Impacts of Pelagic Fish on Organic Carbon Cycling as Recorded in Marine Sediments

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Abstract

The field of biogeochemistry has established that life plays a key role in dictating the chemical regime of the world's oceans. Focus has been placed on primary producers and microbes but the role of upper trophic levels and overall ecosystem structure remains uncertain. In contrast, the link between fish stocks and lake eutrophication in fresh water ecology has been well established for decades and numerous observations demonstrate similar dynamics are possible in the marine environment. To gain a long-term perspective of natural fish fluctuations and marine biogeochemical dynamics, published high-resolution coastal sediment records were compiled and concentrations of fish scales, a proxy for pelagic fish abundance, were compared with total organic carbon, a proxy for export production. Despite the challenges of using sediment records and the potential convolution of ecological and climatic signals, statistically significant relationships are observed at four out of eight sites. The strongest of these correlations are negative, an intriguing result as the opposite would be expected from bottom-up control of an ecosystem or a purely preservation related signal. These negative relationships could be due to upwelling-driven oxygen and nutrient dynamics or a result of pelagic fish stocks increasing the recycling of carbon in the upper ocean. Correlations are strongest with counts of scales belonging to specific species, rather than aggregates of all fish scales, implying that the trophic level of the fish is of key importance. The results point to an underexploited opportunity to quantify the relationships between marine fish populations and biogeochemical cycles on timescales that cannot be observed directly.

Résumé

Le domaine de la biogéochimie a établi que la vie joue un rôle clé dans la détermination de la composition chimique des océans mondiaux. À ce jour, davantage d'attention a été portée aux producteurs primaires et microbes, mais le rôle des niveaux trophiques supérieurs et de la structure de l'écosystème en son ensemble demeure incertain. Toutefois, l'association entre les populations marines et l'eutrophication des lacs a été démontrée depuis plusieurs décennies dans le domaine de l'écologie des eaux douces, et de nombreuses observations ont prouvé que des dynamiques similaires existent dans l'environnement marin. Afin d'acquérir une vision à long terme sur les fluctuations naturelles des espèces pélagiques et des dynamiques biogéochimiques marines, des registres de sédiments côtiers de haute résolution sont compilés afin de comparer les concentrations d'écailles de poisson, un proxy de l'abondance des poissons pélagiques, avec la totalité du carbone organique, soit un proxy de la production pour l'exportation. Malgré que l'utilisation des carottes de sédiments demeure un défi, notamment en raison de la convolution des signaux écologiques et climatiques, des relations statistiquement significatives ont été observées à quatre des huit sites. La plus forte et plus fréquemment observée de ces corrélations est négative, ce qui constitue un résultat intriguant, puisqu'une relation inverse serait attendue avec le contrôle ascendant d'un tel écosystème ou d'un signal de préservation. Ces corrélations pourraient être reliées à des dynamiques d'oxygène et de nutriments causées par les remontées d'eaux, ou pourraient être secondaires au fait que les populations d'espèces pélagiques augmentent le recyclage de carbone dans les niveaux supérieurs océaniques. Les corrélations négatives étaient davantage observées avec les ensembles d'écailles appartenant à des espèces spécifiques, plutôt que celles appartenant à toutes espèces confondues, ce qui implique que le niveau trophique du poisson est d'importance primale. Des proxys dans les carottes

de sédiment à haute résolution ont l'aptitude d'enregistrer les effets qui peuvent être attendus avec la fluctuation des populations pélagiques, et ceci représente une opportunité hors pair de quantifier les pleines répercussions des populations pélagiques marines sur le cycle du carbone et des éléments biogéochimiques.

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Preface & Contribution of Authors

This thesis contains one manuscript, "Relationships Between Pelagic Fish Stocks and Organic Carbon in the Marine Sediment Record" by Lucas Kavanagh and Eric Galbraith, in preparation for submission to PLOS ONE. Lucas Kavanagh was responsible for data compilation, analysis, and manuscript writing. Eric Galbraith was responsible for the initial concept, and provided constant advice, editing, and review of interpretations and results.

1 Introduction

The dynamics of nutrients, carbon, and oxygen through the worlds oceans are profoundly affected by microbial, plant, and animal life. The carbon cycle is of particular importance as the marine biological pump is a key mechanism for the short-term drawdown of atmospheric carbon dioxide (*De La Rocha*, 2003). Over the past three decades our understanding of the marine carbon cycle has grown to include phytoplankton, zooplankton, microbes, and most recently fish (*Stemmann and Boss*, 2012). Fish can impact organic carbon export through their production of fast-sinking fecal pellets (*Staresinic et al.*, 1983) as well as through their direct transport of organic matter during vertical migrations (*Davison et al.*, 2013). Their role as predators can have significant effects on the zooplankton community whose fecal pellets often dominate organic carbon collected in sediment traps (*Turner*, 2002). *Wilson et al.* (2009) have estimated that fish may be responsible for 3-15% of global carbonate production through precipitation in their guts.

Currently a long-term perspective of the effects of fish populations on marine biogeochemistry is lacking, largely due to insufficient observations of fish stocks prior to 60 years ago (*FAO Department of Fisheries*, 2014). Similar data constraints exist in many fields of oceanography, and are often rectified through the use of proxies in sediment cores. The ocean floor is subjected to a constant gradual accumulation of biogenic and terrigenous sediment. This allows timeseries to be constructed through analysis of sediment cores, the deeper in the core, the further back in time. This depth-time relationship may be quantified using radiometric dating or by counting seasonal layers in the sediment. Sedimentary records tend to be interpreted as reflecting climatic and oceanographic changes. This work explore the possibility that if upper marine trophic levels can exert a control over the chemical properties of an ecosystem; relationships between proxies of these should be recorded in the sediments.

This study began with a global search of high-resolution sediment cores in order to determine the availability of potential data. Due to the complexity of both the marine ecosystem and carbon cycle, the nature of biogeochemical interactions with fish is unknown and will likely vary depending on local ecological and oceanographic properties. A total of 24 locations identified as promising were searched (Appendix A); these all sites with high productivity and potential for excellent sedimentary preservation.

The criteria for individual sedimentary records was that they had a published age model, covered the late holocene (last 5000 years), data was available for proxies of interest, and these measurements were made with at least sub-centennial resolution. Our initial list of target proxies included counts of fish bones or scales, measurement of total organic carbon (TOC), calcium carbonate (CaCO3), opal, elements (particularly those related to primary production or redox conditions), bulk sedimentary ^{15}N, counts of primary producers (dinoflagellate cysts, foraminifera, diatoms, coccoliths), and records of sea surface temperature (SST, found using an alkenone undersaturation index). Data from a total of 120 cores meeting the criteria were found (Appendix B); however, many individual sites lacked a sufficient number of cores to reasonably expect to observe signals of interest.

To find relationships between fish populations and signals in sedimentary proxies, a record of fish abundance is needed. An attempt was made to compile historical and archeological data in order to constrain this before modern catch or biomass records were kept; however, this was quickly determined to be unrealistic due to a sparsity of data. To address this issue, sites with published counts of fish scales were found and the perspective of the study was narrowed to these eight areas (Figure 1, Table 1). The only biogeochemical proxy also present at all of these sites was TOC, which is subject to variable preservation, but nonetheless a conceptually straightforward quantity for studying the relationship between fish and carbon export.

Correlations between timeseries of TOC and fish scale counts are taken as indicators of the potential relationships between fish stocks and carbon export. In addition to these, proxies of redox conditions from most sites were examined to determine preservation potential of both organic carbon and scales in the sediments, as well as to determine if changing conditions could influence correlations. A series of mechanisms, both causal and external are discussed as potentially being responsible for these relationships.

This is, to our knowledge, the first systematic compilation of marine sediment records to search for relationships between fish abundance and biogeochemical cycling. By comparing correlations between available proxies, we identify what relationships exist and speculate on what mechanisms may be responsible. The aim is to investigate both the links between pelagic fish and carbon cycling and to test the ability of high-resolution sediments to record whatever interplay may exist between upper ecosystem trophic levels and biogeochemical proxies.

This document consists of the manuscript “Relationships Between Pelagic Fish Abundance and Organic Carbon in the Marine Sediment Record”, which begins by theorizing mechanisms of potential upper trophic level influence on marine biogeochemistry by drawing from fresh water observations and their applicability to the marine environment. Potential influences of fish stocks and their expected response in sedimentary proxies are reviewed and the methods used in this study are outlined. Eight sites containing fish scale counts are focused on; these may be seen in Figure 1. Background as well as sediment core information for each site is detailed in Appendix C and plots of downcore records may be found in Appendix D. Finally, a series of potential ecological and oceanographic mechanisms are proposed and discussed in the context of the observed correlations. This provides both plausible explanations for the sedimentary observations and paths of potential future research.

2 Relationships Between Pelagic Fish Abundance and Organic Carbon in the Marine Sediment Record

By Lucas Kavanagh and Eric Galbraith

2.1 Introduction

The fundamental role that microbes, phytoplankton, and zooplankton play in marine biogeochemistry is well appreciated (*Sarmiento and Gruber*, 2006) but it is largely unknown what part is played by higher trophic levels such as fish. How does overall ecosystem structure relate to important element cycles such as the export of carbon from the surface ocean? This question gains a sense of urgency in the context of anthropogenic fishing, which may have depleted predatory fish biomass by 90% since preindustrial times (*Myers and Worm*, 2003). To understand the full effects of fish depletion, the impact that fish can have on the chemical environment around them must be understood.

To do this, records of both fish abundance and the biogeochemical property of interest are needed. Sufficient timeseries of fish catch do not go back more than 60 years (*FAO Department of Fisheries*, 2014) and high quality oceanographic data has only been routinely collected over the past 40 years, Yet, prior work has shown that natural pelagic fish variability over time can be reconstructed from counts of fish scales in sediment cores. These were first counted in the Santa Barbara Basin by *Soutar* (1967) and correlated to standing stock biomass by *Soutar and Isaacs* (1974). Total organic carbon (TOC) is the focus of this analysis as it is a direct proxy of export production, represents an amalgamation of the carbon exported by all trophic levels in an ecosystem, and is one of the most commonly measured sedimentary proxies. To our knowledge, this is the first compilation of these records with the goal of assessing the biogeochemical impacts of marine fish.

Using and interpreting the sediment record presents considerable challenges. Proxy signals are convolutions of climatic, oceanographic, sedimentary, and ecological influences, between which it can be difficult to differentiate. In addition, sedimentary records are inherently complex; age models are uncertain, diagenetic alteration is common in young sediments, and even the simple recovery of the most recent material at the top of cores requires careful attention. It is possible that any signals resulting from upper trophic level influence on biogeochemistry may simply be too small in magnitude to be preserved in sediments or may be dwarfed by climate changes.

2.1.1 Background: Top-Down Control of Marine Ecosystems

Bottom-up control describes an ecosystem in which primary productivity varies due to environmental changes and higher trophic levels respond to the consequent availability of food. As such, all trophic levels tend to flourish and decline together. Top-down control describes an ecosystem structure in which biomass is significantly altered by predation. Top-down control occurs where prey populations are regulated through predation and as a result, predator-prey pairings tend to have abundances that vary inversely over time (*Frank et al.*, 2006). Top-down control provides a potential mechanism for fish to impact biogeochemistry by controlling the abundance of the trophic levels below them. Top-down control is widely recognized in fresh water ecosystems; trophic cascades result when the reduction of biomass at one trophic level releases their prey from predatory pressure, causing them to increase in abundance. The next trophic level down would be depleted, in turn. This pattern of depleting the biomass of every other trophic level was first observed in fish removal experiments (*Carpenter et al.*, 1985; *Carpenter and Kitchell*, 1993) and was shown to have profound biogeochemical impacts in lakes. Trophic cascades induced by the addition or removal of fish can abruptly increase phytoplankton biomass, which lowers water column transparency, reduces the depth of light penetration and causes the thermal stratification and mixing depth to shoal (*Mazumder et al.*, 1990a). The increased thermal stratification, combined with a greater amount of slow-sinking phytodetritus can increase sub-surface respiration and significantly deplete hypolimnetic oxygen concentrations (*Mazumder et al.*, 1990b).

The simple trophic cascade mechanism documented in lakes is not directly transferable to marine ecosystems due to their higher diversity, less discrete trophic levels, and the relative ease with which organisms can migrate. Nonetheless, there are indications that some forms of trophic cascades can occur in the marine environment. *Frank et al.* (2006) found evidence for top-down control in many North Atlantic ecosystems by looking for negative correlations between predator-prey pairings of species. Trophic cascades have been documented as a result of human activities including cod fisheries in the Baltic Sea (*Casini et al.*, 2008), Black Sea (*Daskalov et al.*, 2007), and the Scotian Shelf (*Frank et al.*, 2005). All three of these trophic cascades correspond to observed and documented biogeochemical changes, an increase in chlorophyll *a* concentrations in the Baltic Sea, oxygen depletion in the Black Sea, and an increase in water column nitrogen on the Scotian Shelf. These observations suggest that upper trophic levels can exert a significant influence on the marine biogeochemical environment.

It would be expected that carbon export would be altered by a trophic cascade through a variety of mechanisms. *Turner* (2002) found that zooplankton fecal pellets account for a highly variable (between 0 and 100%) but often significant amount of carbon collected in sediment traps. Zooplankton biomass, size, and community structure can have a significant influence on the remineralization profile of the water column and thus the export efficiency of particulate organic carbon (*Wilson et al.*, 2008). Planktivorous fish can exert influence over the zooplankton community such as was observed in the Scotian Shelf trophic cascade (*Frank et al.*, 2005). This has also been observed in fresh water systems where a shift towards smaller zooplankton results in less efficient grazing of phytoplankton and smaller, slower sinking particulate matter (*Mazumder et al.*, 1990b).

2.1.2 Background: Potential Impacts of Fish Populations

In addition to controlling the biomass of the trophic levels below them, previous studies provide evidence that fish can exert a direct control on carbon export. Fish create large, fast sinking fecal pellets, up to an order of magnitude faster than those from zooplankton (*Saba and Steinberg*, 2012). Few studies distinguish fish pellets from zooplankton faeces but *Staresinic et al.* (1983) found that anchovy fecal pellets account for up to 17% of organic carbon in sediment traps placed in the Peruvian Upwelling Zone.

Pelagic fish also engage in widespread diel vertical migrations that facilitate the active transport of carbon out of the upper ocean by feeding near the surface at night and resting at depth during the day. This behaviour accounts for 15-17% of carbon export in the California Current (*Davison et al.*, 2013). The depth of migration is closely related to the top of the oxygen minimum zone (OMZ), which smaller fish and zooplankton may use as a refuge from larger predators (*Bianchi et al.*, 2013). *Bianchi et al.* (2013) suggests that the congregation of migratory fish at the top of the OMZ can increase respiration at these depths, resulting in a further depletion of oxygen concentrations.

2.1.3 Background: Proxy Signals

The potential effects of fish stocks could produce a variety of responses in the sediment record. Commonly measured sedimentary proxies that might reveal relevant processes generally fall into three categories: primary and export production, oxygenation state, and fish abundance. Productivity proxies include Total Organic Carbon (TOC), calcium carbonate, opal, and counts of phytoplankton (e.g. diatoms, foraminifera, and dinoflagellate cysts). These may be used to interpret changes in primary productivity resulting from trophic cascades as well as export production, which is controlled by both ecosystem structure and the remineralization profile. Redox proxies include bulk ^{15}N, redox sensitive elements, and counts of redox sensitive species of phytoplankton. These may be used to test for relationship between fish stocks and oxygen concentrations and are also essential for detecting changes to the preservation potential of the aforementioned productivity proxies. Fish abundance proxies include counts of fish bones or scales in sediment cores. Fish scales are composed of hydroxyapatite and can be preserved in anoxic sediments (*Field et al.*, 2009). The only other proxy present at all sites with fish scale counts is TOC; since this is a direct proxy of carbon export, it was chosen as the focus of this study. If the presence of pelagic fish facilitates organic carbon export, or if we are observing a bottom-up ecosystem control, or a preservation related signal, positive correlations between downcore records of these two proxies can be anticipated. If the presence of pelagic fish inhibits export and enhances recycling of organic carbon in the upper ocean, negative correlations are expected.

Many proxies represent convolutions of various signals; however, this is particularly true for TOC. The proxy is dictated by a combination of primary productivity (that fixes the carbon, determined by phytoplankton growth), export (sinking of this matter out of the upper ocean, determined largely by ecosystem structure), and preservation (the fraction that avoids remineralization in the water column or sediments, determined largely by redox conditions). This presents the challenge of deconstructing observed signals into their most likely components; however, it also may allow for many indirect effects to be recorded. For example, if fish stocks exert a control on oxygen concentrations, this may affect the preservation of sinking organic matter and therefore the signal of TOC seen in the sediment record. Deconstruction of TOC records can be aided through supporting information from other proxies of redox conditions, productivity and climate.

2.2 Methods

An extensive search was performed using four online databases, the PalaeOceanographc Integrated SEdiment (POISE) database (*Cartapanis et al.*, 2013), Pangaea (pangaea.de), Web of Science (webofscience.com), and Google Scholar (scholar.google.com) for high resolution records of fish scales and TOC. Each site (Figure 1) was also searched for other palaeocanographic data available on a similar time scale, to help constrain primary productivity and redox conditions; all records are listed in Table 1.

Retrieved data is separated by sites, areas chosen based on groupings of data in previous palaeoceanographic, ecological, and oceanographic studies. Some of these possessed sufficient data to allow for comparisons of TOC and scale counts to be made in multiple cores. Within each site, published age models were carefully examined to allow for cross-core correlations and for all records to be plotted on a common time axis; this process is detailed for each site in Appendix C. As fish scale and TOC records often had different sampling resolution, the finer was always interpolated to the resolution of the coarser. For comparison within the same core, measurements were interpolated linearly; for adjacent cores, an average of all finer resolution points within the coarser sampling interval was taken. This accounts for a certain degree of uncertainty in the two age models. The potential for relationships between fish scales and TOC was examined using linear regression; correlations with p values less than 0.05 were taken as statistically significant. Each timeseries was also linearly detrended and correlations recalculated in order to determine they could reflect overall long-term trends with no causal link, if the p value remained below the threshold of 0.05 the correlation was considered robust. With the exception of one site, comparison were always made between concentrations within sediments as opposed to accumulation rates, to avoid false positive correlations due to changes in the estimated sedimentation rate at chronological tie points. This was not possible in the Soledad Basin due to raw fish scale counts being unavailable.

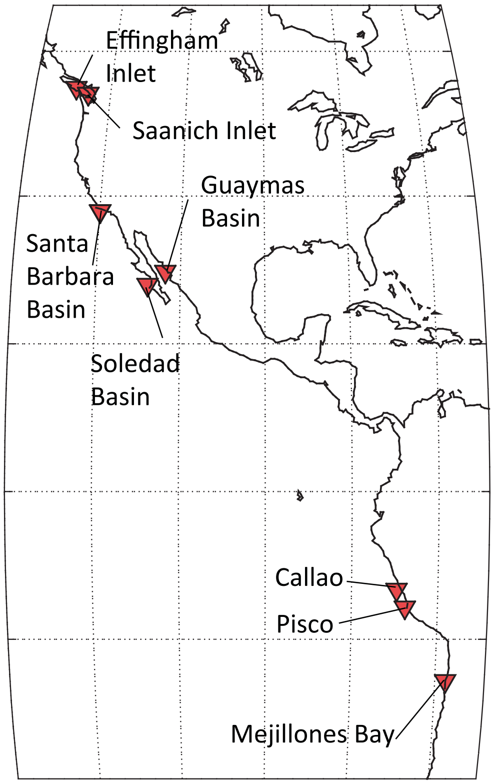

Figure 1: A map of sites containing records of fish bone or scale counts. These records correspond to the papers cited in Table 1.

Whenever an original study identified individual species in fish scale counts, correlations were examined with each species as well as an aggregate of all scales counted. This could help indicate if a particular species is most likely to exert a control over carbon export. TOC is an aggregate of the carbon export occurring from all trophic levels and as such it is not possible to separate it into its various source components.

2.3 Preservation Concerns

Preservation of both TOC and fish scales depends highly on the redox conditions of the water column and sediment. If there is a significant change in oxygenation over the time period examined, the preservation potential of both proxies could change dramatically, invalidating

Table 1: Data sources for the eight sites examined.

Site	**Core**	**Data Source**	**Data Used**
Effingham Inlet, Canada	TUL99B03	*Patterson* (2004)	Fish scale counts
		Wright et al. (2005)	Age model
	MD02-2494	*Ivanochko et al.* (2008)	TOC, Opal, CaCO3, total N, N-15, redox sensitive elements
		Enkin and Dallimore (2013)	Age model
Saanich Inlet, Canada	ODP 1034	*Tunnicliffe et al.* (2001)	Fish bone counts
		Bornhold and Firth (1998)	TOC
	ODP 1033	*Calvert et al.* (2001)	TOC, Opal, CaCO3, total N, N-15, redox sensitive elements
Santa Barbara Basin, USA	214	*Soutar and Isaacs* (1969)	Fish scale counts
	SABA87-1	*Zhao et al.* (2000)	TOC, alkenone SST
	ODP 1017	*Hendy et al.* (2004)	TOC, N-15
Soledad Basin, Mexico	244	*Soutar and Isaacs* (1974)	Fish scale counts
		Van Geen et al. (2003)	Age Model
	TUL (unnamed)	*Anderson* (2012)	TOC
Guaymas Basin, Mexico	7807-1305	*Holmgren-Urba and Baumgartner* (1993)	Fish scale counts
	BC50	*Dean et al.* (2004)	TOC, Opal, total N, redox sensitive elements
Callao, Peru	106KL	*Rein et al.* (2005)	Alkenone SST
	ODP 1228	*Agnihotri et al.* (2006)	N-15, total N
	W7706-40	*Higginson and Altabet* (2004)	N-15, total N
	SO78_173-4	*Muller* (2014)	TOC, alkenone SST
	B0405-13	*Gutiérrez et al.* (2009)	Fish scale counts, fish bone counts, TOC, CaCO3, opal, total N, N-15
Pisco, Peru	B0405-06	*Gutiérrez et al.* (2009)	Fish scale counts, fish bone counts, TOC, CaCO3, opal, total N, N-15
		Gutiérrez et al. (2011)	Alkenone SST
		Salvatteci et al. (2012)	Fish scale counts
	B0506-14	*Salvatteci et al.* (2014a)	Opal, N-15, TOC, redox sensitive elements
	C0329	*Díaz-Ochoa et al.* (2009)	Fish scale counts, P_fish, TOC, CaCO3, Opal, total N
Mejillones Bay, Chile	F981A	*Valdés et al.* (2008)	Fish scale counts
	BC3D	*Díaz-Ochoa et al.* (2011)	TOC

correlations across such a transition. As an example, all four Peruvian cores examined (Figures A3, A4, A5, A6) display an abrupt shift at approximately 1820 towards more anchovy scales and higher TOC values (*Gutiérrez et al.*, 2009). This transition is seen most prominently in proxies of redox conditions (^{15}N and redox sensitive elements); an example record is shown in Figure 2, with the shaded region indicating higher oxygen conditions indicated by lower ^{15}N values. Nitrogen loss occurs through denitrification and anaerobic ammonium oxidation (anammox), both are bacterially mediated processes occurring in low oxygen waters and preferentially remove ^{14}N, leaving the waters enriched in ^{15}N.

The 1820 event has been interpreted as a shift in atmospheric circulation, increasing upwelling and bringing increased nutrient rich, oxygen depleted water to the surface. This shift has also been observed in salinity, Sea Surface Temperature (SST), and precipitation proxies on both sides of the equatorial pacific (*Gutiérrez et al.*, 2009; *Sachs et al.*, 2009); for more information see Appenix C. This change likely had a significant impact on fish stocks and the greater abundance of anchovies may have impacted other proxies in the cores. However, due to the magnitude of the climatic shift, it is difficult to separate signals at this transition into climate and ecosystem related components.

Lower scale counts and TOC concentrations before the 1820 transition are clear in Figure 2; as an increase in upwelling is expected to both increase primary production and preservation of these proxies, it is important to attempt to distinguish these effects. *Salvatteci et al.* (2012) found that scales before this transition were more degraded than those afterwards. To test the relationships between these proxies through each period of time, correlations are shown in Table 2. Taking data over the entire core produces a positive correlation, likely due to the comparison of low values in both proxies before the transition to high values afterwards. The positive relationship holds if only the data before 1820 is taken, however the record of ^{15}N indicates considerable variability in oxygenation over this period, which approximately corresponds to peaks in scale counts and TOC, suggesting this correlation could be due to preservation of both proxies varying together. This is supported by a moderate positive correlation between all fish scales and ^{15}N before 1820 ($r = 0.36$, $p = 0.039$) and a strong positive correlation between TOC and ^{15}N over the same period ($r = 0.52$, $p = 0.0021$). In contrast, taking only the data after 1820 during the period of optimal preservation produces a negative correlation between these two proxies. Caution should be taken interpreting this relationship in particular due to possibilities of spurious correlations discussed later; however, due to the observations of better preservation by *Salvatteci et al.* (2012) and stability of the ^{15}N, only post-1820 data is used for all Peruvian cores.

Table 2: Correlations produced from different preservation regimes in Core B0405-06, Pisco, Peru.

Core Section	r	p
Complete Core	0.51	0.00000084
Pre-1820 (more oxic)	0.43	0.0013
Post-1820 (less oxic)	-0.51	0.0034

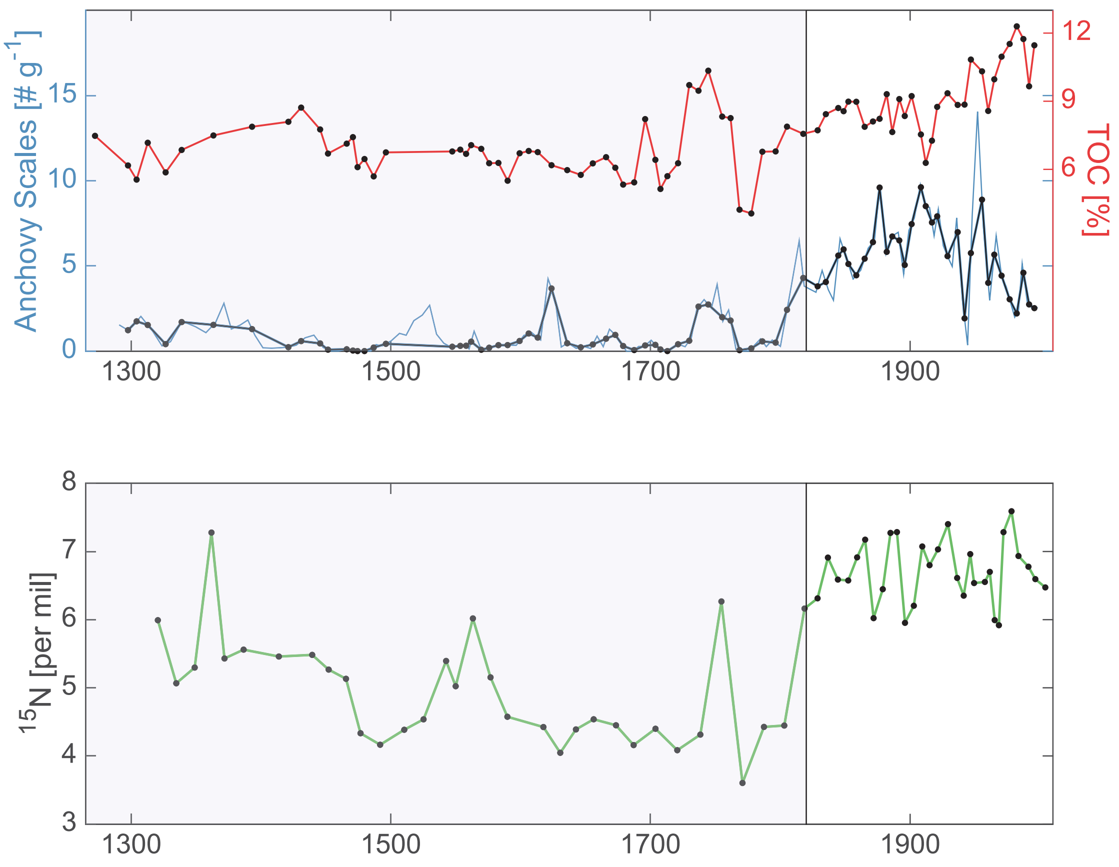

Figure 2: Downcore records from Core B0405-06, Pisco, Peru. The shaded area indicates the period of higher oxygenation, supported by ^{15}N data.

2.4 Observed Relationships

Counts of fish bones or scales exists at eight sites along the west coast of North and South America (Figure 1). All downcore records in Table 1 were plotted and carefully examined for signals related to changes in fish abundance (see Appendix C for details and Appendix D for figures). Figure 3 shows fish scale and TOC records from four example sites. Correlations between these two proxies were examined at all sites, three examples are shown in Figure 4 and all are summarized in Table 3. Of the eight sites examined, statistically significant negative correlations were seen at three locations (Santa Barbara, Soledad, Saanich Inlet), positive correlations at one location (Mejillones), both positive and negative relationships in separate cores at one location (Pisco), and no significant relationships at three (Callao, Guaymas, Effingham). The negative relationships are the strongest and most frequent in Table 3 and are the opposite of what would be expected from simple bottom-up control of an ecosystem or a signal related to preservation.

The Santa Barbara Basin has one of the best developed fish scale records (Figure 3a). Comparing anchovy scales to high resolution TOC data from *Zhao et al.* (2000) produces a significant negative correlation ($r = -0.45$, $p = 0.00097$, Figure 4a). This relationship is particularly robust as it occurs over numerous boom-bust cycles in anchovy scales; this is the only site where the record is long enough for this to occur. The correlation remains strong when both records are linearly detrended ($r = -0.44$, $p = 0.0013$). An aggregate of all fish scales produces a somewhat poorer correlation ($r = -.34$, $p = 0.014$), due to a lack of a pattern between sardine scales and TOC. Attempts have been made to relate the TOC record to ${U^{k\prime}}_{37}$ derived SST (*Zhao et al.*, 2000) but no meaningful relationship was found and anchovy scales produce a much stronger correlation.

Further south at Soledad Basin (Figure 3b), accumulation rates of hake scales have the strongest negative correlation to TOC ($r = -0.75$, $p = .0084$, Figure 4b), which also is relatively unaffected by detrending ($r = -0.75$, $p = .0071$). Note that scale accumulation rate is being used at this site due to a lack of published concentration data. In contrast, the correlation with anchovies is positive ($r = 0.35$, $p = 0.30$). Hake are positioned tropically higher than anchovies, level ∼4.4 as opposed to ∼3.1 (*Froese and Pauly*, 2000) and anchovies can account for a large fraction (>50%) of hake diet in the California Current (*Buckley and Livingston*, 1997). The dominant relationship with hake, rather than anchovies at Santa Barbara may indicate different ecosystem structure between the two sites.

Two more cores also display negative relationships between fish scales and TOC, however supporting information indicates these should be viewed with caution. The first is Saanich Inlet on the southern tip of Vancouver Island. At this site, fish bone counts and TOC values come from a long Ocean Drilling Program core, providing a record of the entire Holocene (Figure A7). A gradual increase in TOC over this period and decrease in fish bones from approximately 7500 to 3000 BCE produces an overall negative correlation ($r = -0.64$, $p = 0.002$) but which is insignificant when detrended ($r = -0.36$, $p = 0.12$). Isostatic rebound following the last deglaciation had a tremendous local effect by gradually isolating the fjord from the open ocean, increasing productivity and lowering oxygen conditions (*Calvert et al.*, 2001). This major bathymetric change likely dominates the trends in these records, masking any potential relationships between fish and organic carbon cycling.

The second site displaying a questionable negative correlation is one of the cores from Pisco, in the Peruvian Upwelling Zone. All correlations in Peruvian cores only use data in the region of optimal preservation, after the 1820 biogeochemical shift. Core B0405-06 (Figure 3c) displays a negative relationship between anchovy scales and TOC ($r = -0.51$, $p = 0.0034$, Figure 4c), but this largely reflects the increase in TOC and decrease in anchovy scales in the uppermost section of the core. Another concern is that the second core from the same site (B0506-14, sampled 18.7 km away) displays a weak positive relationship between fish scales and TOC ($r = 0.29$, $p = 0.0016$, Figure A4). The fact that the relationship between TOC and scales differs over such a short spatial scale, despite the fact that the ecosystem would be expected to be similar, suggests that sedimentary processes in the active current system of the Peruvian shelf may differentially affect the deposition of proxies between these two cores.

The other site displaying a positive correlation is Mejillones Bay in Northern Chile (anchovy scales, $r = 0.36$, $p = 0.000016$, Figure A10). At this site, records of both fish scales and TOC closely follow the trends displayed by ^{15}N (*Valdés et al.*, 2008), suggesting this positive correlation could be due to redox conditions varying the preservation of both proxies.

Four sites did not yield any statistically significant correlations, meaning either the ecosystem structure does not include a relationship, the sediments do not preserve it, or existing data is insufficient to observe it. The downcore record from Guaymas Basin is plotted in Figure 3d as an example of a site with no relationship. Two high points in fish scale counts roughly correspond to low points in TOC but this is not enough to generate a statistically significant correlation. Two cores were examined at Callao (Figures A5 and A6), a second Peruvian site where the 1820 biogeochemical transition was clearly present and did not yield any significant relationships. Effingham Inlet, a small (<1 km wide) isolated fjord on the west coast of Vancouver Island, showed overall low scale counts with no clear periodicity or trend (Figure A9).

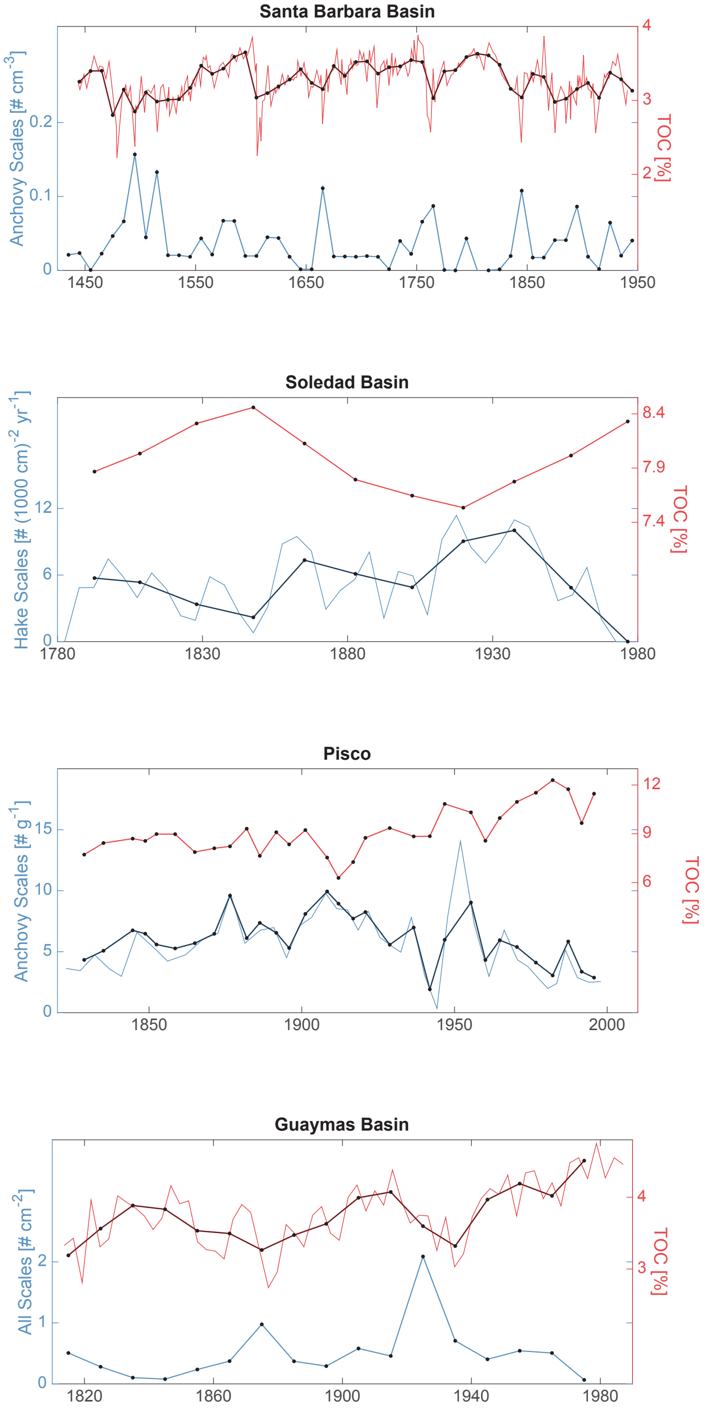

Figure 3: Downcore records of fish scales and TOC from four example areas. The solid black line represents the interpolation of the finer timeseries to the resolution of the coarser. a) a strong negative correlation in the Santa Barbara Basin b) a strong negative correlation in the Soledad Basin c) a suspect negative correlation in Pisco d) no significant correlation in the Guaymas Basin.

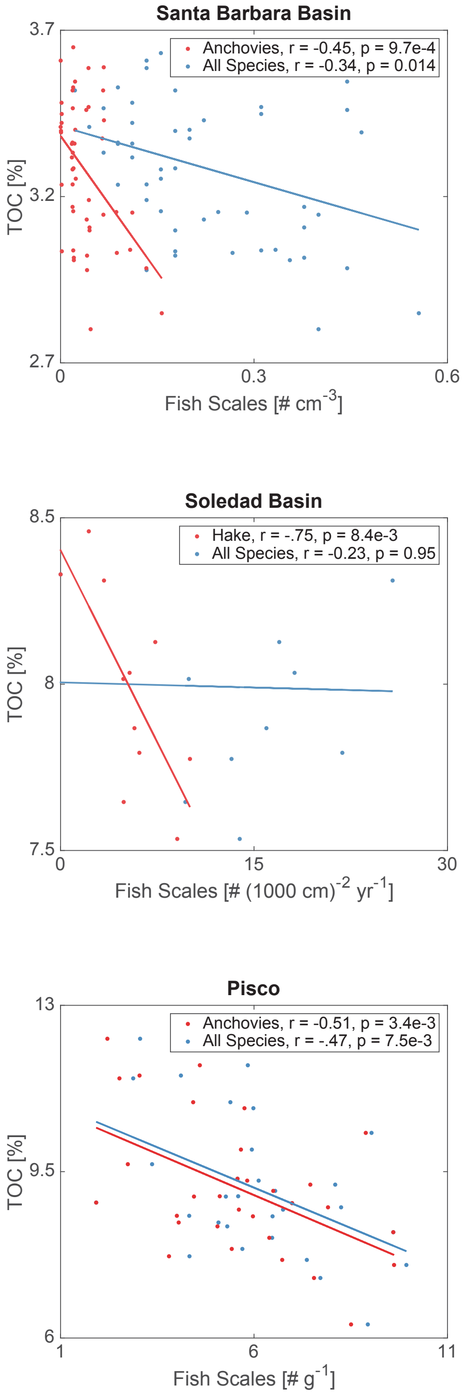

Figure 4: Three statistically significant negative relationships between fish scales and TOC.

Table 3: A summary of all relationships between fish scales and TOC. Bold indicates statistical significance.

Site	**Core(s)**	**Species**	**r**	**p**	**r (detrended)**	**p (detrended)**
Santa Barbara	214, 87-1, 87-2, 88-1	Anchovy	**-0.45**	**0.00097**	**-0.44**	**0.0013**
		Hake	-0.27	0.051	-0.27	0.051
		Sardine	-0.001	0.99	-0.0082	0.95
		Other	0.0036	0.98	0.062	0.66
		All	**-0.34**	**0.014**	**-0.32**	**0.023**
Soledad	455, unnamed	Anchovy	0.35	0.3	0.33	0.32
		Hake	**-0.75**	**.0084**	**-0.75**	**0.0071**
		All	-0.23	0.95	-0.21	0.54
Pisco	B0405-06	Anchovy	**-0.51**	**0.0034**	**-0.45**	**0.012**
		All	**-0.47**	**0.0075**	**-0.38**	**0.034**
	B0506-14	Anchovy	**0.29**	**0.0016**	0.051	0.59
		All	**0.34**	**0.00024**	0.11	0.25
Callao	B0405-13	Anchovy	0.26	0.15	0.086	0.64
	C0329	Anchovy	0.33	0.23	0.049	0.86
		All	0.38	0.16	0.23	0.4
Saanich	ODP 1033	All	**-0.64**	**0.002**	-0.36	0.12
Guaymas	7807-1305, BC50	Anchovy	-0.4	0.12	-0.37	0.15
		Hake	0.14	0.60	-0.074	0.78
		Mackerel	0.12	0.63	-0.24	0.35
		Myctophid	-0.19	0.45	-0.45	0.069
		All	-0.29	0.25	-0.56	0.02
Effingham	TUL99B03, MD02-2494	Anchovy	0.024	0.85	-0.091	0.47
		Herring	0.12	0.35	0.04	0.75
		All	0.073	0.56	-0.99	0.43
Mejillones Bay	F98-1A, BC-3D	Anchovy	**0.46**	**0.000016**	**0.36**	**0.0011**
		Sardine	0.11	0.32	0.089	0.43
		Mackerel	0.11	0.31	0.12	0.3
		Other	0.17	0.12	0.19	0.085
		All	**0.4**	**0.00021**	**0.32**	**0.0035**

2.5 Discussion

Correlations between fish scale counts and TOC are observed in four of the eight sites at which records are available, while the remainder did not produce significant relationships or lost significance when detrended. Given that variability of climate, the preservation of organic matter and fish detritus, and sedimentation processes could all obscure relationships between fish abundance and biogeochemical cycling, the presence of significant correlations at numerous sites is intriguing.

In order to consider the possible mechanisms that could result in correlations between proxies of fish abundance and those of export, we divide them into four categories (Figure 5): bottom-up control where production of organic matter drives fish stocks, top-down control where fish stocks control carbon export, common drivers of both proxies, and the possibility of spurious correlations.

2.5.1 Bottom-Up Control

A positive correlation would be expected from the classic bottom-up view of marine ecosystem control. Higher primary production would percolate up the food chain, resulting in greater fish abundance and carbon export from all trophic levels. This might be seen in Core B0506-14, the second core from Pisco that has a positive relationship between scale counts and TOC. In the period after the 1820 transition and before the onset of industrial fishing, scale counts and TOC vary together in the uppermost portion of the core when redox proxies remain relatively constant (*Salvatteci et al.*, 2014a). This suggests these proxies are not being controlled by oxygen-related preservation conditions and are presumably recording carbon and fish scale deposition.

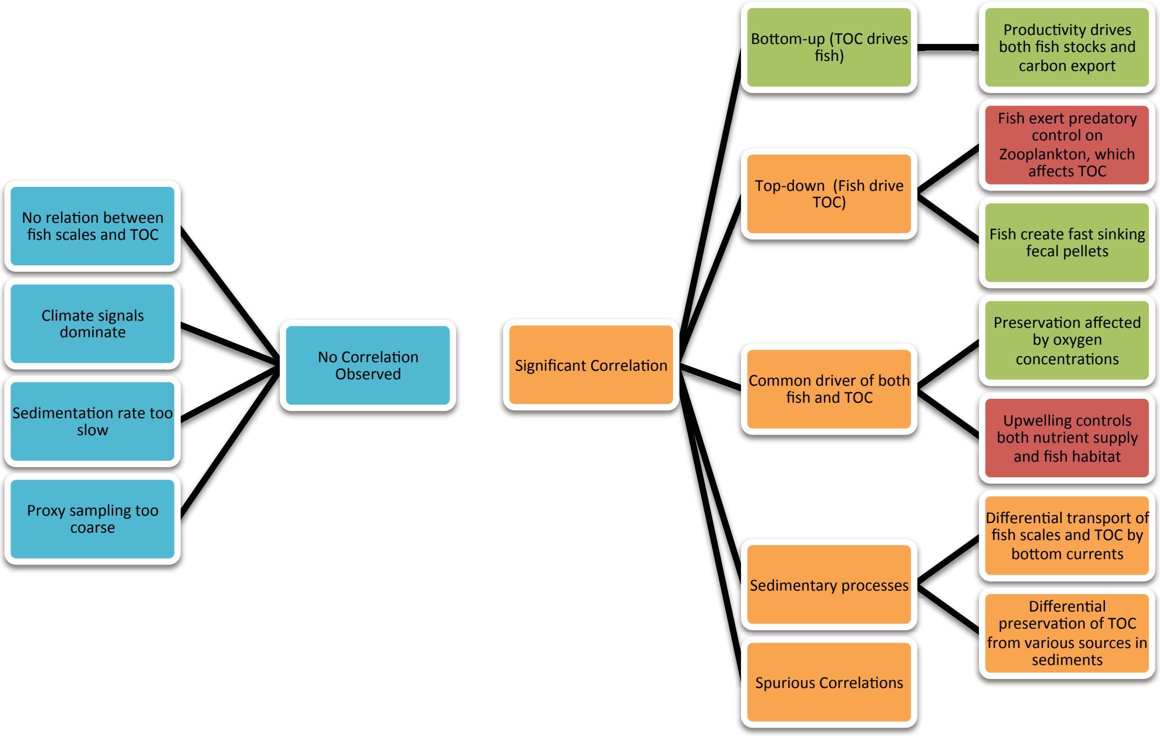

Figure 5: Potential mechanistic explanations of observed correlations. Green indicates a positive correlation is expected, red a negative correlation, and orange indicates either is possible.

2.5.2 Top-Down Control

In contrast, top-down mechanisms raise the possibility that pelagic fish could be exerting a control on carbon export. Every negative correlation observed is strongest when TOC is related to the scale counts of a single fish species, rather than an aggregate of all scales (Figure 4). This could point to top-down control as it indicates a particular species or trophic level is more closely related to carbon export than the ecosystem as a whole. In addition, it indicates that when a key species is depleted, there is no compensatory response from another, at least in terms of a relationship to TOC. This control on carbon export could be a result of predation on lower trophic levels or due to the behaviour or the species itself.

Fish predation could deplete zooplankton stocks, potentially reducing their repackaging of phytodetritus as fecal pellets as well as the active transport of carbon through vertically migrating plankton. This would result in the negative correlations seen at three sites. However, pelagic fish themselves are also creators of fast sinking fecal pellets and facilitate active transport through diel vertical migrations. This means the presence of fish stocks could enhance or diminish carbon export based on the roles zooplankton or pelagic fish play in generating carbon export in the local community. We may see evidence of this ecosystem dependance in comparing Santa Barbara and Soledad Basins, anchovies (planktivores) have the strongest relationship to TOC in Santa Barbara and hake (dominantly piscivores, one trophic level higher) have the strongest relationship in Soledad. In addition, a change in zooplankton biomass through predation may not be reflected directly in fluxes of carbon. Predation by fish could also alter the composition or size structure of the zooplankton community; however, the effects that such a change would have on carbon export are difficult to predict.

2.5.3 Common Drivers

The changes observed in fish scale counts and TOC may also be driven by a common factor, without a direct causal link between the two. Oxygen concentrations affect both proxy preservation and habitat range for pelagic fish. All sites examined are directly or indirectly affected by coastal upwelling and thus changes in wind-driven upwelling can significantly change water column oxygen and organic matter production.

For example, the positive correlation seen in Mejillones Bay may be due to preservation of both proxies being affected by variable redox conditions, as both of them follow the same trend as ^{15}N (*Valdés et al.*, 2008). Upwelling intensity is the strongest external driver for oxygen variability at this site and is also a source of nutrient rich waters which likely results in increased primary productivity. The combination of enhanced preservation due to low oxygen and increased primary production could strengthen positive correlations between TOC and fish scales.

Oxygen conditions can have impacts beyond preservation, a depletion of oxygen within the water column could cause habitat depth range of a pelagic fish to shoal, making them more venerable to predation. This mechanism was invoked by *Koslow et al.* (2014) to explain positive correlations between oxygen concentrations and fish stocks in the California Current over the last 60 years. As more oxygen-poor, nutrient-rich waters are upwelled, primary production is expected to increase. This would result in increased phytodetritus and higher preservation potential corresponding to depleted fish populations. This introduces a large degree of uncertainty in how a change in water column oxygen would affect carbon export as it is also a feasible mechanism to create negative correlations between TOC and fish scales.

2.5.4 Sedimentary Processes

Once TOC or fish scales are deposited on the seafloor, preservation is not instantaneous and sedimentary processes act upon these proxies differently. Local currents transport sediment along the seafloor and winnow the finer sediments away from the coarser; this may differentially transport the fine fraction of TOC relative to fish scales. A potentially important issue is any preservation differences in the sediment of organic carbon originating from phytodetritus or marine snow versus fecal pellets from zooplankton or fish. This effect is currently unstudied but could have important implications not only for the methods used in this study but for general contributions of different trophic levels to the biological pump.

A potential driver of negative correlations is the dilution of TOC concentrations by the presence of fish scales or vice versa. However, as a specific species most often gives better correlations than an aggregate of all scales, this possibility is unlikely. If dilution were the driving factor, we would expect the strongest negative correlation to always be with an aggregate of all scales counted.

2.5.5 Spurious Correlations

The possibility of spurious correlations must be considered, particularly considering the small sample size of sites where fish scale counts are currently available. A likely example of this is the negative correlation seen in the first Pisco core, B0405-06. In this example, TOC increases towards the core-top, which could relate to the downcore decay of organic carbon. This section of young sediment was largely deposited since 1950, the same period as a rapid intensification of industrial fishing in the area (*Thorp and Bertram*, 1978), feasibly causing a decrease in scales towards the top of the core. These unrelated effects could provide a reasonable explanation for the negative correlation found in this part of the core. On the other hand, if fish do exert a top-down control, the onset of industrial fishing could have caused in the observed increase in TOC.

2.5.6 No Correlation Observed

At the sites where no correlation between the proxies can be seen, ecosystem structure may not allow for a relationship between fish abundance and carbon export. Relationships may also be masked by larger climate signals (such as the large shifts seen in Saanich or at the Peruvian sites) or high-frequency effects may not be seen due to low sedimentation rates or insufficient sampling resolution.

2.6 Conclusions

Given the significant impact fish stocks can have on fresh water systems, it is plausible that they can exert influence on carbon export and other aspects of marine biogeochemical cycles. By compiling existing sediment records, significant negative relationships were found between counts of fish sales and TOC at three of eight sites. The negative correlations could be driven by upwelling dynamics; however, these observations also open a door to the possibility that the presence of fish could enhance the recycling of carbon in the upper ocean and this begs further investigation. Sediment cores represent a valuable archive of information that can be applied to help bridge the gap between marine ecology and biogeochemistry.

This study cannot definitively distinguish between the causal mechanisms behind the observed sedimentary correlations. However, as Figure 5 summarizes, the mechanisms that can conceivably produce negative correlations are few, suggesting that predation on zooplankton stocks or oxygen control on habitat range are likely mechanisms by which inverse relationships between pelagic fish abundance and carbon export may arise. If indeed fish are capable of exerting a control on carbon export, this could have important implications for anthropogenic fish depletion and be essential to understand the full ecological impacts of human fishing. The sediment record represents an important archive of data that can be used to help examine long-term relationships between marine fish and the environment around them. To take full advantage of this opportunity, more datasets of high resolution fish abundance should be developed as they are currently sparse relative to other sedimentary proxies. All of the sites examined here are underlain by coastal upwelling; of particular interest would be fish abundance records in dramatically different oceanographic regimes to examine ecosystem-carbon dynamics in other settings.

3 Conclusions

Through a compilation of published sediment core data, fish scale counts and TOC measurements were compared at eight eastern pacific sites in order to assess potential impacts of pelagic fish stocks on carbon export from the upper ocean. Relationships between these proxies vary between sites; two sites had robust negative correlations, one positive, four did not have significant relationships and one showed conflicting results between two cores. The sites with negative correlations indicate a potential deviation from classic bottom-up ecosystem control or preservation related signals. These relationships could be due to ether a common external driver or the fish themselves exerting a control on ecosystem structure and carbon export.

While these mechanisms cannot be differentiated at this time, each has significant implications for the role of pelagic fish in the marine ecosystem. Upwelling driven oxygen dynamics may be the common factor controlling the habitat range of small pelagic fish, nutrient supply to primary producers, and the preservation potential of carbon in sediment cores. If this is the case, the long-term perspective provided by this sediment compilation lends support to the work of (*Koslow et al.*, 2014). If, on the other hand, these relationships are a result of fish exerting a predatory control on the zooplankton community and inhibiting the export of carbon from the surface ocean, human fishing may have consequences for the marine carbon cycle. Either way, the sediment record represents a wealth of data that can be applied to examine the relationship between pelagic fish and carbon dynamics. To take advantage of this opportunity, more records of fish scales should be developed alongside existing biogeochemical proxies and a modelling based approach should be taken to examine the plausibility of mechanisms relating fish stocks and carbon export.

A Initial List of Searched Sites

What follows is a list of all sites where a search for sediment records took place. Bold sites indicate sufficient data for analysis was found, italic sites indicate a fish biomass proxy exists. Due to the need for a proxy of pelagic fish abundance, the bold and italicized sites were the ones used for analysis. Cores recovered are listed in Table A1.

- **Arabian Sea**
- **Baltic Sea**
- Barents Sea
- Black Sea
- ***Mejillones Bay, Chile***
- ***Effingham Inlet, Canada***
- England (Celtic-Biscay Shelf)
- Georges Banks/Chesapeake Bay, US
- Grand Banks, US
- ***Gulf of California (Guaymas basin)***
- **Iberian Shelf**
- Icelandic Shelf
- **Mediterranean Sea**
- **Namibian Shelf**

- North Pacific Coastal
- **North Sea**
- ***Callao, Peru***
- ***Pisco, Peru***
- ***Saanich Inlet, Canada***
- ***Santa Barbara Basin, US***
- Scotian Shelf (Emerald and La Have Basins), Canada
- Sea of Japan
- ***Soledad Basin, Canada***
- Yellow Sea

B Complete Core List

Table A1: A complete list of cores retrieved from the initial search of areas listed in Appendix A. Abbreviations are as follows, fish scales (scales) Total Organic Carbon (TOC), Calcium Carbonate ($CaCO_3$), Phytoplankton Counts (PC), bulk sedimentary Nitrogen 15 (^{15}N), Redox Sensitive Elements (RSE).

Location	**Source**	**Data**
Arabian Sea	*Böll et al.* (2014)	TOC, ^{15}N, SST
Arabian Sea	*Agnihotri et al.* (2003)	TOC, ^{15}N, RSE
Arabian Sea	*Kessarkar et al.* (2010)	TOC, $CaCO_3$
Arabian Sea	*Agnihotri et al.* (2008a)	TOC, ^{15}N
Arabian Sea	*Altabet et al.* (2002)	TOC, ^{15}N
Arabian Sea	*Suthhof et al.* (2001)	TOC, ^{15}N
Arabian Sea	*Ivanochko et al.* (2005)	TOC, ^{15}N, RSE
Arabian Sea	*Pichevin et al.* (2007)	TOC, ^{15}N
Arabian Sea	*von Rad et al.* (1999)	SST
Arabian Sea	*Kim et al.* (2004)	SST
Baltic Sea	*Neumann and Leipe* (1997)	TOC, RSE
Baltic Sea	*Funkey et al.* (2014)	TOC, ^{15}N, RSE
Baltic Sea	*Funkey et al.* (2014)	TOC, ^{15}N, RSE
Baltic Sea	*Kabel et al.* (2012)	TOC, SST
Baltic Sea	*Kabel et al.* (2012)	TOC, Si, SST
Bay of Biscay	*Mojtahid et al.* (2013)	PC
Black Sea	*Sperling et al.* (2003)	TOC, PC, SST
Black Sea	*Arnold et al.* (2012)	TOC, RSE
Black Sea	*Bahr et al.* (2008)	TOC
Black Sea	*Filipova-Marinova et al.* (2013)	PC
Black Sea	*Fulton et al.* (2012)	TOC, ^{15}N
Chilean Margin	*Díaz-Ochoa et al.* (2011)	TOC, SI, PC, RSE
Chilean Margin	*Lamy* (2002)	TOC, Si, PC, RSE

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Table A1 – continued from previous page

Location	Source	Data
Chilean Margin	*Ortlieb et al.* (2000)	Scales, PC
Chilean Margin	*Rebolledo et al.* (2008)	TOC, Si, RSE
Chilean Margin	*Valdés et al.* (2008)	Scales, TOC
Chilean Margin	*Vargas et al.* (2004)	Scales, TOC, Si, PC
Chilean Margin	*Vargas et al.* (2007)	TOC, ^{15}N, SST
Chilean Margin	*Mohtadi et al.* (2007)	PC, SST
Chilean Margin	*Muratli et al.* (2010)	TOC, Si
East Brazil Shelf	*Almeida et al.* (2013)	TOC
Effingham Inlet	*Chang* (2004)	PC
Effingham Inlet	*Patterson et al.* (2005)	Scales, PC
Effingham Inlet	*Patterson et al.* (2011)	PC, SST
Effingham Inlet	*Ivanochko et al.* (2008)	TOC, $CaCO_3$, Si, RSE
Gulf of California	*Dean et al.* (2004)	TOC, $CaCO_3$, RSE
Gulf of California	*Holmgren-Urba and Baumgartner* (1993)	Scales
Gulf of California	*Soutar and Isaacs* (1974)	Scales
Gulf of California	*Anderson* (2012)	TOC, ^{15}N
Iberian Shelf	*Abrantes et al.* (2011)	SST
Iberian Shelf	*Rodrigues et al.* (2009)	SST
Iberian Shelf	*Abrantes et al.* (2005)	SST
Iberian Shelf	*Kim et al.* (2004)	SST
Iberian Shelf	*Segl and Alt-Epping* (2005)	TOC, $CaCO_3$
Iberian Shelf	*Alt-epping* (2008)	TOC, $CaCO_3$
Iberian Shelf	*Alt-epping* (2008)	TOC, $CaCO_3$, ^{15}N
Iberian Shelf	*Diz et al.* (2002)	TOC, SST, PC
Icelandic Shelf	*Moossen et al.* (2013)	TOC
Icelandic Shelf	*Solignac et al.* (2006)	PC
Mediterranean	*Möbius et al.* (2010)	TOC, $CaCO_3$, ^{15}N
Mediterranean	*Emeis and Dawson* (2003)	SST
		Continued on next page

Table A1 – continued from previous page

Location	**Source**	**Data**
Namibian Shelf	*Shackleton* (1987)	Scales
Namibian Shelf	*Emeis et al.* (2009)	^{15}N, SST
Namibian Shelf	*Struck et al.* (2002)	Scales, TOC, ^{15}N
Newfoundland-Labrador Shelf	*Solignac et al.* (2011)	PC
Newfoundland-Labrador Shelf	*Solignac et al.* (2011)	PC
North Sea	*Dale et al.* (1999)	PC
North Sea	*Dale* (2009)	PC
North Sea	*Alve* (1996)	PC
North Sea	*Filipsson and Nordberg* (2010)	PC
North Sea	*Brückner and Mackensen* (2008)	PC
North Sea	*Brückner and Mackensen* (2008)	PC
North Sea	*Dähnke et al.* (2008)	^{15}N, PC, RSE
North Sea	*Erbs-Hansen et al.* (2012)	TOC, $CaCO_3$, PC
North Sea	*Gil et al.* (2006)	PC
North Sea	*Hebbeln et al.* (2006)	PC
Northeast US Continental Shelf	*Wainright et al.* (1993)	Scales
Northeast US Continental Shelf	*Willard et al.* (2003)	PC
Northeast US Continental Shelf	*Karlsen et al.* (2000)	PC
Northeast US Continental Shelf	*Sherwood et al.* (2011)	^{15}N
Peruvian Upwelling Zone	*Agnihotri et al.* (2008b)	Si, ^{15}N, RSE
Peruvian Upwelling Zone	*Díaz-Ochoa et al.* (2009)	Scales, TOC, RSE
Peruvian Upwelling Zone	*Salvatteci et al.* (2012)	Scales, TOC, ^{15}N
Peruvian Upwelling Zone	*De Vries and Pearcy* (1982)	Scales
Peruvian Upwelling Zone	*Gutiérrez et al.* (2011)	TOC, SST
Peruvian Upwelling Zone	*Gutiérrez et al.* (2009)	Scales, TOC, Si, PC, ^{15}N
Peruvian Upwelling Zone	*Salvatteci et al.* (2014a)	TOC, Si, ^{15}N
Peruvian Upwelling Zone	*Sifeddine et al.* (2008)	TOC
Peruvian Upwelling Zone	*Agnihotri et al.* (2008b)	TOC, ^{15}N

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Table A1 – continued from previous page

Location	**Source**	**Data**
Peruvian Upwelling Zone	*Agnihotri et al.* (2006)	^{15}N
Peruvian Upwelling Zone	*Chazen et al.* (2009)	Si, ^{15}N, SST
Peruvian Upwelling Zone	*Rein et al.* (2005)	SST
Peruvian Upwelling Zone	*Muller* (2014)	TOC, SST
Saanich Inlet	*Calvert et al.* (2001)	TOC, $CaCO_3$, Si, RSE
Saanich Inlet	*McQuoid and Hobson* (2001)	TOC, Si
Saanich Inlet	*McQuoid et al.* (2001)	PC
Saanich Inlet	*Elvert et al.* (2001)	TOC
Saanich Inlet	*Russell and Morford* (2001)	TOC
Saanich Inlet	*Filippelli* (2001)	TOC
Saanich Inlet	*Bornhold and Firth* (1998)	TOC
Saanich Inlet	*Tunnicliffe et al.* (2001)	Scales
Saanich Inlet	*O'Connell and Tunnicliffe* (2001)	Scales
Santa Barbara Basin	*Soutar* (1967)	Scales
Santa Barbara Basin	*Soutar and Isaacs* (1969)	Scales
Santa Barbara Basin	*Soutar and Isaacs* (1974)	Scales
Santa Barbara Basin	*Ohkushi et al.* (2013)	TOC, $CaCO_3$, PC
Santa Barbara Basin	*Grelaud et al.* (2009a)	PC
Santa Barbara Basin	*Hendy et al.* (2004)	TOC, ^{15}N
Santa Barbara Basin	*Emmer and Thunell* (2000)	TOC, ^{15}N
Santa Barbara Basin	*Gardner and Dartnell* (1995)	TOC, $CaCO_3$
Santa Barbara Basin	*Grelaud et al.* (2009b)	PC
Santa Barbara Basin	*Barron et al.* (2010)	Si, PC
Santa Barbara Basin	*Zhao et al.* (2000)	TOC, SST
Santa Barbara Basin	*Barron et al.* (2010)	Si, PC
Santa Barbara Basin	*De Bernardi et al.* (2008)	PC, RSE
Santa Barbara Basin	*Deutsch et al.* (2014)	^{15}N
Santa Barbara Basin	*Huguet et al.* (2007)	SST

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Table A1 – continued from previous page

Location	**Source**	**Data**
Costa Rica Margin	*Martinez and Robinson* (2010)	TOC, ^{15}N
Scotian Shelf	*Keigwin et al.* (2003)	SST
Scotian Shelf	*Levac* (2001)	PC
Sea of Japan	*Kuwae et al.* (2007)	TOC, ^{15}N

C Background Information and Sediment Record Details

C.1 Santa Barbara Basin

The Santa Barbara Basin is a 600 m deep anoxic basin in the California Current, which flows southwards bringing cold, nutrient rich water to the region. This is met by the Davidson current, flowing northwards and consisting of cold, nutrient depleted waters. The southward flow is strongest in the spring and summer, the Northward flow is strongest in the winter (*Emmer and Thunell*, 2000; *Zhao et al.*, 2000). On top of this interaction, northerly winds drive upwelling of cold, nutrient-rich Pacific Intermediate Waters.

Upwelling results in high primary productivity, driving biogenic sedimentation in the spring and summer. These light layers alternate with terrigenous sedimentation that dominates during the winter months, forming consistent annual varves in the basin (*Hendy et al.*, 2013). *Schimmelmann and Tegner* (1991) proposed that productivity in the region is largely controlled by ENSO events; during El Nino phases more warm nutrient-poor water flows northward, suppressing the upwelling of nutrient rich intermediate waters. However, these links have been difficult to establish in the palaeoceaographic record; *Zhao et al.* (2000) found a poor relationship between ENSO events and $\mathrm{U}^{k\prime}{}_{37}$ derived SST and could not find a link to TOC records that are indicative of productivity.

This was the first area to have fish populations reconstructed through scale counts in a sediment core (*Soutar*, 1967), setting off a series of similar work in the area (*Soutar and Isaacs*, 1969, 1974; *Baumgartner et al.*, 1992). *Baumgartner et al.* (1992) compiled data from a number of cores to produce a 1700 year record of pelagic fish stocks that revealed 9 collapse and recovery cycles with anchovy and sardine stocks varying over periods of 60 and 100 years respectively. Figure A1 reveals the scales, TOC, and SST all undergo fluctuations on multidecadal timescales. This data comes from two different cores in the basin, correlated with varve-based age models. A longer, coarser resolution record to TOC from *Hendy et al.* (2004) was also examined but this did not capture the periodic fluctuations seen in the record from *Zhao et al.* (2000). Nevertheless, the negative trend between anchovy scales and TOC holds up over the longer time period.

C.2 Soledad Basin

The Soledad Basin a 540 m deep, flat-bottomed basin located on the shelf off western coast of Baja California (*Van Geen et al.*, 2003). Preservation is excellent due to anoxic bottom waters but due to the lack of regular rainfall on Baja California, varves in the sediment are not annual or temporally consistent, limiting age models to radionuclide dating (*Soutar and Isaacs*, 1974). Despite the excellent preservation potential in the basin, palaeoceanographic studies are few. Fish scale counts were performed by *Soutar and Isaacs* (1974), dated with a ^{210}Pb age model and accumulation rates were calculated (unfortunately the raw content data is not available at this site). In Figure A2, this is compared to TOC data from *Anderson* (2012), dated with a ^{14}C age model from *Van Geen et al.* (2003).

C.3 Peruvian Upwelling Zone

The coastal region of the Peruvian Upwelling Zone consists of two main currents, the shallow equator-ward Peru-Chile Coastal Current and the poleward Peru-Chile Undercurrent beneath it. Offshore, the Peru-Chile Counter Current runs to the south (*Sifeddine et al.*, 2008). The undercurrent supplies the region with nutrient-rich, oxygen-poor water at depths of approximately 50-400m (*Salvatteci et al.*, 2014a). A combination of respiration of organic matter and long residence time of water masses results in further oxygen depletion and a very large sub-surface oxygen minimum zone (OMZ). Wind driven upwelling dominates the oceanographic regime up to 200 km from the shore (*Sifeddine et al.*, 2008) and is an important source of nutrients to the surface. This continues all year long but is strongest in the austral winter and spring and between 14°S and 16°S. The strength of upwelling also varies along with the strength and position of the South Pacific Subtropical High (SPSH) and Intertropical Convergence Zone (ITCZ) to the North, which affects the strength of alongshore winds. The region is also profoundly influenced by ENSO dynamics; during El Nino phases the thermocline deepens and suppresses upwelling of cold, nutrient-rich waters. This is observed in warm anomalies in SST, lower productivity, and a deepening of the oxycline (*Agnihotri et al.*, 2008b).

The high rates of primary productivity feed a short but highly efficient food chain. Small pelagic fish (dominantly anchovies) consume both zooplankton and phytoplankton; stomach content studies indicated that phytoplankton accounts for over 99% of the items ingested by anchovies but zooplankton accounts for 98% of the carbon consumed (*Espinoza and Bertrand*, 2008). These small pelagic fish are in turn consumed by marine mammals, seabirds, and a limited number of larger fish.

Unconformities in the sediment due to slumps are common, making age models difficult to construct (*Salvatteci et al.*, 2014b). Recently a suite of studies examining multi-decadal to centennial scale trends in the Peruvian Upwelling Zone have emerged and fish scale counts have been a key component of a number of these. These studies use multiple dating techniques such as ^{210}Pb, ^{241}Am, ^{14}C (on bulk organic matter), and correlation of varves between cores in an attempt to overcome the uncertainty due to slumps in the region.

Gutiérrez et al. (2009) identified a drastic biogeochemical shift at approximately 1820, causing rapid change in nearly all sedimentary proxies. This was interpreted as the product of a northward movement of the ITZC, SPSH, and strengthening of the Walker circulation (the atmospheric cell connecting the east and west sides of the tropical Pacific) by *Gutiérrez et al.* (2009). This shift in atmospheric circulation would increase alongshore winds and thus upwelling, increasing the source of cold, nutrient-rich, oxygen-poor water. This interpretation implies a large-scale signal and was originally based on salinity and SST proxies in the Makassar Strait. It has since been strengthened by δD records from Palau and the Galapagos (*Sachs et al.*, 2009).

This transition is shaded in Figures A3 and A5 and the approximate point is shaded in Figures A4 and A6. Proxies of oxygenation show a rapid shift to lower oxygen conditions after 1820 and proxies of productivity tend to show an increase at the same point. *Salvatteci et al.* (2012) closely examined the preservation of fish scales in Core B0506-14 and found that scales before this transition were significantly more degraded but the increase around 1820 is unlikely to be purely higher preservation and anchovy populations likely increased at this time as well. Because of these two separate regimes of preservation, analysis here is restricted to after the transition, when preservation conditions are optimal.

C.4 Saanich Inlet

Saanich Inlet is 240 m deep enclosed basin on Southern Vancouver Island; bottom waters are anoxic for the vast majority of the year with the exception of episodic spring and fall oxygen renewal events (*Manning et al.*, 2010). The dominant sources of freshwater are located outside the inlet, creating a reverse estuarine flow with freshwater entering the inlet near the surface, mixing with saline waters within the inlet and exiting at depth. This inflow, combined with tidal forces is an important supply of nutrients, supplying a large spring bloom (*Gargett et al.*, 2003). This bloom is responsible for significant silicious sediment deposition, which alternates with greater terrigenous sources in the winter, creating clear annual varves and excellent age models (*Gross et al.*, 1963).

Saanich Inlet provides a unique record of pelagic fish as counts of bones were performed on a long core (55 m) taken as part of the Ocean Drilling Program and provide a complete

Holocene record (*Tunnicliffe et al.*, 2001). This is plotted in the top panel of Figure A7; fish abundances increased in the early Holocene with a peak at 7500 BCE, followed by gradual decrease until 3000 BC with the sub-millennial scale fluctuations continuing until present. This is compared with records of TOC (low resolution from the same core and high resolution from an adjacent core), opal %, and Mo/Al. These reveal a gradual trend of increasing productivity and anoxia over the entire Holocene. *Calvert et al.* (2001) attribute this to isostatic rebound gradually isolating the fjord, creating the anoxic, high-productivity regime that exists today.

C.5 Guaymas Basin

The Guaymas Basin is a depression in the central Gulf of California. The region is strongly seasonal with strong winter winds focused from the northeast that causes a net outwards transport of surface water from the Gulf (*Thunell et al.*, 1994). This drives mixing, upwelling of nutrient rich water, and thus high rates of productivity from the late fall to early spring. During the summer and fall, winds are significantly less focused but largely shift to southerly, brining in warm tropical pacific surface waters that are depleted in nutrients and as a result, decrease productivity. The summer also brings increased precipitation in the region, increasing the flux of terrigenous material to the basin. This seasonality results in annual varves composed of alternating biogenic material in the winter and terrigenous material in the summer being deposited. Preservation is excellent due to the oxygen depleted North Pacific Intermediate Waters dominating depths between 500 and 1000 m in the Gulf (*Dean et al.*, 2004).

Holmgren-Urba and Baumgartner (1993) counted fish scales and found a significant negative relationship between anchovy and sardine populations; mackerel and myctophid scales also fluctuated in a way similar to the sardines. The myctophid scales (which were not differentiated by species) accounted for by far the highest counts of scales and were the only group present throughout the entire record. The core was dated using a combination of varve counting and ^{210}Pb dating, producing a high confidence age model to allow for comparison with other cores in the region. This record is plotted in Figure A8, along with TOC and Mo/Al data from *Dean et al.* (2004). This proxy data comes from core BC50, taken from the slope between the Guaymas and adjacent Carmen basin and dated with a ^{210}Pb age model. Fish scales concentrations have two notable peaks, neither of which consist of more than one data point. The TOC record shows sub-centennial scale fluctuations with a steady increase since the mid 1900s. The record of Mo/Al shows a decrease with consistent low values over the last 150 years. This decrease indicates an increase in oxygen concentrations which *Dean et al.* (2004) attribute to decreased organic productivity and thus lower respiration. Thus the recent increase in TOC may largely reflect a preservation signal.

C.6 Effingham Inlet

Effingham Inlet is 17 km long and branches off of Barkley Sound on the west coast of Vancouver Island. It is a well mixed estuary with freshwater coming from the Effingham river at its head (*Patterson et al.*, 2011). Upwelling occurs seasonally during the summer, outside the mouth of the inlet, bringing waters from the Alaska Current System or California Undercurrent Regime up and often into the inlet. The bathymetry of the inlet consists of two depressions, an outer basin (210 m deep) near the mouth and an inner basin (120 m deep) closer to the head of the inlet (*Patterson et al.*, 2011). Both cores examined here are from the inner basin which has more consistently anoxic bottom waters.

Fish scale counts come from core TUL99B03, dated through an age model incorporating ^{210}Pb, ^{137}Cs and ^{14}C points. A wide variaty of species were identified including Northern anchovy, Pacific herring and lesser abundances of rockfish, hake, elasmobranchs, and surfperch

(*Patterson*, 2004; *Wright et al.*, 2005). There is no correlation between the anchovy and herring populations in this record (*Wright et al.*, 2005) but *Patterson et al.* (2005) did suggest that the anchovy regime is associated with cold waters and overall higher productivity. *Patterson* (2004) and *Patterson et al.* (2005) suggests sunspot cycles as a potential driving mechanism behind these ecological changes. An aggregate of the anchovy and herring counts is plotted in Figure A9 but no regular periodicity or trend is evident. Other proxy data come from core MD02-2494 (*Ivanochko et al.*, 2008); this core covers the entire Holocene and last deglaciation and is dated using ^{14}C dates. Over the interval that corresponds to the fish scale counts, TOC and $CaCO_3$ show centennial scale fluctuations but no overall trend. Information on redox conditions can be gained through the ratios of U/Al and Mo/Al, both of which fluctuate slightly (and together) but confirm that the inner basin remained overall anoxic throughout the Holocene.

C.7 Mejillones Bay

Mejillones Bay is a shallow (125 m deep), northward facing bay in northern Chile. The surface waters of the region consists of the Peru-Chile Current that transports Subantarctic water towards the equator both along the coast and offshore, with the Peru-Chile Countercurrent running in-between, bringing subtropical water southwards (*Díaz-Ochoa et al.*, 2011). Beneath this, the Peru-Chile Undercurrent also moves polewards, bringing oxygen depleted waters that originated as equatorial surface waters to depths between 50 and 300 m off the coast of northern Chile. It is this source of oxygen depleted water that is responsible for the very shallow oxygen minimum zone in the region and the hypoxic bottom waters in Mejillones Bay. Oxygen concentrations in the bay are further reduced by the respiration of organic matter from the high productivity region, driven by the strong upwelling cell immediately to the west of the bay (*Ortlieb et al.*, 2000).

Extensive work has been done examining records of fish scale deposition in the region (*Ortlieb et al.*, 2000; *Vargas et al.*, 2004; *Valdés et al.*, 2008; *Guiñez et al.*, 2014) and the sum of all scale counts performed by *Valdés et al.* (2008) is plotted in Figure A10. Sardine and anchovy scales were counted, with anchovy scales accounting for the vast majority of these. An age model for this core was constructed using ^{210}Pb and ^{14}C ages. The record of TOC is from Core BC3D, dated using ^{210}Pb and a $CaCO_3$ correlation to Core F98-1A (*Díaz-Ochoa et al.*, 2011); the previous correlation of these two cores gives us a high degree of confidence in the comparison between them. Two distinct periods of increased anchovy abundance can be seen in the 1890s and 1970s; *Valdés et al.* (2008) suggests there is some degree of a variable preservation factor preserved in this record due to the similar patterns in a record of ^{15}N (see cited paper for this data). The record of TOC shows a small increase at 1820, corresponding to a decrease in oxygenation seen in ^{15}N and redox sensitive elements (*Díaz-Ochoa et al.*, 2011).

D Supplementary Figures

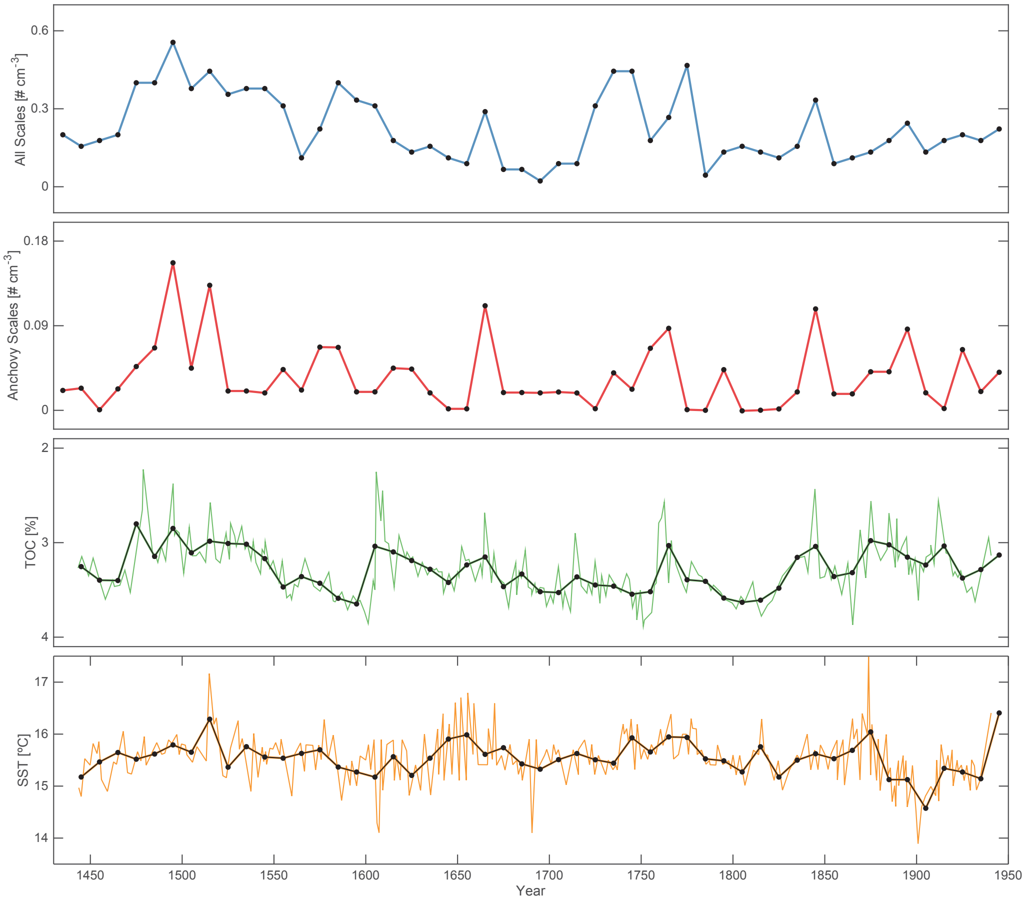

Figure A1: A timeseries of fish scales from Core 214 (*Soutar and Isaacs*, 1969) and TOC and SST from Cores SABA 87-1, 87-2, and 88-1 *Zhao et al.* (2000) from Santa Barbara Basin. Note the inverted vertical scale on the TOC plot.

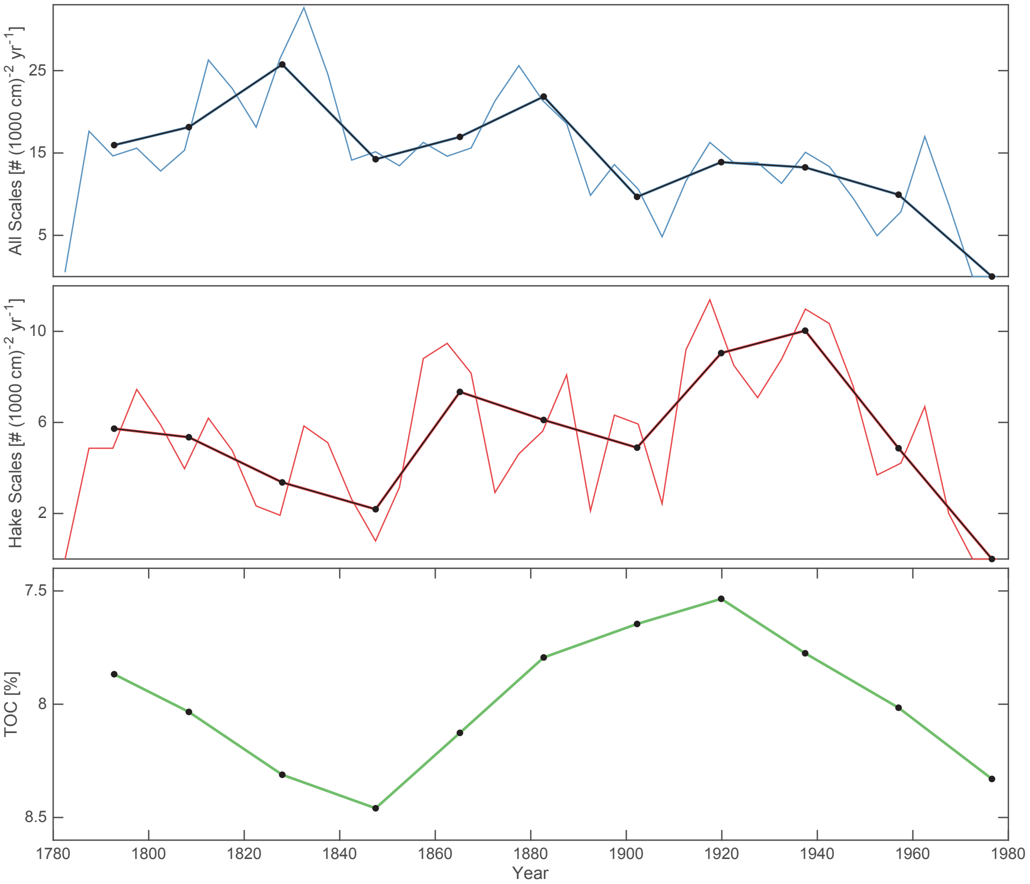

Figure A2: A timeseries of fish scale accumulation rates from Core 455 (*Soutar and Isaacs*, 1974) and TOC from an unnamed core (*Anderson*, 2012) from the Soledad Basin. Note the inverted vertical scale on the TOC plot.

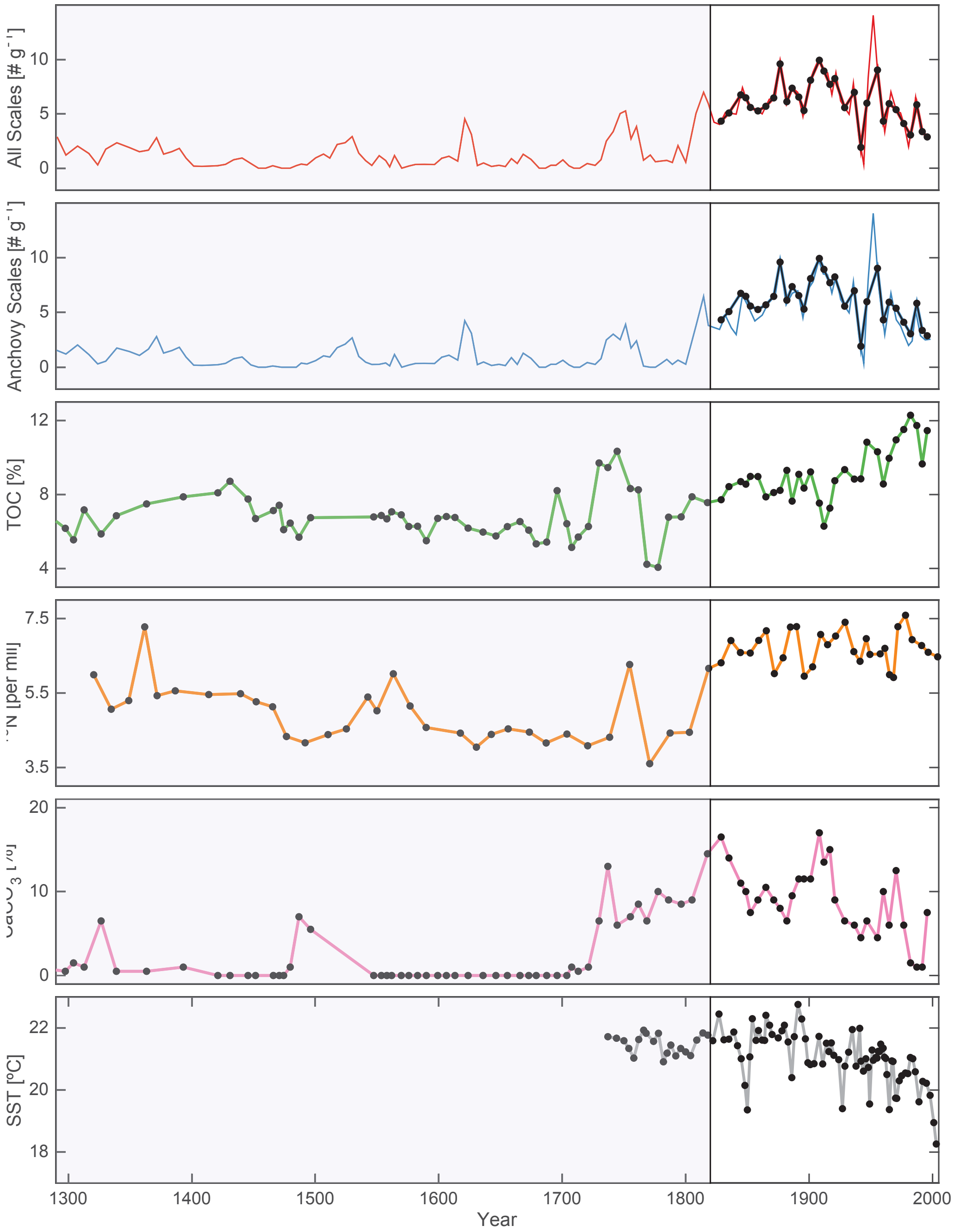

Figure A3: Fish scale and geochemical proxy records from core B0405-06, Pisco, Peru. All data from *Gutiérrez et al.* (2009) except SST, which is from *Gutiérrez et al.* (2011). The shaded region indicates the period of lower anoxia leading up to a biogeochemical transition at 1820, identified by *Gutiérrez et al.* (2009).

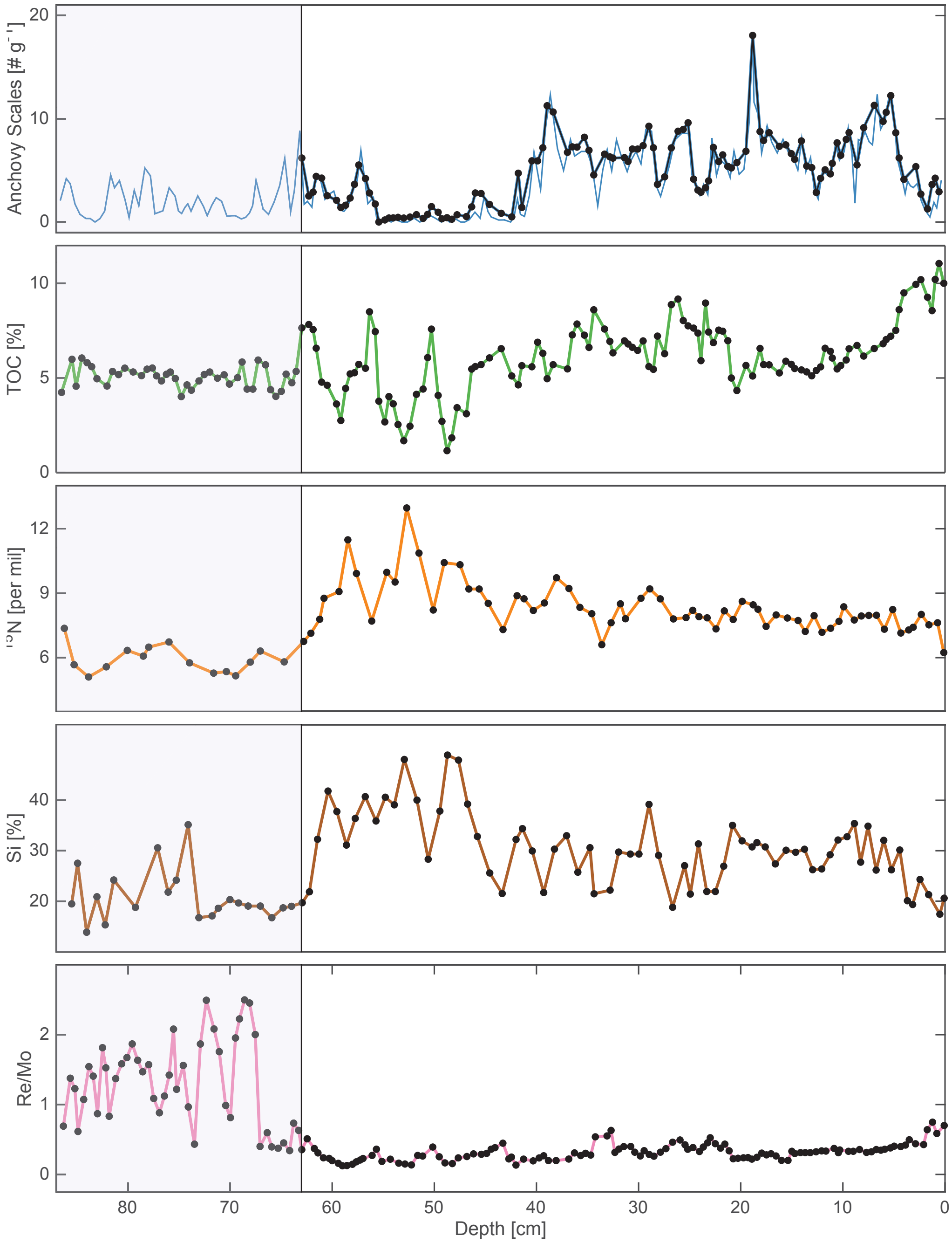

Figure A4: Fish scale counts from *Salvatteci et al.* (2012) and geochemical proxy data from *Salvatteci et al.* (2014a) in core B0506-14, Pisco, Peru. Comparisons are made based on core-depth due to uncertainty in the age model, the shaded region indicates the approximate period of lower anoxia identified by *Gutiérrez et al.* (2009).

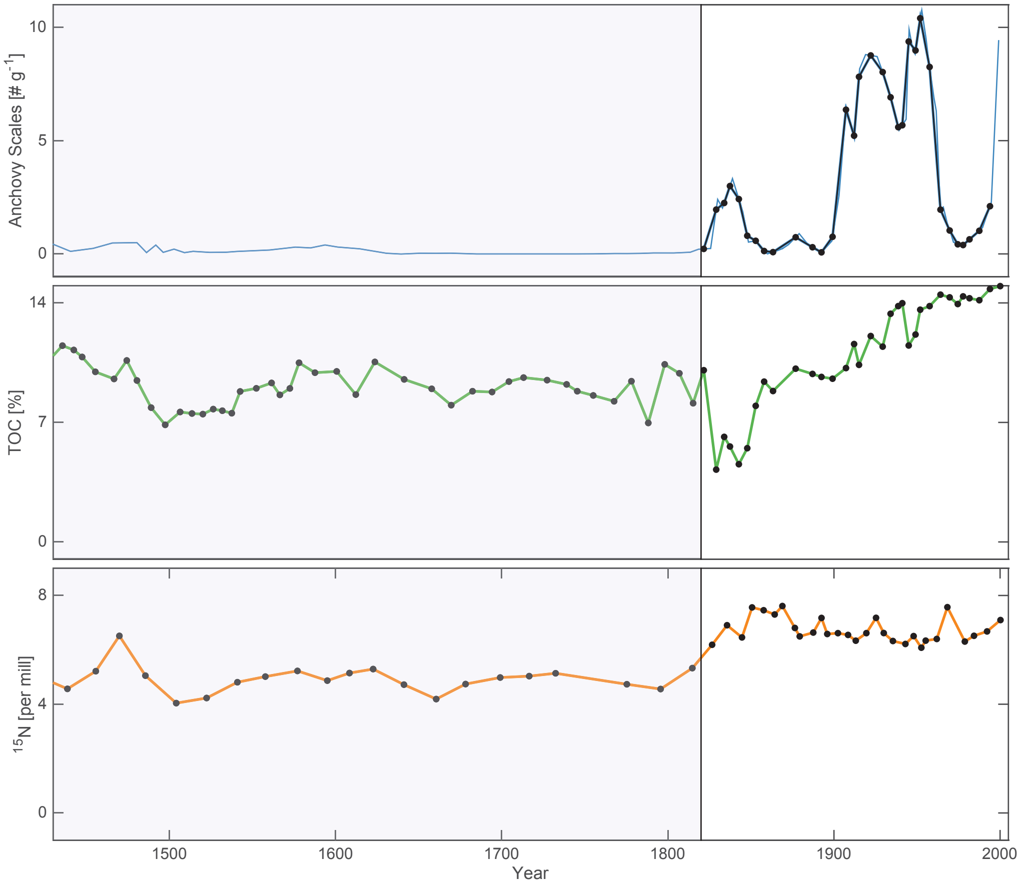

Figure A5: Fish scale counts and geochemical proxy data from core B0405-13, Callao, Peru (*Gutiérrez et al.*, 2009). The shaded region indicates the period of lower anoxia leading up to a biogeochemical transition at 1820, identified by *Gutiérrez et al.* (2009).

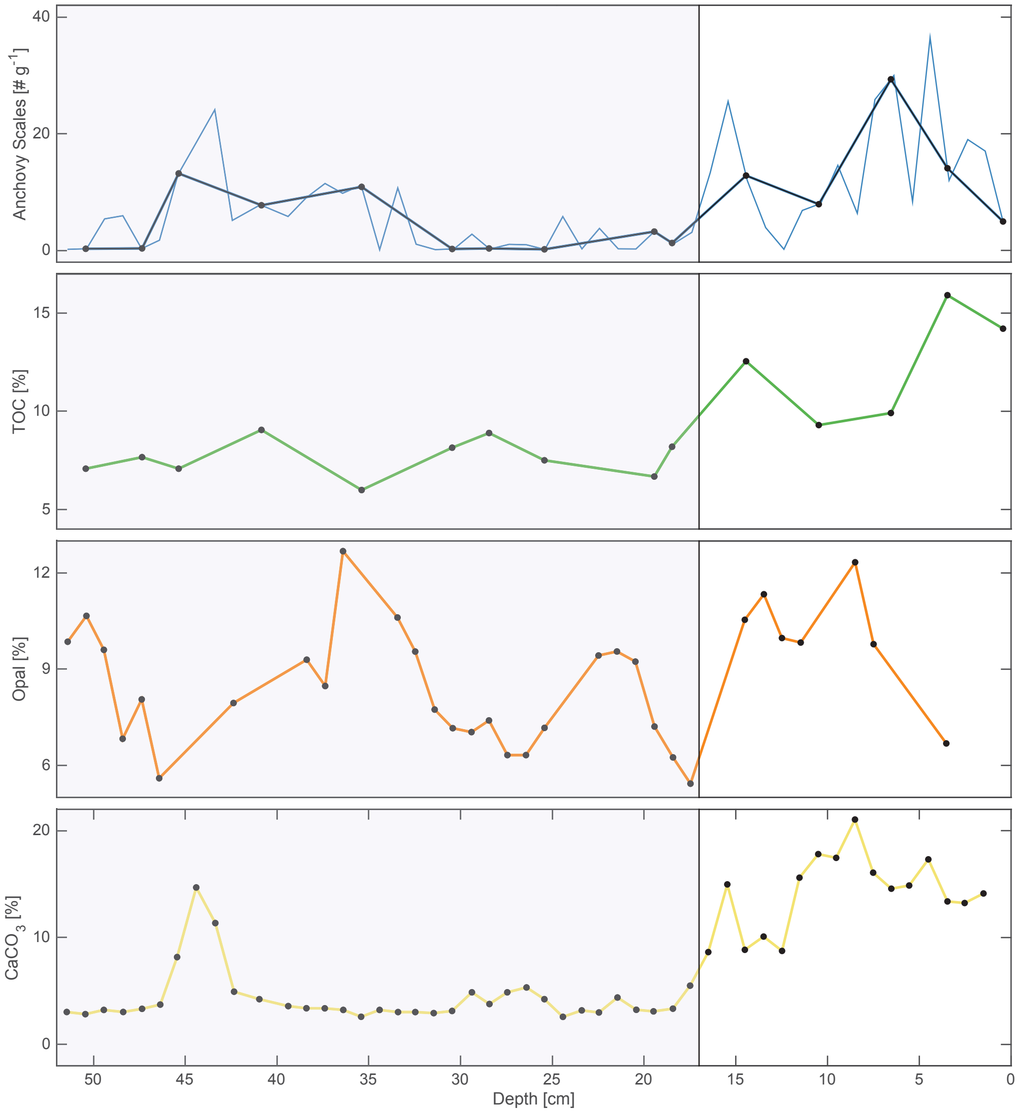

Figure A6: Fish scale counts and geochemical proxy data from core C0329, Callao, Peru (*Díaz-Ochoa et al.*, 2009). Comparisons are made based on core-depth due to uncertainty in the age model. The shaded region indicates a lithological shift identified by *Díaz-Ochoa et al.* (2009) which corresponds approximately to the 1820 shift identified by *Gutiérrez et al.* (2009).

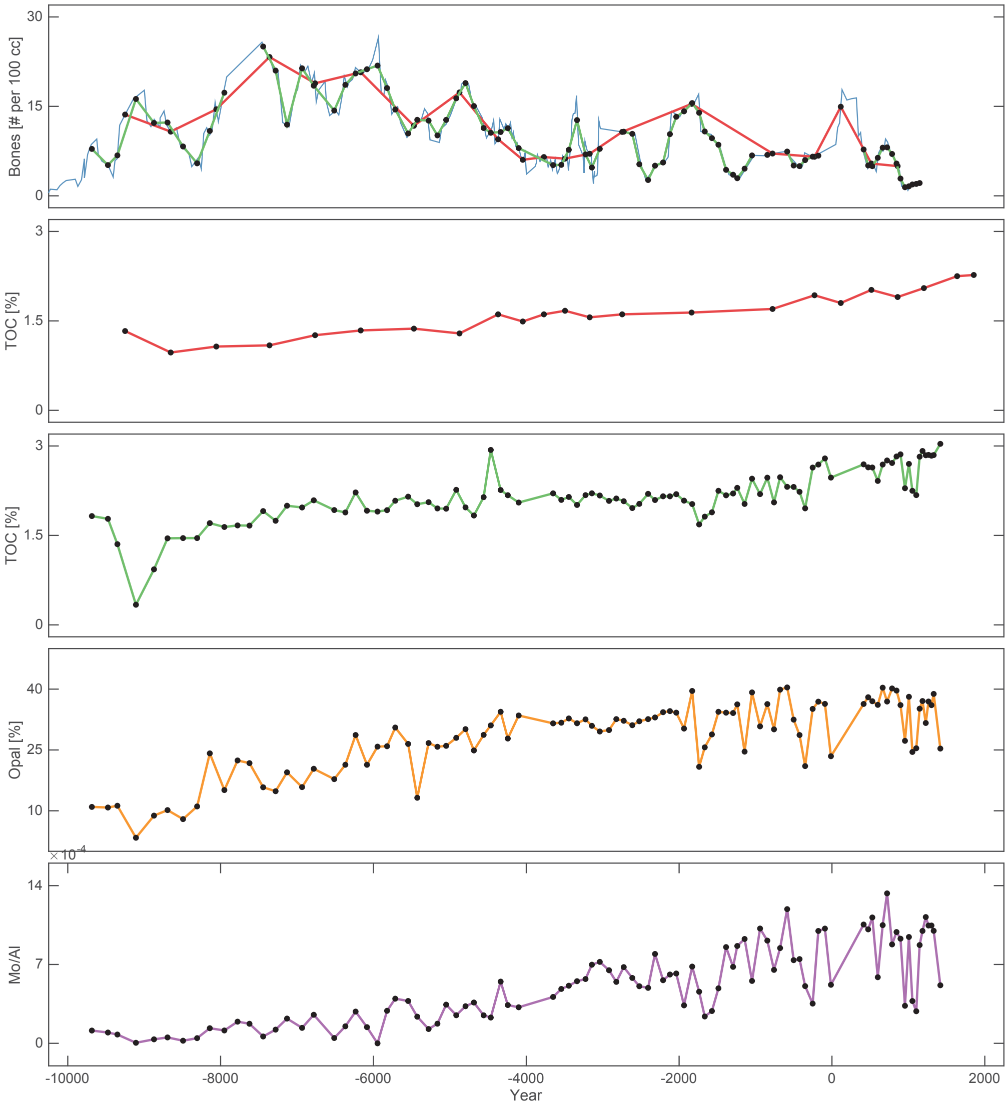

Figure A7: Counts of fish bones from core ODP 1033 in Saanich Inlet Canada (*Tunnicliffe et al.*, 2001). The first TOC data is from the same core and the rest of the proxy data is from the adjacent core ODP 1034 (*Calvert et al.*, 2001).

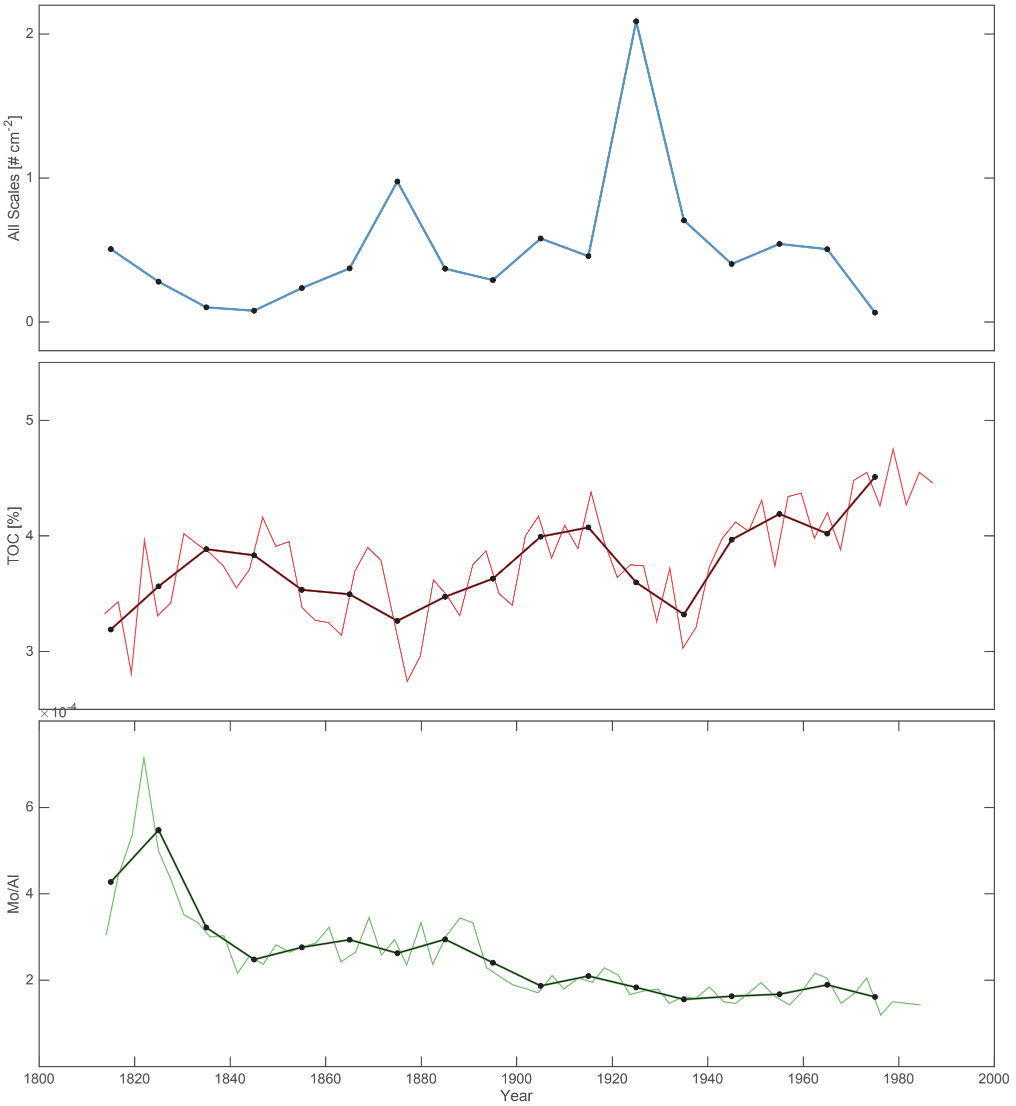

Figure A8: Fish scale counts from core 7807-1305 (*Holmgren-Urba and Baumgartner*, 1993) and TOC and Mo/Al data from core BC50 (*Dean et al.*, 2004), Guaymas Basin, Mexico. Scale counts are normalized to the surface area of sediment samples analyzed. No statistically significant relationships exist between the fish scales and proxies examined.

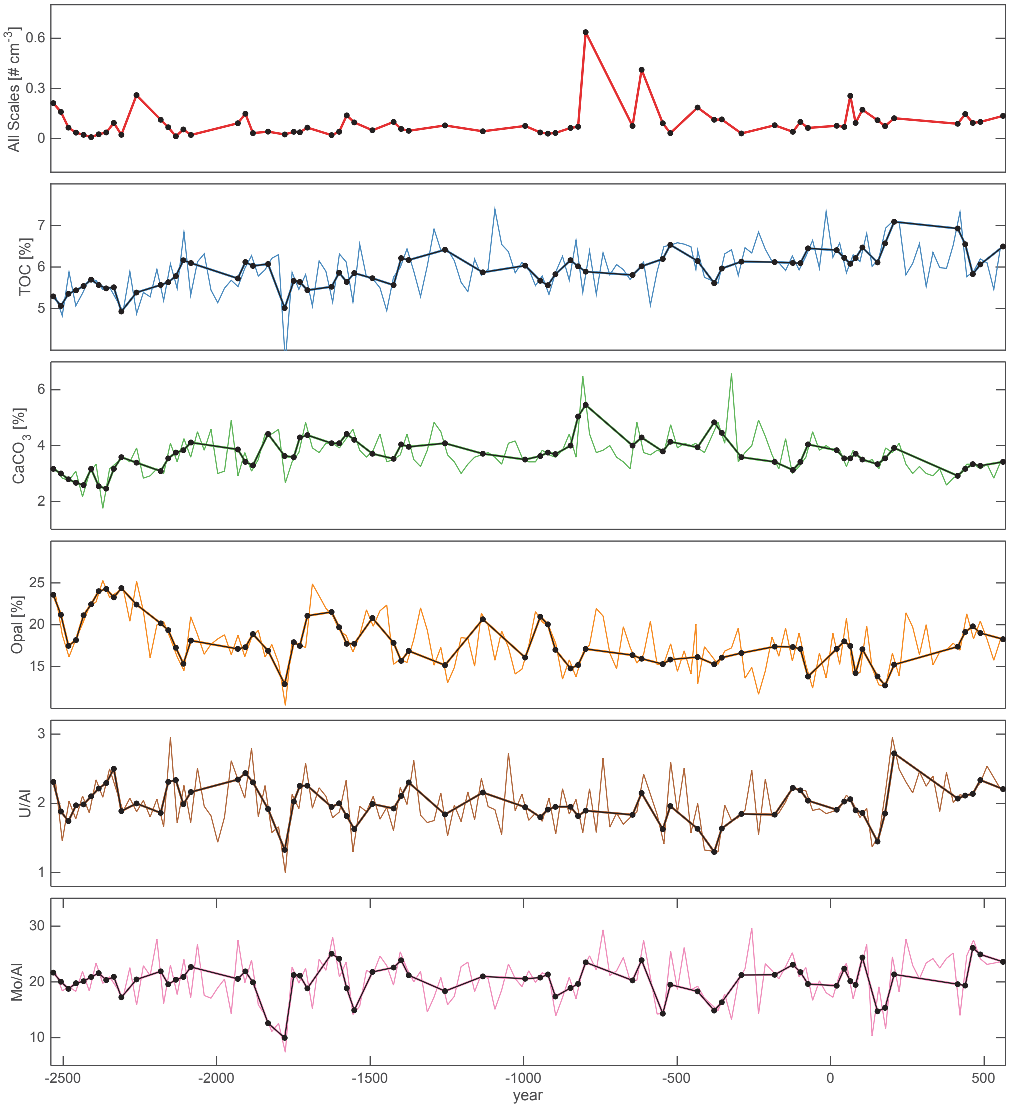

Figure A9: Fish scale counts from core TUL99B03 (*Patterson*, 2004) and geochemical proxies from core MD02-2494 (*Ivanochko et al.*, 2008), Effingham Inlet, Canada. No statistically significant relationships exist between the fish scales and proxies examined.

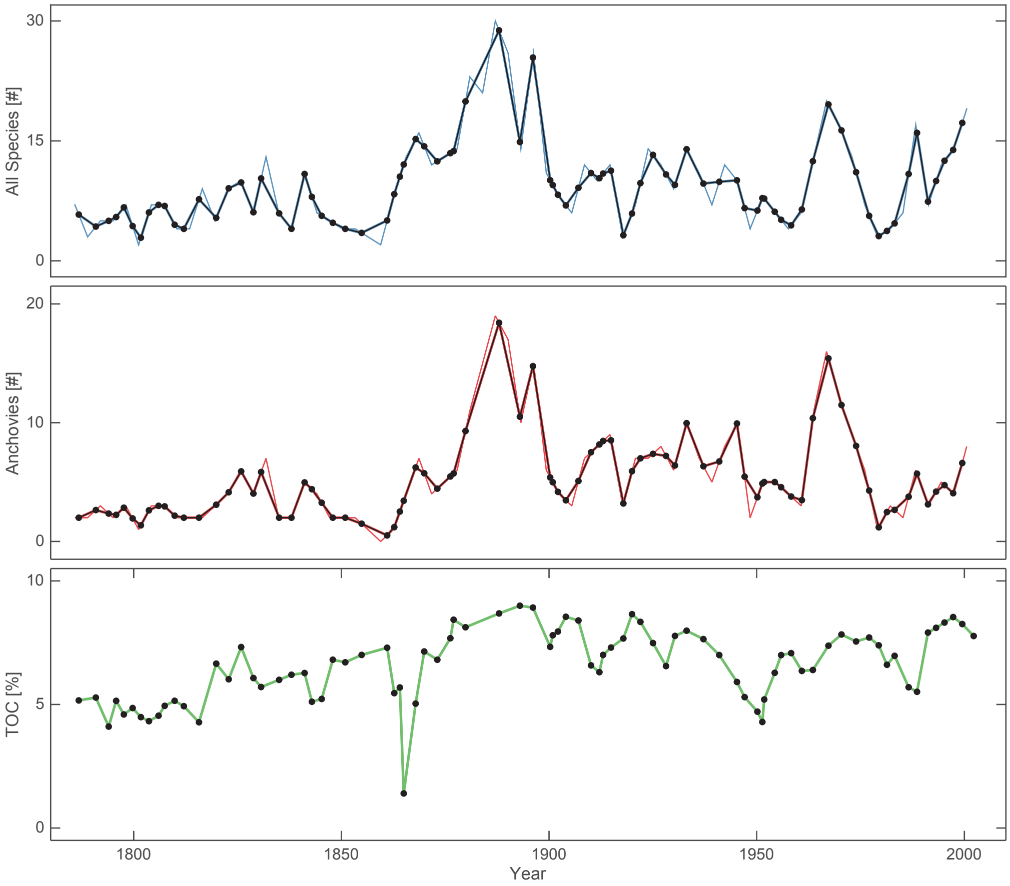

Figure A10: Fish scale counts from core F98-1A (*Valdés et al.*, 2008) and TOC from core BC-3D (*Díaz-Ochoa et al.*, 2011), Mejillones Bay, Chile.

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