparison of the flux of ichthyoliths to the sea floor between sites with different sedimentation rates and overall oceanographic conditions.

Sedimentation rates for each site were determined by established age models for the Pleistocene. The age models for ODP Sites 664, 677, 982 and 1123 were developed by correlation to the LR04 global benthic $\delta^{18}O$ stack (61). The adjusted composite depth model and time scale for IODP Site U1313 (62) is based on a combination of benthic foraminiferal $\delta^{18}O$ and sediment lightness for the last 1 Ma, and tuning of lightness to the LR04 global benthic $\delta^{18}O$ stack (61) for the earlier Pleistocene record. For ODP Site 704, two age models were considered: one chronology is based on correlation of the oxygen isotopic record with the SPECMAP stacked record (63) for the last 750 Kyr. The age model for the interval before 750 Ka was constructed from a combination of magnetostratigraphic and oxygen isotope stratigraphy (64).

Composite depth models were taken from published or shipboard stratigraphic frameworks, as applicable to age models (62, 64–68). AnalySeries software (69) was used for each site to identify tie points in samples depths with age model chronology. All sites used shipboard dry-bulk-density, calculated as averages of the same sample intervals used in the Pleistocene records, in the IAR calculations (52–57). The development of timescales for EO records has been previously presented in Sibert et al. (51).

Calculated IAR data do not meet the assumption of normality, so to compare IAR between sites across the Pleistocene as well as the Eocene and Oligocene, the Kruskal-Wallis and Pairwise Wilcoxon non-parametric rank-based tests were utilized. All analyses were carried out using the R statistical software.

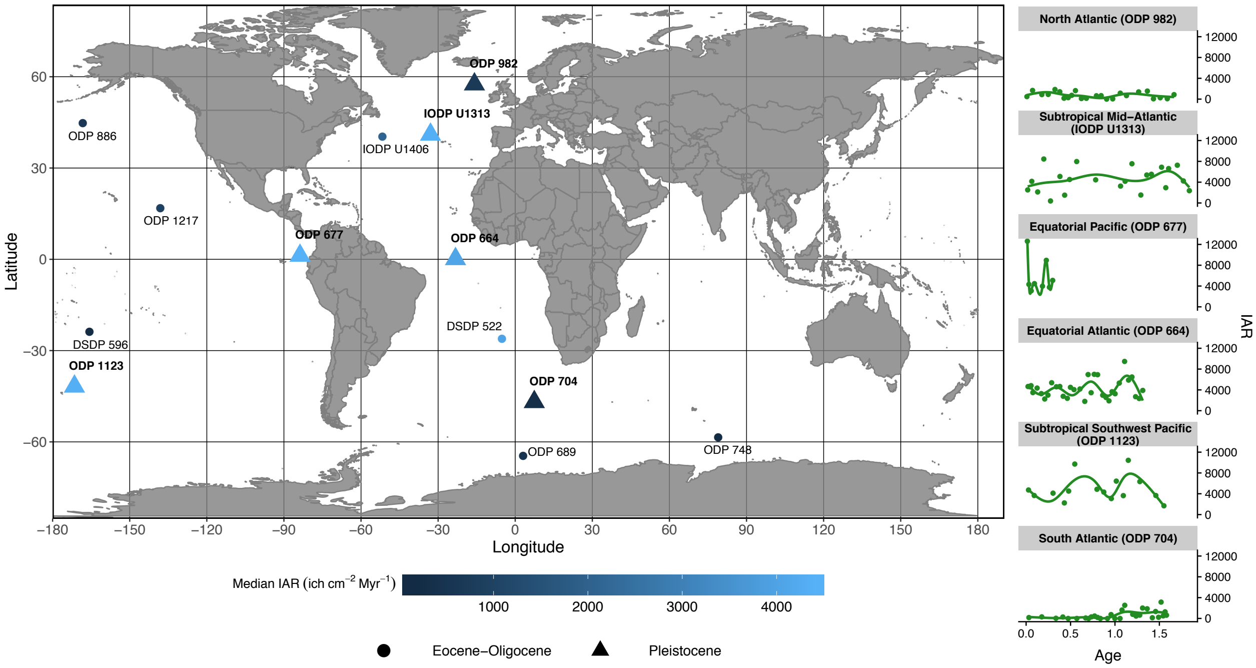

Figure 1. Map of study sites in the Pleistocene and Eocene-Oligocene (EO) records (left) and Ichthyolith Accumulation Rates (IAR) for individual Pleistocene records (right). Left: Study site locations for sites included in the Pleistocene (triangles and bold) and EO (circles) (51) records. Sites are colored based on their median IAR through respective intervals, with higher IAR in light blue and lower IAR in dark blue. Right: Line graph depicting IAR through the Pleistocene for study sites ODP 982, IODP U1313, and ODP 677, 664, 1123, and 704 (from top to bottom). All lines are smoothed using GAM (general additive modeling) fit.

RESULTS

Pleistocene Records

The global ichthyolith production record points to a strong latitudinal gradient in pelagic fish productivity through the Pleistocene (Fig. 2 and 3). We statistically compared overall baseline productivity at locations with analogous environmental structure, oceanography and latitude. Polar sites (ODP 982 and 704) have statistically comparable ichthyolith abundance ($p = 1.0$). Additionally, statistically significant comparisons in IAR were also found between equatorial (ODP 664 and 677) and gyre margin (ODP 1123 and IODP U1313) locations ($p = 1.0$), hereafter referred to collectively as “low latitude sites”.

Absolute IAR values between polar and lower latitude sites are statistically different ($p < 0.05$). The low latitude sites have collectively higher IAR [mean = 4,590 ich cm^{-2} myr^{-1} (SD = ±2,236), n = 78] relative to polar sites (mean = 692 ich cm^{-2} myr^{-1} (±728), n = 54]). Low latitude IAR values generally range from 3,000-6000 ich cm^{-2} myr^{-1}, with peaks ranging between ~7,000-12,600 ich cm^{-2} myr^{-1} throughout the individual records. Mean values between equatorial sites [4,530 ich cm^{-2} myr^{-1} (±2,172), n = 41] and gyre margin sites [4,657 ich cm^{-2} myr^{-1} (±2,334), n = 37] were statistically comparable, and considerable fluctuations were observed throughout all individual records (see Fig. 1 and 3).

In contrast, polar sites [mean = 692 ich cm^{-2} myr^{-1} (±728), n = 54] have IAR about a tenth that of lower latitude sites and range from approximately 300-700 ich cm^{-2} myr^{-1}, with generally less variability relative to low latitude sites (see Fig. 1 and 3). Of note, zero ichthyoliths were recovered in 23% of samples from the ODP 704 record, all of which spanned from 1.05 Myr and later. ODP 982 is the only other record with a minimum IAR value of 0 ich cm^{-2} myr^{-1}.

In some cases, there is considerable within-site variance. We are unable to resolve possible orbital signals in IAR, such as glacial-interglacial variation owing to our low sample spacing. Instead our study design is focused on interpretation of long-term trends over the course of evolutionary time rather than analysis of temporal variability.

Equatorial Sites

At ODP 664 (Equatorial Atlantic), 33 samples were processed across a ~1.31 million-year interval, spaced ~ 40 Kyr in a time series between 21,506 Kyr and 1.3 Ma. The mean IAR is 4,227 ich cm^{-2} myr^{-1} (±1,744), and median IAR is 4,053 ich cm^{-2} myr^{-1}, and the record generally fluctuates between 2,000-5,500 ich cm^{-2} myr^{-1}. Considerable variation in IAR is observed between 1.3 Myr and 660 Kyr, with occasional peaks of ~7,000-9,500 ich cm^{-2} myr^{-1} deviating from IAR values of ~1,800-3,900 ich cm^{-2} myr^{-1}. Variability is reduced thereafter and IAR generally fluctuates between ~2,500-5,000 ich cm^{-2} myr^{-1}.

At ODP Site 677 (Equatorial Pacific), eight samples were processed between ~300-14 Kyr, spaced about 41 Kyr apart. The mean IAR is 5,781 ich cm^{-2} myr^{-1} (±3,290) and the median is 4,392 ich cm^{-2} myr^{-1}. IAR generally fluctuates around 4,000 ich cm^{-2} myr^{-1}, with two peaks of ~8,950 ich cm^{-2} myr^{-}

^{1} at 227 Ka and ~12,600 ich cm^{-2} myr^{-1} at 13.8 Kyr. Though ODP 677 has the highest mean and median IAR values throughout the Pleistocene record, caution must be taken in interpretation, as this record is limited by the sample size.

Gyre Margin Sites

At ODP 1123 (South Pacific subtropical gyre margin), 15 samples were processed covering a ~1.55 million-year record, which resulted in a spacing of ~109 Kyr between samples. This site has a high mean IAR of 4,896 ich cm^{-2} myr^{-1} (±2,459) and median IAR of 4,323 ich cm^{-2} myr^{-1}. The record fluctuates between ~3,000-5,000 ich cm^{-2} myr^{-1}, with the exception of two peaks of ~10,000 ich cm^{-2} myr^{-1} observed at 1.15 Myr and again at 548 Kyr.

At IODP U1313 (North Atlantic subtropical gyre margin), 22 samples were processed over ~1.55 million years, with a spacing of 87 Kyr between samples. This record has a mean IAR value of 4,493 ich cm^{-2} myr^{-1} (±2,288) and a median IAR of 4,345. IAR values vary between ~2,000-7,500 ich cm^{-2} myr^{-1}.

Polar Sites

At ODP Site 704 (South Atlantic), 30 samples were processed over a ~1.58 million-year period, with a spacing of 53 Kyr between samples. In comparison to other records, ODP 704 has the lowest mean IAR of 657 ich cm^{-2} myr^{-1} (±827) and median IAR of 302 ich cm^{-2} myr^{-1}. The record shows a decrease in ichthyolith accumulation through the Pleistocene, with a stark difference in mean IAR and variability before 1.08 Myr and thereafter. Prior to 1.08 Myr, IAR generally fluctuates around a mean of 1,223 ich cm^{-2} myr^{-1} (±909), generally between ~200-2,000 ich cm^{-2} myr^{-1}, with peak values of up to 3,150 ich cm^{-2} myr^{-1}. Following 1.08 Myr, the mean value decreases to 161 ich cm^{-2} myr^{-1} (±214), a 24% reduction, and IAR generally fluctuates between 0-300 ich cm^{-2} myr^{-1}.

At ODP 982 (North Atlantic), 24 samples were processed over ~1.67 million years, with an average spacing of 72 Kyr. The mean IAR value of 670 ich cm^{-2} myr^{-1} (±595) and median IAR of 670 ich cm^{-2} myr^{-1}, were slightly higher than ODP 704, although still 15% that of the low latitude sites. IAR was generally below 1,000 ich cm^{-2} myr^{-1} excepting elevated excursions between ~1,550-1,850 ich cm^{-2} myr^{-1}.

Comparisons between Pleistocene and Eocene and Oligocene Records

A similar latitudinal trend in IAR was observed between the Pleistocene and the EO record (Fig. 4). Similar to the Pleistocene record, Eocene and Oligocene IAR in the Southern Ocean sites, approximately 100-400 ich cm^{-2} myr^{-1}, are about a tenth that of lower latitude sites (4000-5000 ich cm^{-2} myr^{-1}). The only sites outside of the Southern Ocean with comparably low IAR are the North and South Pacific gyre sites ODP 886 and DSDP 596, respectively, which are ultra-oligotrophic regions with notably low productivity in the modern ocean. The similar latitudinal trend observed in both the Pleistocene and EO records suggests that baseline fish productivity in high latitudes has been consistently low relative to low latitude sites, without substantial change in ichthyolith production rates over the last ~42 Myr.

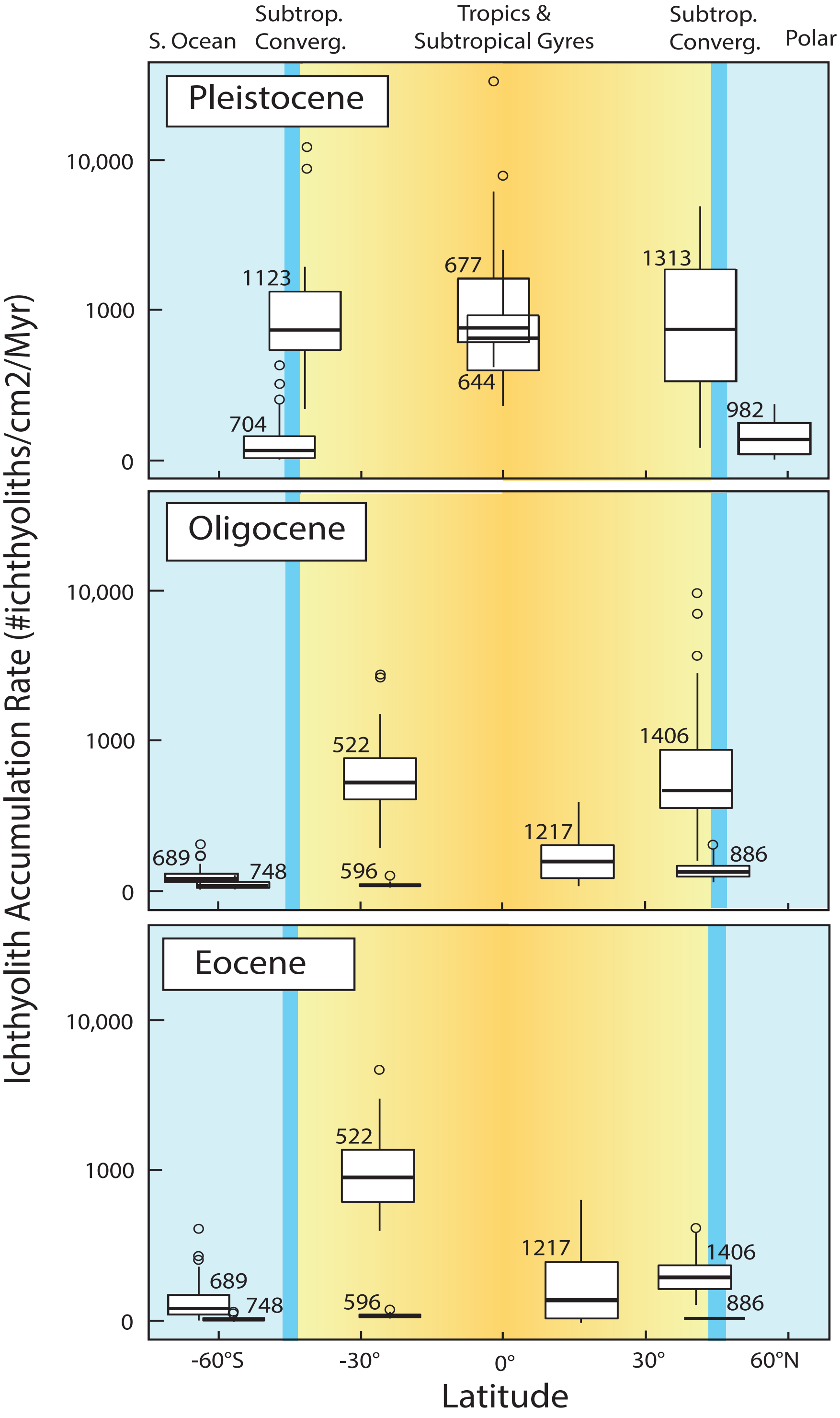

Figure 2. IAR by site plotted against latitude within Pleistocene, Oligocene, and Eocene intervals. Latitudes (x-axis) are representative of study site locations. The box plot components are solid line, median; box, interquartile range (IR); whiskers, most extreme point less than 1.5 times the IR from the 75th percentile; circle, outlier values beyond the whiskers. IAR values through the Oligocene and Eocene intervals are taken from Sibert et al. (51).

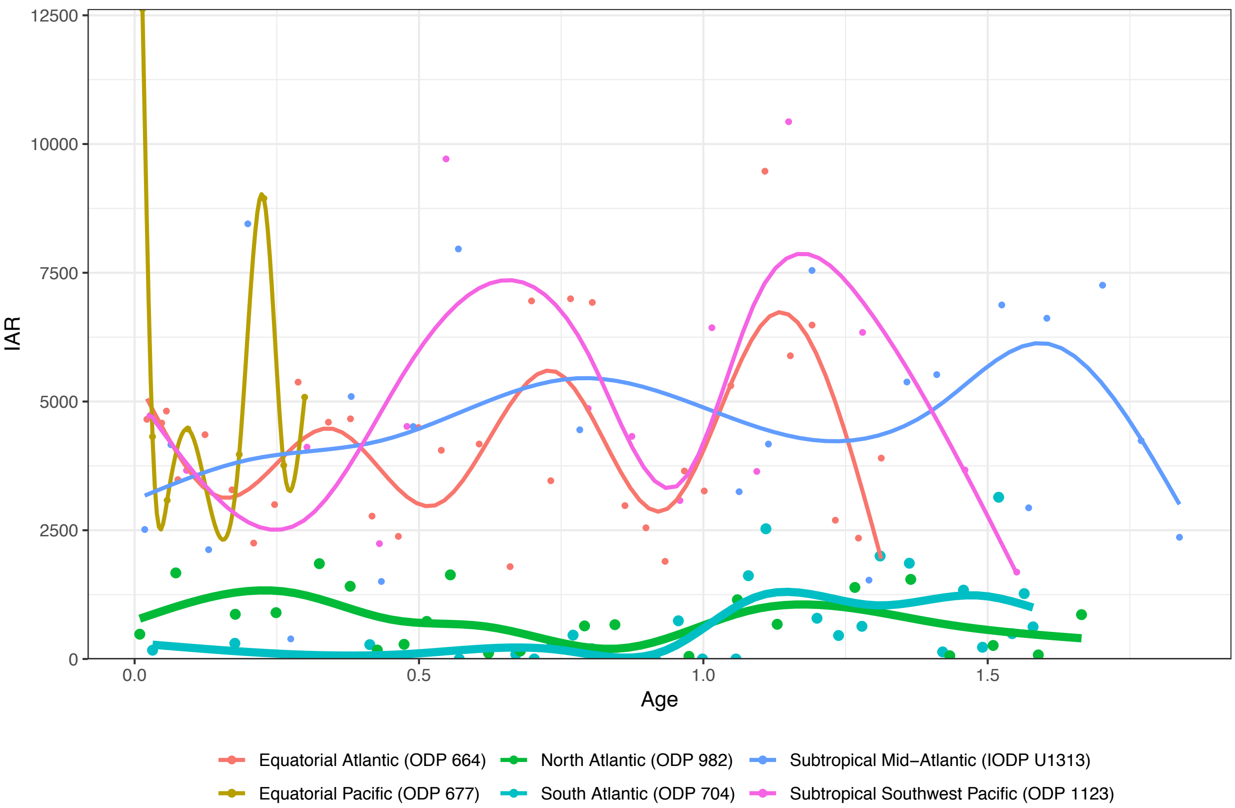

Figure 3. IAR for all Pleistocene sites. All lines are smoothed using GAM fit to show trends.

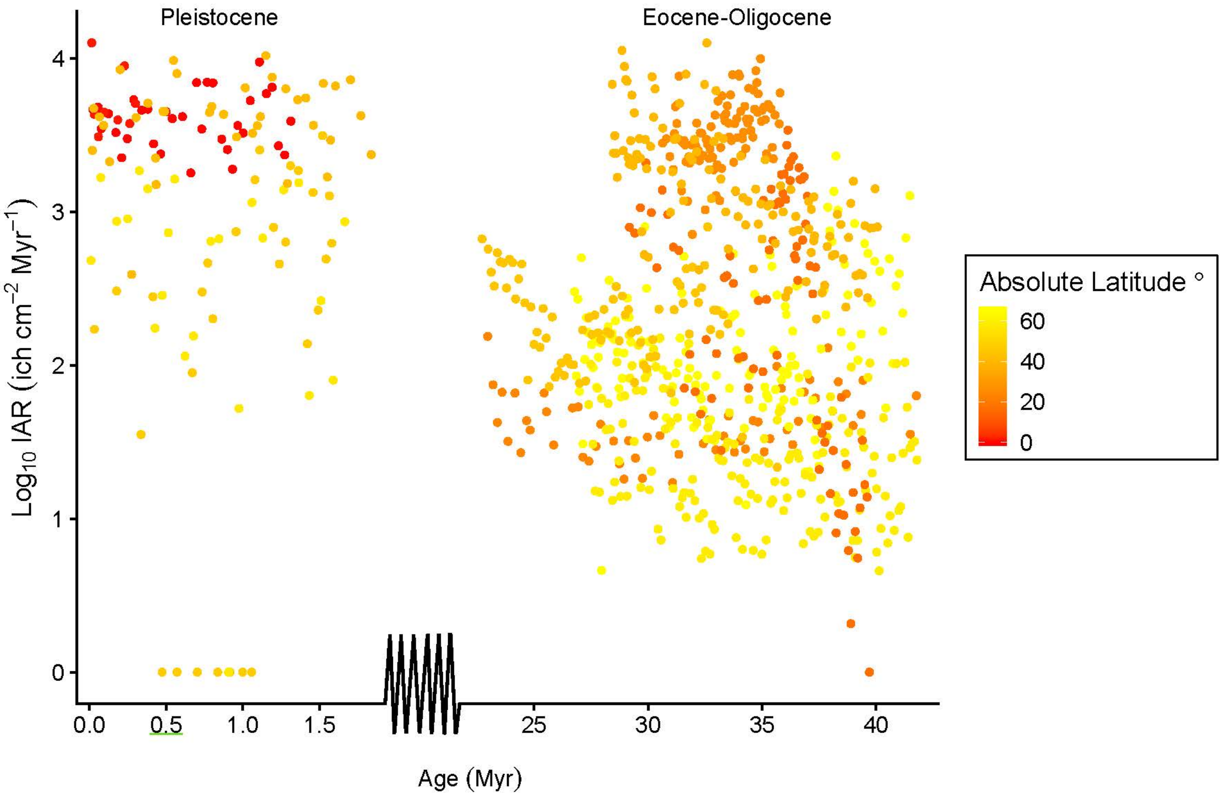

Figure 4. IAR-Absolute Latitude Plot through the Pleistocene and EO. Each dot represents Log_{10} IAR (y-axis) for one sample, plotted against the age (x-axis) of the sample (see Methods for age model sources). Dot are colored based on the study site locations with respect to distance from the equator (i.e., absolute latitude), with red indicative of proximity to the equator and yellow indicative of proximity to the poles.

DISCUSSION

We find that the contrast in IAR between high and low latitudes are consistent with environmental and oceanographic conditions. The pelagic equatorial and gyre margin regions exhibit similar records in fish production, with high, fluctuating IAR relative to polar sites. The equatorial sites presumably support a large capacity for fish production, as fish biomass is positively correlated with species richness and functional diversity (70), which increase with proximity to the equator (71). Further, warm temperatures, such as those in the low latitude oceans, directly increase biomass, presumably by raising metabolism, and indirectly by increasing functional diversity (70). Similarly, biophysical coupling at gyre fronts can lead to the formation of pelagic foraging hotspots, drawing an array of fish species (72, 73). Frontal convergence and along-front advection contribute to the aggregation of nutrients and increases in primary production that supports higher trophic levels (74–77) .

In contrast, the consistently low ichthyolith production observed in the high-latitudes introduces a 'counter-narrative' to the classical paradigm of high productivity in polar ecosystems (78). Indeed, enhanced fish productivity seems to be at odds with the major evolutionary radiations of mammals, seabirds and krill in the polar marine realm, short and efficient food chains, and summer pulses of high productivity that characterize the polar regions. Here we identify the factors and processes supporting sustained low fish production in the polar regions.

Extreme Seasonality

Environmental seasonality is a critical factor in structuring polar marine ecosystems, and it is perhaps unsurprising that resource constraints, energetic demand, and cold temperatures would result in the low IAR observed in our high-latitude records. The Arctic and Southern Oceans feature strong seasonal extremes in solar radiation, ice cover, and nutrients, which in turn supports intense Spring-Summer phytoplankton blooms (79). Biological productivity is minimal in the high latitudes during the boreal and austral winters due to limited light availability. As the ice cover retreats, there is a short period in the spring and summer when intense phytoplankton blooms develop in the open ocean, beginning in mid-latitudes and spreading polewards (7). Vertebrates in higher trophic levels must fully utilize the short spring and summer blooms to breed and survive during winter months with low primary productivity (5, 80).

Polar conditions appear to be incompatible for fish with an overt sensitivity to seasonal variations in photoperiod. The abundance of large mesopelagic fish has been found to have an inverse relationship with latitude in the Northern Hemisphere due to unfavorable light conditions relative to vertical foraging and predator avoidance (81–83). At high latitudes, short summer nights expose animals to predators that are foraging in the constantly illuminated upper ocean during the productive summer periods (81, 84), while constant darkness during winters hampers visual feeding in deep waters and makes it difficult for mesopelagic fish to exploit abundant prey (85). However, gadoids (Atlantic cod, haddock, and polar cod) are able to catch prey during the polar night, suggesting that the ability to reproduce despite resource limitations rather than the inability to feed during long periods of darkness is a key adaptation that may allow only a few fish species to colonize the polar oceans (86).

Polar pelagic fish have been able to survive seasonal resource constraints at a cost to individual growth rates and population productivity. The short, seasonal pulses of primary productivity have required fish to reduce metabolic costs in order to withstand extended periods of low food availability or undertake migrations during the austral and boreal winters (87). The polar oceans also exhibit very cold temperatures, a factor that reduces basal metabolic rates and food demands but also reduces growth rates and increases longevity of polar fish (88, 89). Physiological limitations on polar fish metabolic rates can be seen in the age distributions of species from some of the largest Southern Ocean fisheries. For example, orange roughy *Hoplostethus atlanticus* has been shown to live for about a century based on dating of otoliths (90). Likewise, Antarctic toothfish *Dissostichus mawsoni*, has a longevity of 39 years or older (91). Indeed, ecosystems dominated by slow growing fish species are expected to have low intrinsic rates of production even if the biomass of relatively long-lived individuals is high.

Phenological Responses

Low fish production in the high latitudes may also have its roots in phenological mismatches between trophic levels and functional groups. Polar organisms are adapted to exploit a narrow time window for growth defined by strong seasonality of environmental forcing; a small timing mismatch between an individual's life strategy and their physical environment can propagate through an entire food web, eventually resulting in changes in the abundance and distribution of fish through its influence on recruitment (92, 93). Pelagic phytoplankton blooms in the high latitudes has a strong dependence on the seasonal onset of ice retreat and released ice algae (11, 94), the timing of which is sensitive to temperature perturbations. Reproductive cycles of consumers (e.g., zooplankton and fish) are synchronized to the timing of the spring phytoplankton bloom in order to provide maximum food supply during the critical period of larval development (92, 93, 95–101). Consequently, short-term oceanographic variability and long-term climatic changes can decouple the phenological relationship between egg hatching and bloom development, thereby reducing successful fish recruitment that is highly dependent on synchronized production across trophic levels.

Fish productivity is thus influenced directly or indirectly by changes in the abiotic environment depending on prey composition and trophic linkages. Fish reliant on planktonic prey will be directly influenced by changes in the timing of spring blooms, whereas higher trophic level fishes will be indirectly affected by the temporal synchrony of successive trophic production peaks. Within polar food webs, a small number of intermediate trophic level species perform most of the core ecological functions and dominate the energy flow between lower and upper trophic levels, including fish (102–107). For example, in the Southern Ocean, Antarctic krill *Euphausia superba* represent an important link between primary producers and top predators (fishes, seabirds, seals, and whales) (10, 108). The dependence of so many higher trophic level species on krill results in a "wasp-waist ecosystem," (109, 110), where fluctuations in krill populations have a disproportionately large effect on trophic levels below and above. Fish within some areas of the Southern Ocean rely almost exclusively on Antarctic krill (111); therefore, spatial and temporal variation in krill production will act as a direct control to the biomass of fish and other predators relying on the same prey. Though fluctuations in krill abundance allow for the expression of alternative pathways to krill links (104, 112–116), these alternative prey sources cannot substitute for the krill-predator food chain in the long-term, because more complex pathways involve more trophic transfers and associated energy losses at each step (114, 116).

Pleistocene Climatic Variability

Glacial-interglacial cycles drive large variations in sea-ice cover and shelf habitat area that could suppress glacial IAR in our high latitude records. During glacial phases, fauna were driven down the slope to deeper bathyal waters or they migrated toward the equator to refugia in unglaciated, sub-polar regions (117). During interglacial periods, the reduction in sea ice and rising sea levels would have allowed fish to recolonize areas formerly covered by ice or exposed by glacial low stands of sea level. For instance, under today's warming conditions in the modern Arctic, large, long-lived and piscivorous boreal fish communities are rapidly replacing and reducing the biomass of small-sized, less fecund, bottom-dwelling benthivore Arctic species (118). It is plausible that Arctic fish faunas showed similar community shifts in the past (119, 120). The net result, seen in our IAR data is that fish production integrated across Glacial-Interglacial cycles is very low compared to lower latitude sites.

In contrast, most surviving marine fauna in the Southern Hemisphere persisted throughout Quaternary glacial maxima in local refugia, apparent in the high levels of endemism in Antarctic continental shelf habitats (24). Biological production in the Southern Ocean adjacent to the Antarctic margin has been found to be insignificant during the last glacial period due to the development of multi-year ice close to shore (121). There was also significant northward extension of the seasonal sea-ice zone during the last glacial period, prompting broadscale shutdowns of primary production close to shore and hampering any secondary productivity (122). It may be that the extreme variability in temperature and biological production throughout the Pleistocene incurred a compounding effect on polar fish populations already prone to low production. The combination of low and variable food availability and shifts in community structure on fish populations unsuited for rapid turnover (88) may explain the consistently low IAR observed in our high latitude records.

Consistency of Low Polar Fish Production through the Eocene

The ichthyolith abundance records that span the EO reveal a strikingly similar latitudinal trend to that of our Pleistocene records. Within both the EO and Pleistocene records, high latitude sites have IAR at about a tenth that of low latitude sites. We infer that the basic ecological rules governing fish production have not changed much over the past ~42 million years. High latitude oceans have always been a low productivity system for fish, despite the major structural changes in polar ecosystems brought on by bipolar glaciation and the radiations of numerous groups of polar-associated marine mammals, seabirds, krill and icefish. The establishment of distinctive Southern Ocean and Arctic ecosystems seems to have passed fish by, at least in terms of their rates of production in the open ocean. It is possible that the increased biogenic silica production around the world at the EO transition supported novel diatom-dominated food webs that fish weren't able to effectively exploit. In the Southern Ocean today, most carbon flows to the diatom-krill-large apex predators food chain (benefiting seals, seabirds, and bulk-feeding whales) and largely overshadows the intermediary trophic role of demersal fish in offshore food webs (123). The high latitude oceans may also be intrinsically unable to support abundant fish production owing to the physiological limits on fish growth rates in an environment that is cold and seasonally unproductive.

The only EO records outside of the high latitudes to exhibit consistently low IAR are two Pacific gyre center sites. The gyre sites are expected to have low IAR values due to their location in persistent ultra-oligotrophic, downwelling parts of the gyres. The gyre sites contrast with our other high latitude sites where high polar summer production is balanced by very low winter production, yielding low annual averaged IAR.

Life Histories of Polar Marine Fish Species

Our records suggest that there are intrinsic limitations to primary and secondary production in polar marine ecosystems that have systematically depressed fish productivity since the middle Eocene. Yet fish have persisted in these systems throughout this time, albeit with low production. How have their life histories adapted to survive through the harshest climatic conditions for life on Earth?

Polar fish tend to have a combination of K-selected life history strategies which may increase their vulnerability to ecosystem perturbations (38, 41, 124–126) and result in depressed ichthyolith accumulation rates observed in our records. K-strategists like polar fish are characterized by delayed maturity, slow growth, large body size, short spawning duration, and long life span. In contrast, fish in the equatorial and subtropical gyre fronts are likely r-strategists, characterized by small to medium size, rapid growth, early age-at-maturity, long spawning duration, and short life span (88). R-strategists in the tropical and subtropical oceans are likely to display boom and bust population structure, which provides rationale towards the time-averaged, highly variable, enhanced baseline productivity shown in the equatorial and gyre margin records.

The contrasting life histories of the populations captured in our records is a function of response to different environmental regimes. To compensate for limited year round intake in the polar oceans, metabolism is reduced and less energy is apportioned to year-round growth, resulting in slow growing fish fauna (87). Further, longevity confers a selective advantage in polar regions with prolonged periods of asynchrony between timing of fish larval occurrence and increased microplankton availability (127). A fish population with many year classes (101, 128) can survive long periods of unfavorable recruitment conditions, whereas a fish population with only a few cohorts may collapse before the return of favorable conditions (124). Overall, K-selected life history traits, though tuned to match the problems posed in polar environments, will inherently support fisheries with fewer individuals, greater sensitivity to perturbation, and a proclivity for collapse than fisheries dominated by r-strategists (88) . Indeed, commercial stocks of K-selected species have been subject to extreme exploitation in the last several decades, reduced to historically low levels or, in some cases, virtually extirpated from large regions (129).

Key examples include Patagonian and Antarctic toothfish (130), and orange roughy (131) in the Southern Ocean, and cod (132) in the Arctic.

We should ask then, to what extent are we exploiting historically low fish production in the polar regions? Our data suggests a naturally slow-growing biomass in both polar regions over the past ~42 Myr, which long-lasting, heavy exploitation has depleted in some cases to only a few age-classes of young adults (133). The proclivity for stock collapse is further reinforced by current anthropogenic warming conditions, in that recruitment success of such stocks is inversely related to temperature (101, 128), a relationship amplified by prolonged warming conditions (134). While polar fishes may have persisted through prior warming events in the geologic record by adapting life history traits prone to low biomass, the present situation is different in the sense that anthropogenic climate change is adding to climatic variability (135) and overfishing has grown into an ocean-wide problem (136). These synergistic effects converge towards reductions at the individual, population and ecosystem levels.

CONCLUSION

Our paleorecords of global ichthyolith abundance provides a uniquely powerful test of whether the evolution of the polar ecosystems that facilitated considerable increases in diatom production, efficient trophic transfers, and the diversification of upper trophic levels supports elevated fish production. We find that IAR in the polar regions is an order of magnitude lower than that of lower latitudes. While the remarkable rise of short diatom-based polar food chains is generally agreed to have supported the evolution of polar krill, seals, whales and seabirds, this has not translated to elevated levels of fish production. Some explanations for the historically low polar fish production are (i) seasonal extremes in abiotic conditions and biological production, (ii) phenological mismatch, (iii) low functional redundancy in polar food webs, and (iv) low and variable food availability and community shifts induced by prolonged climatic variability.

These results challenge prior claims based on short-term datasets that suggest sound management can diminish but never eradicate the annualized fluctuations in Arctic fish stock sizes (47). Indeed, the industrial fishing efforts in the polar regions that have prompted mass stock crashes may be driving fish populations with fundamentally low productivity towards the brink of extinction. The low productivity of polar fish clearly raises significant concerns about fishery sustainability. Our data show that low polar fish production has been a constant feature for the last ~42 Myr.

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