Zitteliana

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Series A / Reihe A
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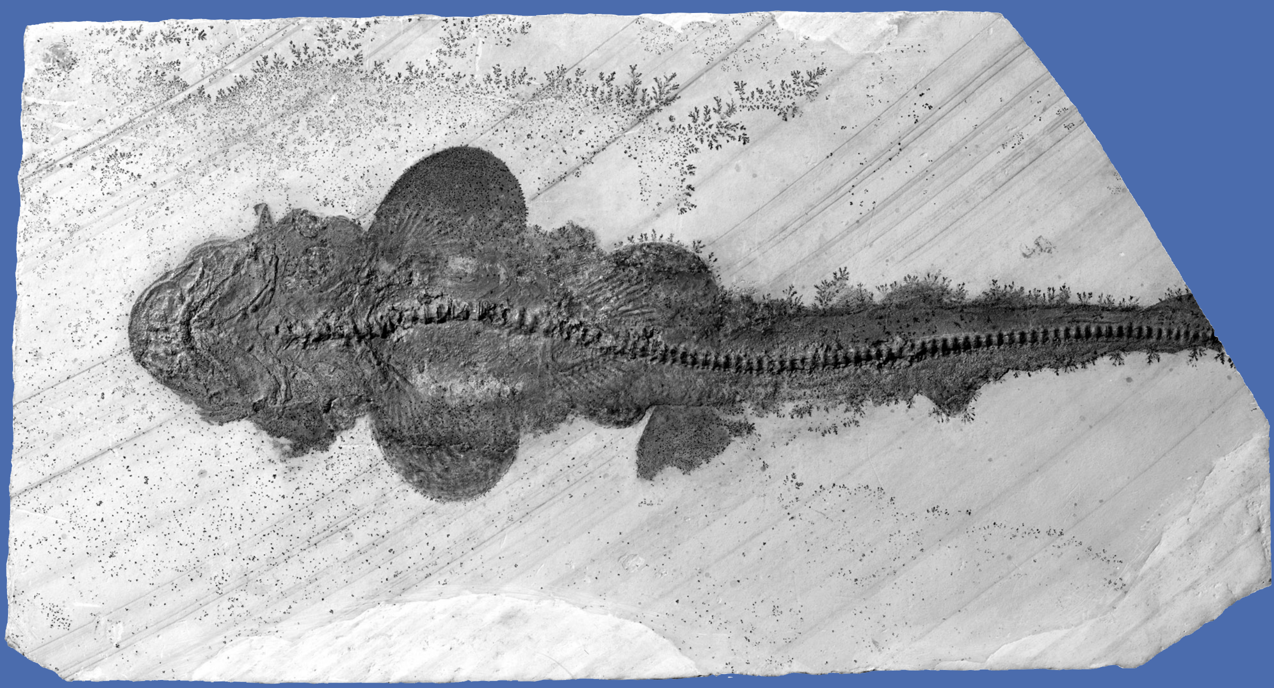

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EDITORIAL NOTE

As of in 2003, the journal *Zitteliana* is published in two series.

Series A: *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) replaces the former „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). The numbering of issues is continued (last published: Heft 43, 2003).

Series B: *Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-4138) continues the previous „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627).

Instructions for authors are included at the end of this volume.

HINWEIS DES HERAUSGEBERS

Vom Jahr 2003 an erscheint die Zeitschrift *Zitteliana* in zwei Reihen.

Die *Reihe A*: *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) ersetzt die bisherigen „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). Die Bandzählung (zuletzt erschienen: Heft 43, 2003) wird fortgesetzt.

Die Reihe B: *Abhandlungen der Bayerischen Staatssammlung für aPaläontologie und Geologie* (ISSN 1612-4138) führt die bisherige „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627) fort.

Hinweise für Autoren beider Reihen sind am Ende dieses Bandes enthalten.

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Cover illustration: *Phorcynis catulina* THIOLLIÈRE, 1854 (BSP 1990 XVIII 51) from the lower Tithonian of Zandt / Denkendorf (Bavaria), ventral view, 25 cm. Photograph: G. JANßEN (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

Umschlagbild: *Phorcynis catulina* THIOLLIÈRE, 1854 (BSP 1990 XVIII 51) aus dem unteren Tithon von Zandt / Denkendorf (Bayern), Ventralansicht, 25 cm. Foto: G. JANßEN (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

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Distribution and nitrogen isotope ratios of fish scales in surface sediments from the upwelling area off Namibia

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Abstract

We investigated the amount and origin of fish scales in 20 surface sediment stations from the diatomaceous mud belt on the shelf offshore Namibia (19°-24° S). Most abundant were scales of four different fish species: Sardine (*Sardinops ocellatus*), anchovy (*Engraulis capensis*), hake (*Merluccius capensis/paradoxus*), and jack mackerel (*Trachurus capensis*), albeit in strongly variable amounts. The total number of scales was highest in samples from approximately 70 m water depth. In total scales of sardines dominate the assemblage, which we attribute to both stability of the scale architecture and high abundance of sardine in the coastal upwelling ecosystem. The peak abundance of sardine- and total scales corresponds to an area of high biological productivity northwest off Walfishbay. The stable nitrogen isotope composition ($\delta^{15}N$) in fish scales clearly reflects the trophic level inhabited by the four species. $\delta^{15}N$ of sardine scales suggests an intermediate position in the food chain between a consumer of first and second order. The average $\delta^{15}N$ signature of anchovy scales suggests a higher position (second order consumer) in the food web. $\delta^{15}N$ of hake and jack mackerel indicate that they are in even higher trophic positions.

Key Words: Benguela, upwelling, fish scales, $\delta^{15}N$, sediment, stable isotopes.

Zusammenfassung

In 20 Proben aus Oberflächensedimenten aus dem Diatomeenschlammgürtel vor Namibia wurden Herkunft und Anzahl der Fischschuppen bestimmt. Am häufigsten, aber mit großen Variationen in der absoluten Häufigkeit, wurden Schuppen von vier verschiedenen Fischarten gefunden: Sardine (*Sardinops ocellatus*), Sardelle (*Engraulis capensis*), Seehecht (*Merluccius capensis/paradoxus*), und Pferdemakrele (*Trachurus capensis*). Die Gesamthäufigkeit von Fischschuppen war in Proben aus ca. 70m Wassertiefe am größten, wobei Sardinenschuppen die Vergesellschaftungen dominierten. Das Häufigkeitsmaximum von Sardinen- und Gesamtschuppenzahl stimmt mit einem ausgeprägten Zentrum biologischer Produktivität vor Namibia überein. Die Stickstoffisotopenzusammensetzung ($\delta^{15}N$) in sedimentären Schuppen überliefert klar die Position des ehemaligen Besitzers in der Nahrungskette. $\delta^{15}N$-Werte in Sardinenschuppen weisen hier darauf hin, dass Sardinen in der Nahrungskette die Position zwischen einem Konsumenten erster und zweiter Ordnung inne haben. Die durchschnittliche Isotopensignatur in Sardellenschuppen weist auf eine höhere Position in der Nahrungskette als Konsument zweiter Ordnung hin. Schuppen von Seehecht und Pferdemakrele zeigen $\delta^{15}N$ Werte, die sie sogar höher in die Nahrungskette ansiedeln.

Schlüsselwörter: Benguela, Auftrieb, Fischschuppen, $\delta^{15}N$, Sediment, stabile Isotope.

1. Introduction

The Benguela coastal upwelling system is one of the classic western boundary current systems, which belongs to the most productive regions of the World Ocean and therefore is one of the prime targets for commercial fisheries. It has recently been established as a "Large Marine Ecosystem" that is jointly managed by the states of Angola, Namibia, and South Africa.

Fishing success was variable during the past five decades (Textfig. 1; Schwartzlose et al. 1999), which is thought to reflect human impact (overfishing) and regional climate and oceanographic change. There is to date no consensus on the question whether human impact or natural variation in climate and upwelling intensity are the overriding causes of the decline in small pelagic fish populations during the past decades (Textfig. 1). One obvious way to shed light on this question would be to investigate sedimentary records of fish variability at times preceding observation, for example through sedimen-

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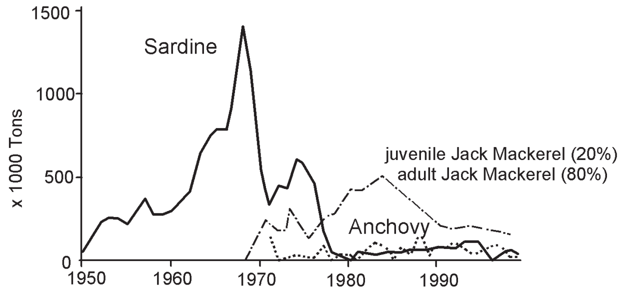


Textfigure 1: Distribution of annual catches of important fish from the upwelling area off Namibia (redrawn from Schwartzlose et al. 1999) in the time span from 1950 until 1998. Catch data of Jack Mackerel are kindly provided by E. Klingelhoeffer, Namibian Ministry of Fisheries.

tary records of fish scale abundance and type.

However, only a few regions in the global ocean have suitable sedimentation environments where fish scales are continuously present in the sedimentary record. Only in western boundary upwelling systems fish populations are large enough to deliver sufficient scales to sediments (Suess 1981). Such areas are located in the western boundary current system of North and South America (summarised in Markgraf et al. 2000), and in the Benguela current system off Namibia, southwest Africa (McLachlan 1994; Shackleton 1987; Struck et al. 2002).

For sardine and anchovy, the two most important fish species for fisheries, the main habitat during large parts of the life span lies in the upwelling area off Walfishbay (Shackleton 1986). In the Walfishbay region juveniles of sardine and anchovy recruit to fishery. Anchovy spawn in winter along most of the Namibian coast. Larvae move inshore in the warmer waters to the North of Walfishbay. Juveniles accumulate in the Walfishbay area from May onwards. Adults again move northwards out of the area (Shackleton 1986). Sardine spawn off northern Namibia and larvae disperse north towards the Angolan border. Juveniles move southwards and are recruited near Walfishbay. Adults are caught in the vicinity of Walfishbay (Shackleton 1986).

The shelf off Namibia (water depths up to approximately 150 m) is characterized by sedimentation of organic rich diatomaceous ooze forming a NNW-SSE striking (coastal parallel) mud layer with a thickness of up to 14 m. The mud belt extends over 700 km in N-S direction and 100 km in E-W direction (Bremner 1983; Emeis et al. 2004). In these sediments fish scales of anchovy and sardine were reported by Shackleton (1986), who examined two short sediment cores from the area off Walfishbay, analyzed their scale content and calculated average scale sedimentation rates. Cyclic changes in the prevalence of sardine and anchovy scales were observed by McLachlan (1994) in a sediment core from the diatomaceous muds off Walfishbay.

These previous investigations relied on only a few sedimentary records of fish scales. No attempt has been made to date to establish the present day spatial distribution of scales, nor has stock been taken of the scale types present and scale assemblages. Here we report on fish scale types and abundance encountered in surface sediments on the shelf off Namibia. We determined stable isotope composition of nitrogen in fish scales to elucidate their significance as indicators for food web position of the fish species (Fry 1988).

An average enrichment of 3-4‰ in $\delta^{15}N$ per trophic level was found throughout the entire food webs in terrestrial as well as marine ecosystems (Peterson & Fry 1987). Isotope ratios of fish scales have previously been used only in a few environmental studies (Estep & Vigg 1985; Wainright et al. 1993). A methodological investigation decribes the preparation of fish scales for isotope studies to be used for retrospective studies on paleontological collection material (Perga & Gerdeaux 2003). Struck et al. (2002) published a limited number of nitrogen isotope data from sedimentary fish scales from the Namibian upwelling area in relation to $\delta^{15}N$ data from a sediment core off Walfishbay.

This methodology is applied here to derive information about the position of fish in the Namibian upwelling food web and potential variation of the food web structure on spatial scales.

2. Material and Methods

Surface sediments were sampled during the R.V. Meteor expedition M 48-2 off Namibia (2000) with a multicorer at 20 stations (Textfig. 2). The top two centimeters of one to three multicorer tubes were sampled per station with volumes ranging from 157 to 471 cm^3. Samples were wet-sieved for the size fractions >250 µm and >63 µm at Munich University. Fish scales and all other components of the coarse size fraction (>250 µm) were counted under a binocular Wild M10 and calculated per sample volume. For stable isotope analysis and measurement of carbon and total nitrogen contents of fish scales, one scale was wrapped into tin foil vessels prior to isotope measurement. For stable isotope analysis of suspended matter 250-500 ml of seawater was filtered on pre-combusted (500 °C for 2 h) glas fibre filters (Whatman GFF 0,8 µm). Carbon and nitrogen concentrations and the stable isotope ratios of nitrogen ($\delta^{15}N$) were determined simultaneously in a Thermo NC2500 Elemental Analyzer connected to an isotope-ratio mass-spectrometer (Finnigan, Delta *Plus*). The reference gas was pure N_2 nitrogen from a cylinder calibrated against IAEA standards N-1 and N-2. The standard deviation for replicate samples was better than 0.2‰.

3. Results

3.1 Fish Scale Systematics

The size fraction >0,250 µm reveals four common types of fish scales. Our taxonomy is based on the morphology of scales only, and thus species names correspond to scale morphology best as possible. We used Patterson et al. (2002) for basic orientation, and discussed our morphotypes with T. R. Baumgartner in 2001 (pers. comm.). It was not possible to dissect the scale morphology of the sibiling species *Merluccius capensis* and *Merluccius paradoxus*; some authors even refer to *Merluccius capensis paradoxus* Franca. An extensive discussion of the ecology and taxonomy of all species given here is provided by Froese & Pauly (2004).

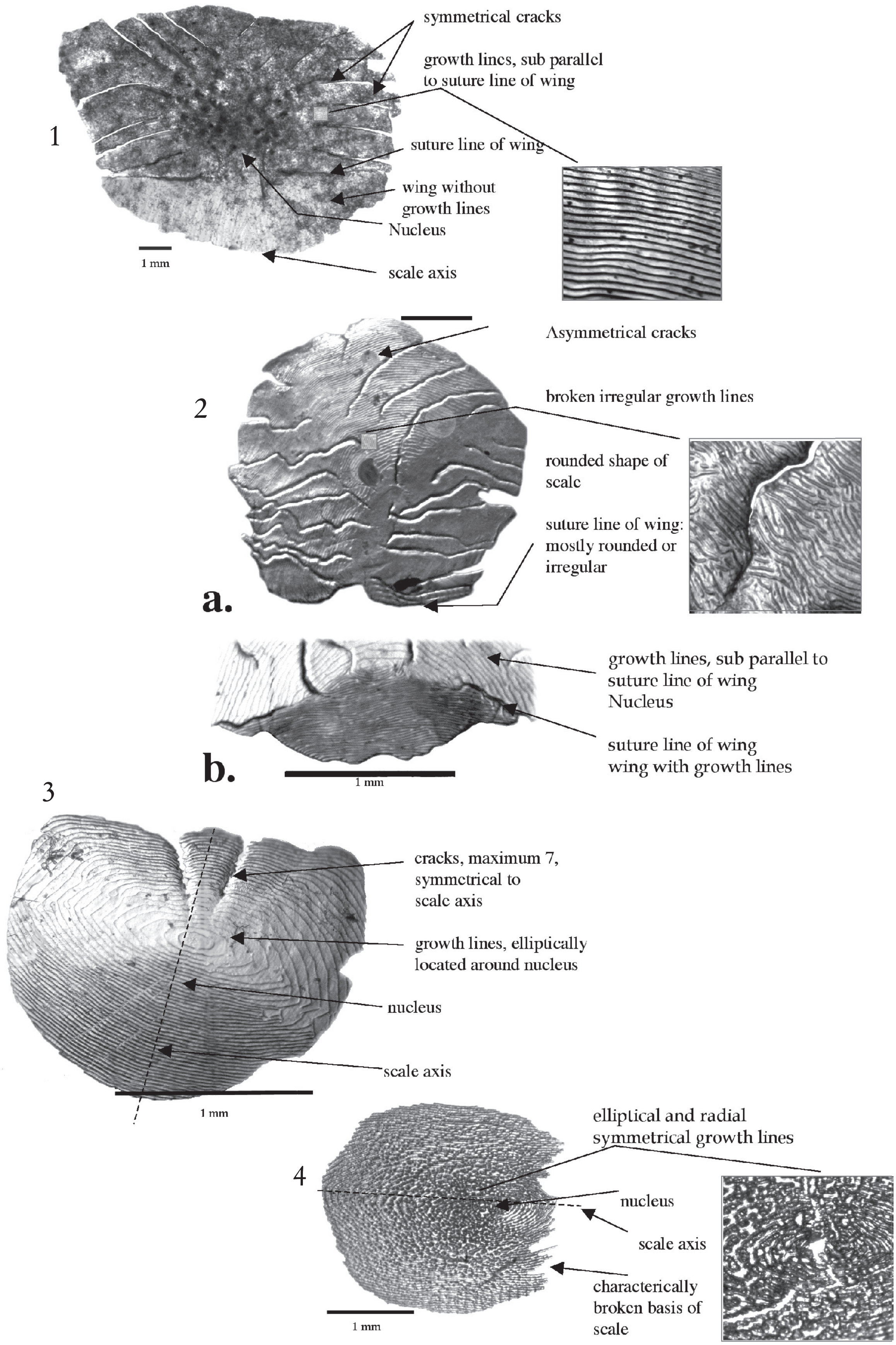


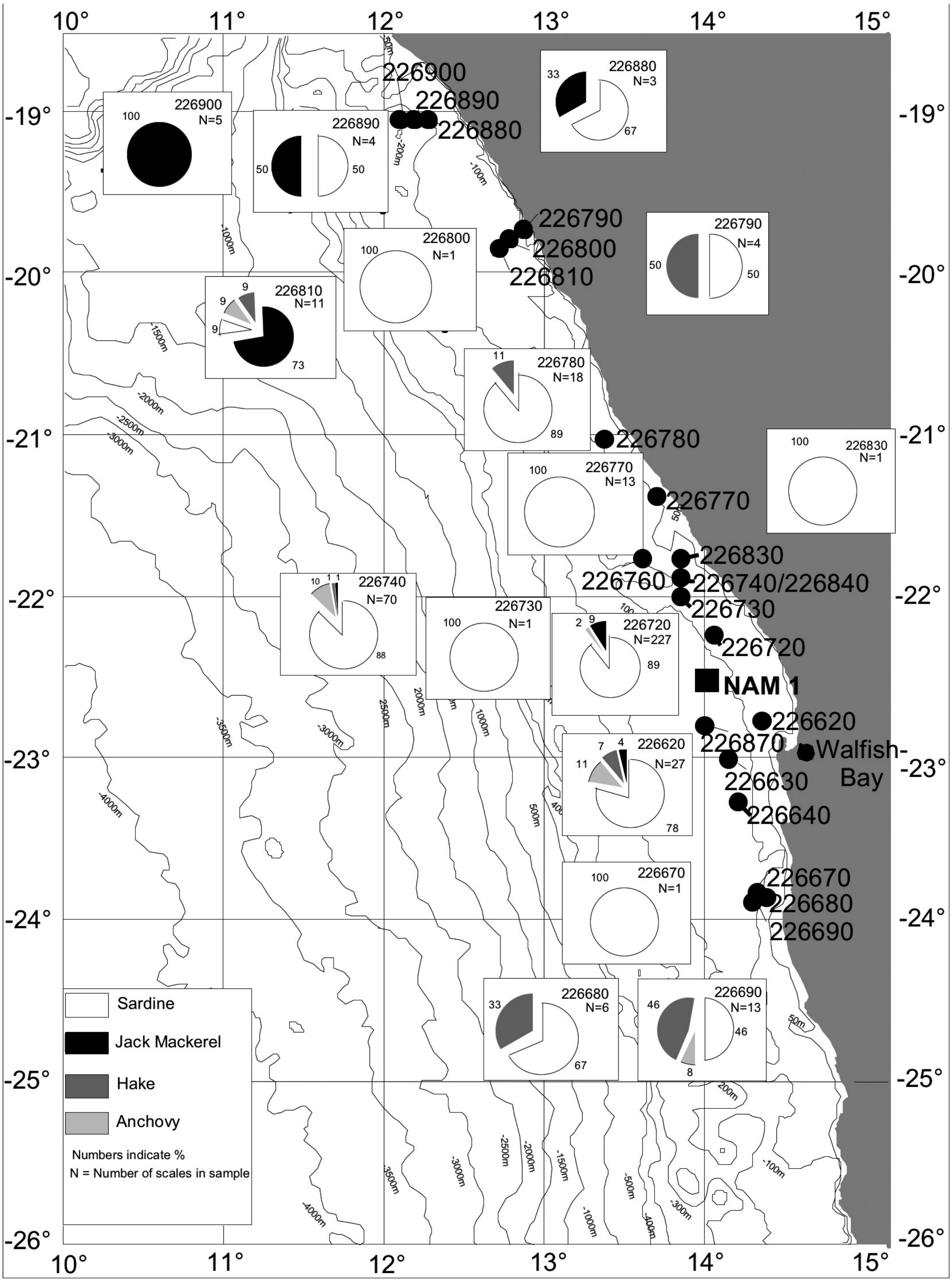
Plate 1: Photographs of typical scales belonging to four important fish species from the upwelling area off Namibia.

Fig. 1: Sardine, *Sardinops ocellatus*.

Fig. 2: Anchovy, *Engraulis capensis*.

Fig. 3: Jack mackerel, *Trachurus capensis*.

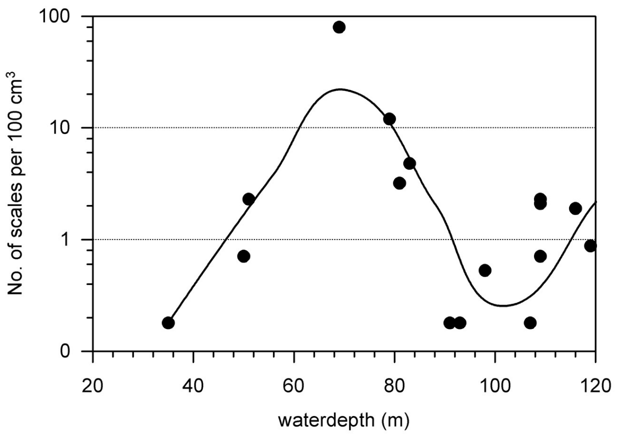
Fig. 4: Hake, *Merluccius capensis / paradoxus*.



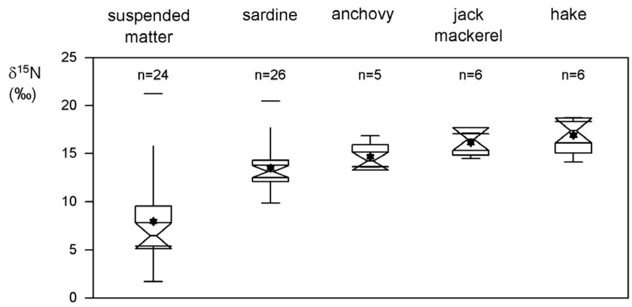
Textfigure 2: Map of relative abundances (%) of the 4 scale types and the total number of scales per $100cm^3$ wet sediment in the fraction >0.250mm. All samples were retrieved during FS Meteor expedition M48 leg 2. The name "NAM1" off Walfishbay indicates the geographical position of a high-resolution sediment core, which will be investigated in the near future for fish scale variations during past climate variations.

Sardine (*Sardinops ocellatus* (Pappe)), Plate 1, Fig. 1

A typical sardine scale is bilaterally symmetrical. It has a rectangular shape and ranges from 3 to 12 mm in length. The scales are relatively resistant to mechanical erosion due to an average thickness of 0.53 mm (Shackleton 1987). The nucleus represents the oldest part of the scale from which concentrical lines of growth are visible. The wing represents the part of the scales that is visible on the skin surface of the



Textfigure 3: Absolute abundance (no. per 100 cm³ sediment) of scales versus water depth (m). The trend line indicates an abundance maximum of scales in water depths around 70 m.



Textfigure 4: Tailed box plots of $\delta^{15}N$-data of fish scales from different fish species from surface sediments from the diatomaceous mud belt off Namibia. The N-isotope signature in fish scales indicates the position of fish in the food chain relative to their prime food source (Fry 1988; Peterson and Fry, 1987). Also indicated is the $\delta^{15}N$-signature of suspended particulate nitrogen from the coastal upwelling system off Namibia, which reflects presumably the isotopic composition of the first trophic level (phytoplankton).

living fish. The wing does not display growth lines. Along the two sides of the scale a variable number of pairs of cracks are located.

Anchovy (*Engraulis capensis* Gilchrist)
Plate 1, Fig. 2

A typical anchovy scale is round and ranges from 2 to 8 mm in diameter. The average thickness of anchovy scales is around 0.21 mm (Shackleton 1987), which makes them relatively sensitive to mechanical erosion. The nucleus represents the oldest part of the anchovy scale from which concentric growth bands extend outwards. In contrast to sardine scales, the lines of growth are broken and irregular. The wing shows typical parallel growth lines. The edge of the round scale shows a number of irregular cracks without any symmetry.

Jack Mackerel (*Trachurus capensis* Castelnau)
Plate 1, Fig. 3

A typical jack mackerel scale is a wingless half-circle ranging from 1 to 6 mm in diameter. The straight part of the scale reveals a variable number of cracks (0-7). Jack mackerel scales are relatively insensitive to mechanical stress. The nucleus represents the oldest part of the jack mackerel scale and is located almost in the center of the scale. Narrow growth lines are arranged concentrically around the nucleus.

Hake (*Merluccius capensis / paradoxus* Castelnau)
Plate 1, Fig. 4

A typical hake scale is ovally shaped and ranges from 2 to 9 mm in length (typically 5 mm). The scales are very fragile and may easily be destroyed by manipulation with tweezers or brush. The nucleus of hake scales typically lies close to the region of the scales that is usually strongly eroded. Growth lines are concentrically arranged around the nucleus. Hake scales do not display wings.

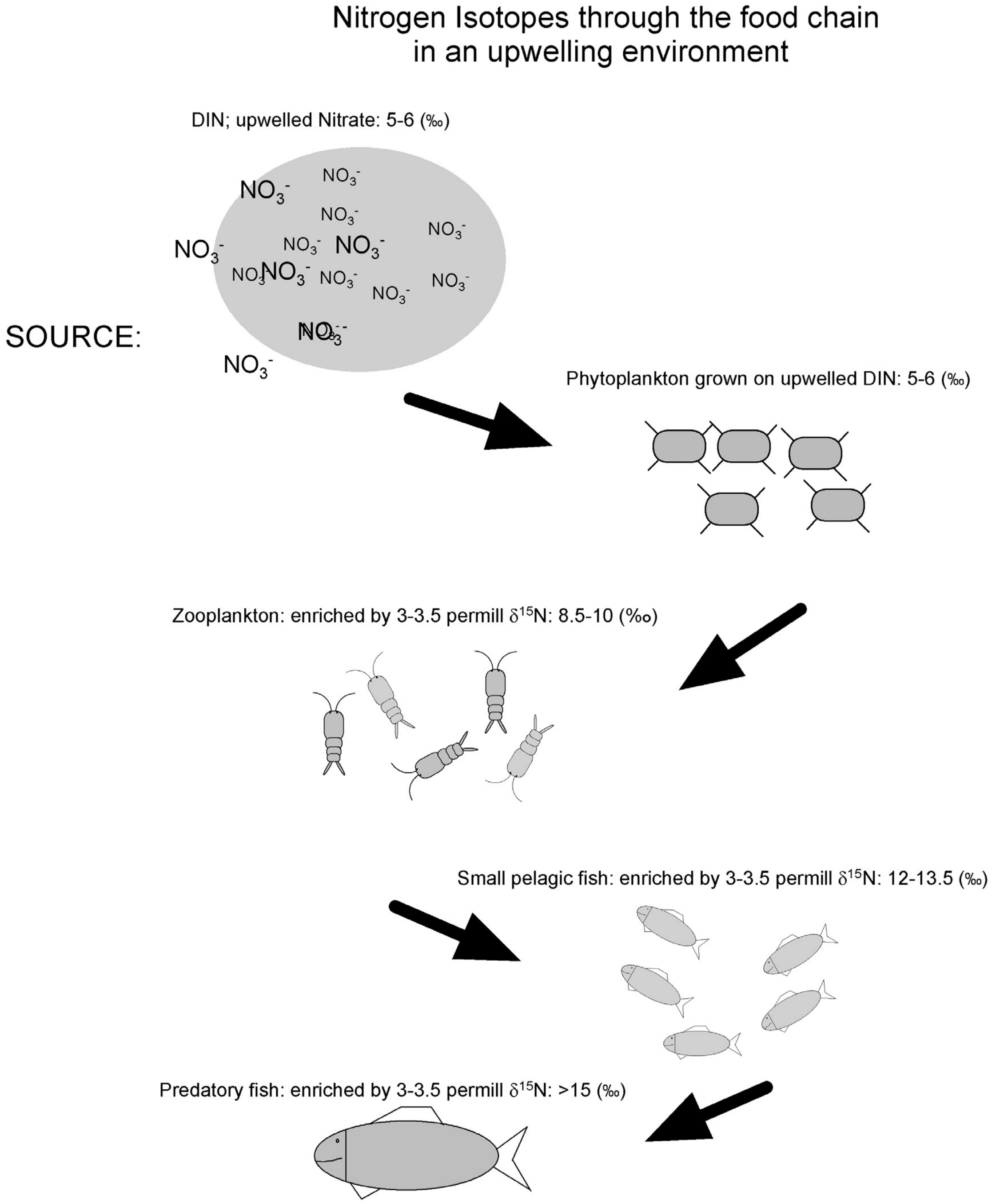
3.2 Areal Distribution of Scales in Sediment Surface Samples

On the basis of the characteristics indicated above, the abundance of fish scales of the four dominant species was counted. Textfig. 2 shows a map of relative abundances (%) of the four scale types and total number of scales per 100 cm³ wet sediment in the fraction >0.250mm. In 16 of 20 sediment samples we found scales in abundances varying between 0.18 to 80 scales per 100 cm³ wet sediment (Textfig. 2). The highest abundance of scales was found in water depths around 70 m (Textfigs 2, 3) in the area with thick diatomaceous oozes offshore Walfishbay/ Swakopmund. In deeper or shallower water the number of scales per 100 cm³ wet sediment decreased rapidly (≤ 1 scale per 100 cm³ wet sediment, cf. Textfig. 3).

The percent distribution of dominant scales reveals clear spatial patterns. In samples of the northern sector (Stations 226900, 266890, 226880, and 266810) jack mackerel and sardine scales strongly dominate the scale assemblage (Textfig. 2; 82-100%), at low total numbers of scales per sample (up to 11 specimens per sample). The samples from the southern sector are dominated by sardine scales with varying contributions by the other three species (Textfig. 2). Only in near coastal samples (Textfig. 2; Stations 226790, 226680, and 226690) the contribution of hake scales is higher than 33%. Anchovy scales were found in low percentages (≤ 11%) in four samples only.

3.3 Stable Nitrogen Isotope Ratios in Scales

Textfig. 4 shows box plots of nitrogen isotope data from fish scales of jack mackerel, hake, anchovy, and sardine. Highest median $\delta^{15}N$ was found in scales of jack mackerels ($\delta^{15}N$ = 14.0 ‰; N = 6). Median $\delta^{15}N$ of hake and anchovy scales are significantly (Textfig. 4) lower: 12.4 ‰ (N = 6) and 11.7 ‰ (N = 5) respectively. Again significantly lower $\delta^{15}N$ values (median = 10.1 ‰) were found in Sardine scales (N = 45) indicating a relatively low position of sardines in the food web of the Benguela upwelling system.



Textfigure 5: Simplified model of the nitrogen isotope distribution in the food web of the Benguela Upwelling System of Namibia (modified from Struck et al. 2002).

The average nitrogen isotope composition of suspended matter ($\delta^{15}N_{PN}$) has a median N-isotope composition of 5.9‰, thus significantly below the median $\delta^{15}N$ composition of fish scales (Textfig. 4).

4. Discussion

Reconstruction of fish stocks under natural conditions is of high relevance for the management of this largest marine resource (http://www.hmapcoml.org/). In the absence of observational records, the only feasible ways are deciphering sediment archives, or using hind casts from numerical models that include higher trophic levels. Both attempts are still in their infancy. We are fairly confident that many of the unknowns in using sedimentary records of fish scales for stock reconstructions will be resolved with growing observational data bases on fish stocks and advancement of such models. The unknowns include such aspects as the species-dependent loss of scales and influences of sediment dynamics and diagenesis on the record preserved in sediments.

Sardine and anchovy live in shoals of millions of individuals. During their life they release scales in continuous rates (deciduousness loss) or during attacks of predators (deciduous loss) (Shackleton 1987). McLachlan (1994) found a deciduousness loss of 0.92 scales per fish per day for sardine and

0.55 scales per fish per day for anchovy, whereas SHACKLETON (1987) found the mean deciduousness fluxes for sardine and anchovy to be 1.5 and 0.48 scales per fish per day respectively. In the same study the deciduous loss of scales amounted to 38% for sardine and only 25% for anchovy. Deciduous scale loss biases any attempt of absolute population comparisons based on scale counts. Sardines are more deciduous than anchovy, so that scale counts are biased towards sardine. Implications from these previous studies are that caution should be exercised when extrapolating from scales numbers to absolute populations. Even more, comparable studies about scaling processes for hake and jack mackerel are lacking.

Nevertheless, significant differences in the areal distribution of scales in the uppermost two centimeters of sediment samples (Textfig. 2) coincide with the average location of specific fish populations in the overlying water mass SHACKLETON (1986). For instance, most of the sardine scales and the highest total numbers of scales were found in the samples off Walfishbay (Textfig. 2). In the sampled area between 19° S and 24° S upwelling intensity is strongest off Walfishbay and Swakopmund as indicated in lowest mean annual sea surface temperatures (SST 14-15 °C; GIRAUDEAU 1993). Mean annual SST increase further north to 18°C around Capo Frio (19° 30' S). Intensive upwelling off Walfishbay and its nutrient supply to the euphotic zone is one of the dominant factors for biological production and thus may be reasonable for highest scale counts in this region (Textfig. 2).

Differences in average sedimentation rates can bias total numbers of scales per sediment volume due to dilution or sorting effects. In the area under investigation an extensive seismic survey and coring program has been carried out by MEYER (1973), ROGERS & BREMNER (1991), and EMEIS et al. (2004), revealing large differences in the average thickness and sedimentation of the diatomaceous mud on the shelf along the Namibian coast. In the area off Walfishbay and Swakopmund the mud belt is both widest and thickest. Highest scale abundance in the area off Walfishbay is thus most likely a result of high primary productivity, high sedimentation rates, and large fish populations in this area. However, establishing quantitative relations between living fish populations and sedimentary scales is impossible at present because observational data of living fish populations (biomass or number of individuals) in the area are still missing. In addition, possible changes in fish stock by seasonal up to centennial cycles are not yet fully documented.

The stable isotope analyses of scales and other sedimentary components can yield valuable information about the past environment (STRUCK et al. 2002). The scales of a fish essentially reflect the average N-isotope signature of muscle tissue (PERGA & GERDEAUX 2003, here: white fish), and thus their isotope fingerprint can be used to clarify the fish's position in the food chain.

Clearly, the statistically significant differences suggest that the four species inhabit different trophic levels (Textfig. 4). Under the assumption that marine nitrate is the basis for primary production yielding a N-isotope signature of 5-6‰ (6.2‰ in the Benguela upwelling, cf. EICHNER 2001), a simplified isotope model for members of the food chain in the Namibian upwelling can be applied (Textfig. 5).

Phytoplankton would have an average N-isotope signature of 5-6‰ under the assumption that nitrate is usually fully depleted after the plankton bloom (MONTOYA 1994). This is indeed indicated by median $\delta^{15}N$ around 6.0‰ in suspended matter from the euphotic zone (Textfig. 4). According to many studies in diverse ecosystems, an increase of 3-3.5‰ in the $\delta^{15}N$-signature can be expected per step in the food chain (e.g., FRY 1988; PETERSON & FRY 1987; STRUCK et al. 2002). For consumers of first order (phytoplanktivorous organisms) a range of nitrogen isotope values from 8.5-10‰ can thus be expected, increasing to 12-13.5‰ for consumer of second order (zooplanktivorous organisms). Predatory fish or seals then should have N-isotope values >15‰.

Mean $\delta^{15}N$ values near 14‰ puts hake into the window for second order consumers predating on small fish, and the same holds true for scales of jack mackerels with slightly lower average values around 13‰ (Textfig. 4). This is in agreement with the exclusively predatory feeding strategy of this two species (LINDSAY et al. 1998).

Anchovy change their trophy during growth (LINDSAY et al. 1998). In young stages (<30mm) individuals show increasing $\delta^{15}N$ values with increasing length ranging from 9 to 11.5‰, reflecting a change in trophy by almost one step in the food web. Anchovy >30 mm to 90mm in length show still increasing $\delta^{15}N$ values with increasing length ranging from 11.5 to 13.5‰ (LINDSAY et al. 1998). This has been attributed to a change in food sources during growth due to selective feeding on different fractions of available plankton (LINDSAY et al. 1998). A similar increase of nitrogen isotope values by 3.5‰ with increasing length (75-125 mm) has been observed in the Benguela Current System for anchovy (*Engraulis capensis*; SHOLTO-DOUGLAS et al. 1991). The relatively low median $\delta^{15}N$ of a number of sedimentary anchovy scales found in this study suggests an intermediate position in the food web between consumer of first and second order and reflects a change in feeding strategy during different development stages (Textfigs 4, 5).

Slightly decreasing $\delta^{15}N$ values (-1.5‰) were observed in sardines surpassing a body length of 18 mm (BODE et al. 2003). During ontogeny, the filter apparatus of sardines is improved by the increasing length of the grill-rakers and the growing number of denticles (ANDREU 1953; ANDREU 1960). Small sized phytoplankton can be ingested more effectively by larger sardines, and thus the amount of this base level $\delta^{15}N$ was supposed to increase in their diet (BODE et al. 2003). The broad spectrum of N-isotope values found for sardine scales off Namibia thus might be influenced in part by such ontogenetic changes (Textfig. 4). For the Benguela Upwelling System, a prevalence of distinct age cohorts seems improbable for sardine, but might be speculated for anchovy.

5. Conclusions

The surface sediments from the diatomaceous mud belt off Namibia reveal fish scales of 4 commercially important fish species in varying numbers: Sardine: *Sardinops ocellatus*; Anchovy: *Engraulis capensis*; Hake: *Merluccius capensis / paradoxus*; Jack Mackerel: *Trachurus capensis*.

The stable isotope signature ($\delta^{15}N$) in scales reflects the trophy of the fish clearly with an enrichment of 3.5‰ $\delta^{15}N$

per trophical level. Hake and jack mackerel were found to be predatory fish, anchovy was mainly feeding on zooplankton, and sardine had an intermediate position in the food web recording a mixed diet of phytoplankton and zooplankton. The $\delta^{15}N$ composition of fish scale records changing food sources, which may be attributed to either ontogeny or to environmental perturbations in the ecosystem off Namibia. Sardine scales are most frequent in the samples investigated, due to the combination of factors such as robustness of scales, shading frequency and overall fish abundance. Future analysis of spatial differences in the amount of scales and the overall maximum of scales in the sedimentary record will depend on increasing knowledge on fish stock in the highly productivity upwelling area off Walfishbay. Even though differences in the robustness of scales and lateral differences in the abundance of scales might bias our results at present, we see high potential in the recovery of climatically linked changes in ancient fish populations from counts and isotopic measures of fish scales in the sedimentary record.

Acknowledgements

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