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FROM THE GEOCHEMISTRY OF CORAL REEF FISH OTOLITHS TO CLIMATE: WHAT CAN WE LEARN FROM THE EXAMPLE OF TAIARO LAGOON?

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CORAL REEF FISH
OTOLITHS
STABLE ISOTOPES
TAIARO ATOLL

ABSTRACT. – The analysis of the C-O stable isotope composition of coral reef fish otoliths from Taiaro, a French Polynesian atoll normally isolated from the Pacific Ocean, has been performed to address two main questions. The first is to confirm previous results which suggest that a lagoonal coral reef fish population is able to achieve its ontogenetic cycle without any open ocean phase. If so, are O isotopic values of otoliths an indicator of temperature fluctuations in the tropical Pacific Ocean related to climate change and in particular temperature variations of water masses? $\delta^{18}O$ and $\delta^{13}C$ values on both lagoon and open ocean fish otoliths caught in 2006 indicated clearly that O-isotopes reached the isotopic equilibrium; in contrast, all $\delta^{13}C$ values exhibited a strong isotopic disequilibrium related to metabolic activity. Stable isotope compositions revealed a clear differentiation between fish from lagoons and those from the open ocean (with a $\delta^{18}O$ enrichment of 1 ‰ in favour of the lagoon). This confirmed a lack of connectivity between habitats and that fish from lagoon lived their entire life cycle in the lagoon. Both $\delta^{18}O$ and $\delta^{13}C$ data indicated differences between nucleus and edge signatures with changes in fish behavior from the larval life to adulthood (habitat, diet, etc.), and a clear adaptation of dietary behavior of lagoon fish. The comparison of the 2006 data set with those of 1994 showed that environmental conditions were stable in the lagoon, leading to a very narrow range of variations in the $\delta^{18}O$ values. $\delta^{18}O$ of fish otoliths of the open ocean exhibited a wider variation (+0.25 ‰) between 1994 and 2006, suggesting a decrease in temperature linked to a change of SST, which can be interpreted in terms of climate change associated with El Nino Southern Oscilation (ENSO). These differences could also be due to a switch of habitats during the life cycle of fish from the open ocean.

INTRODUCTION

In French Polynesia the 9 km^2 uplifted lagoon of Taiaro Atoll is hypersaline due to its isolation from the ocean, but it contains a high diversity of fish. An international multidisciplinary expedition went to this atoll some years ago to establish whether the lagoon fish community could be self-sustaining without regular connection to the ocean (Galzin *et al.* 1998).

Oxygen isotope composition of marine biocarbonates (of tropical reef corals, mollusk shells, foraminifers) is used as a proxy for ocean seawater temperature. They record the specific SST (Sea Surface Temperature) conditions under which they grew. Stable isotope methods have been applied to the otoliths of many fish species. Fish carry their own internal environmental recorders in the form of otoliths (*sagittae*, *lapilli* and *asterisci*) which are aragonitic bodies (aragonite crystals in a protein matrix) of the inner ear of teleosts (Degens *et al.* 1969). The otoliths grow throughout the entire life of a fish and are considered unique in the animal world. Because the otoliths are metabolically inert, the elemental signature embedded in them can be characteristic of the surrounding water masses and can be considered as 'proxies' of environmental conditions (see Campana 1999 for an extensive review). Otolith stable isotope ratios potentially represent an informative and pertinent part of this environmental record (Blamart *et al.* 2002).

Taiaro Atoll is normally isolated from the Pacific Ocean (Galzin *et al.* 1998). This site is well-suited for studying whether the otolith record changes in water temperature. The fish taken from these sites were sufficiently sedentary for their otoliths to reflect the isotopic composition of the water in which they lived. Planes *et al.* (1998), through genetic and demographic studies, confirmed Leis *et al.* conclusion (1998) suggesting that fish may complete their life cycle in the lagoon. Thereafter, Dufour *et al.* (1998) and Blamart *et al.* (2002), on the basis of the physical properties of the mass waters using isotopic composition of waters and fish otoliths, reinforced this hypothesis.

Because the physical and chemical properties of the ocean water and the lagoon water are different, it is possible from the stable isotope (C-O) compositions of the otoliths to identify the habitat used during the fish life history (Blamart *et al*. 2002). It has been shown that otoliths from the lagoon or the ocean are at O-isotopic equilibrium with the surrounding waters (Dufour *et al*. 1998, Blamart *et al*. 2002), and reflect differences in the temperature of the water mass in which they were formed (Campana 1999, Hobson 1999). Thus, the oxygen isotopic composition can be used to estimate temperatures at which carbonates are formed (Kalish 1991, Thorrold *et al*. 1997). Carbon isotopic data can provide information related to metabolic processes and the source of carbon involved in calcification (Kalish 1991, Schwarcz *et al*. 1998, Solomon *et al*. 2006).

The aim of our study was to assess the potential of the stable isotopes (C-O) recorded in otoliths to serve as indicators of climatic change in Pacific tropical waters. For this, the stable isotopic compositions of otoliths from fish collected in 2006 around and in the Taiaro lagoon were measured. Since the lagoonal fish populations of Taiaro can achieved a complete biological cycle without migration at the larval stage to the open ocean (Dufour *et al*. 1998, Planes *et al*. 1998, Blamart *et al*. 2002), data from 2006 were compared to data of the water characteristics (Dufour *et al*. 1998) and from fish otoliths collected in 1994 (Blamart *et al*. 2002) to evaluate the changes in water characteristics.

MATERIALS AND METHODS

Sampling: The Taiaro Atoll (540 km east-northeast of Tahiti 15°45’00”S-144°37’59”O, Fig. 1) is 5 km in diameter with a maximum depth of 29.4 m and is a highly-enclosed lagoon (Chevalier & Salvat 1976). The lagoon water temperature measured during the expedition of 13-19 February 1994 was 30.4 °C at the surface and 29.7 °C at 26.4 m depth (Dufour *et al*. 1998). The salinity of the lagoon water is 42.6 ± 0.2. Ocean water is less saline 36.6 ± 0.2 and consistent with tropical ocean salinity data (Craig & Gordon 1965). Dufour *et al*. (1998) and Chevalier & Salvat (1976) showed based on uniformity of the salinity and of the persistence of lagoon water few centimeter under the ocean level (with no tidal influence) that the lagoon is recharged

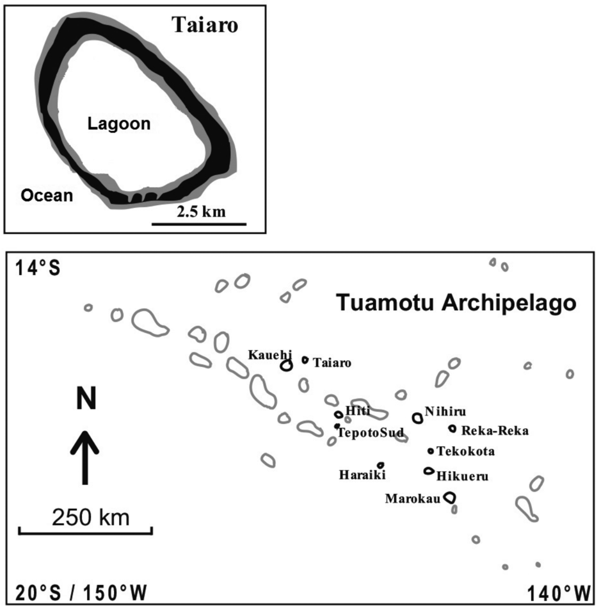

Fig. 1. – Location of Taiaro atoll in French Polynesia.

Table I. – List of coral reef fish collected in 1994 and in 2006 in and around Taiaro Atoll. The number of fish collected was done into brackets.

Date	1994		2006	
Species	Ocean	Lagoon	Ocean	Lagoon
Abudefduf sexfasciatus				+ (5)
Acanthurus triostegus	+ (3)	+ (2)	+ (7)	+ (3)
Centropyge flavissima			+ (5)	+ (4)
Chaetodon auriga			+ (6)	+ (6)
Chaetodon citrinellus				+ (2)
Chaetodon ephippium			+ (1)	+ (5)
Chaetodon lunnulatus			+ (6)	+ (5)
Chaetodon lunula			+ (7)	+ (2)
Chaetodon ulietensis	+ (3)	+ (5)	+ (8)	+ (5)
Cheilinus chlorurus		+ (5)		+ (4)
Cheilinus undulatus				+ (5)
Epinephelus polyphekadion			+ (1)	+ (5)
Epinephelus merra		+ (9)		
Lethrinus atkinsoni				+ (5)
Lethrinus olivaceus	+ (6)	+ (2)	+ (2)	+ (5)
Parrupeneus multifasciatus			+ (5)	

during scarce overtopping of the land barriers or continuous seepage through the reef matrix. A high diversity of teleost fishes, with 125 species belonging to 31 families, was found in this isolated lagoon (Carleton & Doherty 1998, Galzin *et al*. 1998, Leis *et al*. 1998).

Water samples were collected for stable isotope (oxygen) measurements: one sample at 1 m below the surface in the ocean and two samples at 1 m and 23 m in the lagoon. Fishes were collected in the Taiaro lagoon and the adjacent reef slope during the 1994 and June 2006 expeditions (Table I): Acanthuridae (*Acanthurus triostegus*), Chaetodontidae (*Chaetodon auriga, C. citrinellus, C. ephippium, C. lunnulatus, C. lunula, C. ulietensis*), Labridae (*Cheilinus chlorourus, C. undulatus*), Lethrinidae (*Lethrinus atkinsoni, L. olivaceus*), Mullidae (*Parupeneus multifasciatus*), Pomacanthidae (*Centropyge flavissimus*), Pomacentridae (*Abudefduf sexfasciatus*) and Serranidae (*Epinephelus merra, E. polyphekadion*). All *sagittae* were removed from each fish and stored dry in glass vials.

Isotope measurements in water samples: Oxygen isotopes ($\delta^{18}O$) were measured on a Finnigan MAT 252 by equilibration with CO_2. The 1 sigma error of the $\delta^{18}O$ is ± 0.05 ‰. The reference is SMOW, Standard Mean Ocean Water (Craig 1961). The $\delta^{13}C$ value of the dissolve inorganic carbon was not measured.

Isotope measurements in otoliths: In the laboratory, sagittae were cleaned ultrasonically in distilled water, and then fixed on a glass slide. The nucleus (larval life stage) and the outer part or edge (material deposited before sampling) of the otoliths were optically clearly visible and sampled using a dental drill (0.8 mm in diameter). In order to avoid contamination by the organic matter (< 1 wt %), the samples were heated at 380 °C for 45 minutes. Around 100 micrograms of carbonate are needed for the isotopic measurements performed on an Optima-VG mass spectrometer. The results are given in the conventional (δ ‰) notation expressed in per mil against the VPDB standard (Vienna Pee Dee Belemnite, Coplen *et al*. 1983) where:

$$\delta \text{ sample} = (R_{\text{sample}} / R_{\text{Standard}} - 1) \times 10^3$$

Reproducibility is 0.04 ‰ and 0.05 ‰ respectively for the carbon and the oxygen. C and O isotopic equilibrium were calculated using the equation given in Grossman (1982) and Grossman & Ku (1986) for oxygen and carbon. For oxygen, the isotopic fractionation values or the temperatures derived from these two equations are in good agreement with those of Shackleton (1974) and Thorrold *et al*. (1997). The temperature of isotopic equilibrium can be calculated from the following equations respectively for O and C:

$$T°C = 20.19 - 4.56 \times \delta^{18}Oar - \delta^{18}Ow + 0.19 \times \delta 18Oar - \delta^{18}Ow^2$$

$$T°C = 22.22 - 9.25 \times \delta^{13}Car - \delta^{13}Cw$$

Where δ ar and δ w represented the isotopic composition for the C or the O of the aragonite and the water.

Statistical methods and analysis: Isotopic signatures ($\delta^{13}C$ and $\delta^{18}O$) of otolith were compared by Student paired *t*-test to evaluate the differences between both nucleus and edge and between the two areas (lagoon *vs* ocean). In addition, we also compared the isotopic signatures of the two sets of otoliths collected during the expeditions of 1994 and 2006. Before statistical testing, the normality of data was examined by Kolmogorov-Smirnov test.

RESULTS

$\delta^{18}O$ and $\delta^{13}C$ values of the lagoon and ocean waters

A clear isotopic difference of $\delta^{18}O$ values occurred between the surface waters of the Taiaro lagoon and those of the adjacent ocean (Table II). In 2006, $\delta^{18}O$ values of the lagoon waters (~ 1.8 ‰ SMOW) were enriched by around 0.8 ‰ compared to the ocean surface water (~ 0.97 ‰ SMOW). In 1994, $\delta^{18}O$ values of the lagoon waters (~ 1.8 ‰ SMOW) were enriched by around 1 ‰ compared to the ocean surface water, leading to an enrichment of ~ 0.2 ‰ (SMOW) between the years 1994 and 2006. $\delta^{13}C$ values (DIC, dissolved inorganic carbon) of the ocean waters ($\delta^{13}C$ = 1.4 ‰ PDB) were enriched by around 1.2 ‰ compared to the lagoon water (Dufour *et al*. 1998).

Stable isotopes in otoliths

For year 2006, a total of 19 pairs of $\delta^{18}O$ and $\delta^{13}C$ val-

Table II. – Values of $\delta^{18}O$ measured in waters in and around Taiaro Atoll. $\delta^{18}O$ values are expressed relative to international standard: SMOW (Standard Mean Ocean Water). Enrichment in $\delta^{18}O$ corresponds to the ratio lagoonal waters vs ocean waters. $\delta^{18}O$ in 1994 from Dufour *et al*. (1998).

Site	$\delta^{18}O$ in 1994	$\delta^{18}O$ in 2006
Lagoon surface	1.81	1.84
Lagoon 20 m	1.83	1.81
Ocean surface	0.78	0.97
Enrichment Lagoon *vs* Ocean	1.04	0.85

Table III.- Stable isotope values measured in otoliths of fish collected in 1994 and 2006.

Site / Date	Oxygen ‰				Carbon ‰		
	N	Mean ± sd	Min.	Max.	Mean ± sd	Min.	Max.
Lagoon 1994	40	-0.17 ± 0.24	-0.66	0.24	-5.00 ± 1.00	-7.44	-3.33
Ocean 1994	17	-1.19 ± 0.17	-1.47	-0.96	-3.70 ± 2.39	-7.60	-0.47
Lagoon 2006	75	-0.13 ± 0.33	-0.87	0.52	-5.39 ± 1.56	-8.84	-0.94
Ocean 2006	38	-0.94 ± 0.22	-1.55	-0.58	-5.67 ± 1.60	-8.49	-2.36

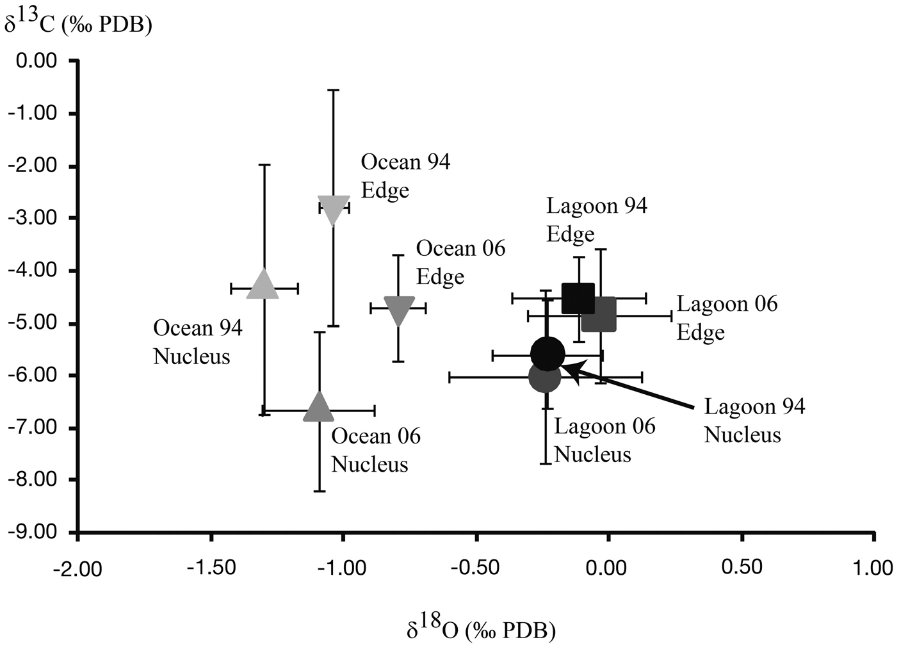

Fig. 2. – Stable isotope ratios of oxygen and carbon measured in nucleus and edge of fish otolith from lagoon and open ocean in 1994 and 2006.

Table IV.- Stable isotope signatures expressed in ‰ PDB of reef fish otoliths from the ocean and the lagoon in Taiaro Atoll in 1994 (from Blamart *et al*. 2002) and 2006 (this study). n = number of otoliths analyzed, SD = Standard Deviation.

		Oxygen (‰)				Carbon (‰)			
		n	Range (Min.; Max.)	mean	SD	n	Range (Min.; Max.)	mean	SD
Ocean 1994	Nucleus	10	-1.47; -1.00	-1.30	0.11	10	-7.60; -1.11	-4.34	2.26
	Edge	7	-1.13; -0.96	-1.04	0.05	7	-5.49; -0.46	-2.78	2.07
Lagoon 1994	Nucleus	18	-0.64; 0.11	-0.23	0.20	18	-7.44; -4.11	-5.58	1.01
	Edge	22	-0.65; 0.23	-0.11	0.24	22	-5.90; -2.81	-4.52	0.79
Ocean 2006	Nucleus	19	-1.55; -0.73	-1.10	0.21	19	-8.49; -2.36	-6.67	1.47
	Edge	19	-0.94; -0.58	-0.80	0.10	19	-6.16; -3.18	-4.70	1.00
Lagoon 2006	Nucleus	35	-0.87; 0.44	-0.24	0.35	35	-8.84; -2.75	-6.01	1.64
	Edge	40	-0.69; 0.52	-0.04	0.26	40	-7.94; -0.94	-4.84	1.26

ues were obtained for both the nucleus and edge of oceanic reef fish otoliths. A total of 40 δ^{18}O and δ^{13}C values at the edge and 35 in the nucleus were obtained for the lagoonal fish. The data are summarized in Table III together with the 1994 data set (Blamart *et al*. 2002). The δ^{18}Ooto mean values of the otoliths from the lagoon (–0.17 ± 0.24 in 1994; –0.13 ± 0.33 ‰ PDB in 2006) are enriched by about 1 ‰ compared to the δ^{18}Ooto mean values of the otoliths from the ocean (–1.19 ± 0.17 in 1994; –0.94 ± 0.22 ‰ PDB in 2006). This difference corresponded to the O-isotopic variation measured between seawaters from the lagoon and the ocean. There is a strong positive correlation between δ^{18}Ow values and salinity, with the lowest δ^{18}Ow values associated with the less saline oceanic waters. The pooling of the 2006 and 1994 datasets clearly showed that the samples from the open ocean and those from the lagoon have their own isotopic signatures (Fig. 2). For the two separate areas considered here, the open ocean and the closed lagoon, stable isotopic composition of otolith nuclei showed distinct δ^{18}O signatures (Table IV) that could separate reef fish into different subpopulations.

In the ocean, globally, the mean δ^{18}Ooto values of coral reef fish were the following (Table IV, Fig. 2): –1.10 ± 0.21 ‰ PDB; range –1.55 to –0.73 in the nuclei and, –0.80 ± 0.10 ‰ PDB; range to –0.94 to –0.58 in the edge. Mean δ^{13}Coto values of the otoliths range from –6.67 ± 1.47 ‰ PDB (range –8.49; –2.36) and –4.70 ± 1.00 ‰ PDB (range –6.16; –3.18) for nuclei and edge respectively. Both C-O isotopic ratios showed an increase from the nucleus to the edge.

In the closed lagoon, the range of variations of δ^{18}Ooto values was the following (Table IV, Fig. 2): –0.24 ± 0.35 ‰ PDB (–0.87; 0.44) and 0.04 ± 0.27 ‰ PDB (–0.69; 0.52) in the nuclei and the edge, respectively. Mean δ^{13}Coto values were: –6.01 ± 1.64 ‰ PDB (–8.84;

Comparison	Isotope	Zone	t	df	P value	
Nucleus vs Edge						
Lagoon 2006	$\delta^{18}O$		-2.79	73	< 0.01	Nucleus < Edge
	$\delta^{13}C$		-3.43	73	< 0.01	Nucleus < Edge
Ocean 2006	$\delta^{18}O$		-5.47	36	< 0.001	Nucleus < Edge
	$\delta^{13}C$		-4.70	36	< 0.001	Nucleus < Edge
Lagoon vs Ocean						
2006	$\delta^{18}O$	Nucleus	9.44	52	< 0.001	Lagoon > Ocean
		Edge	-11.89	57	< 0.001	Lagoon > Ocean
	$\delta^{13}C$	Nucleus	1.43	52	NS	
		Edge	0.42	57	NS	
1994	$\delta^{18}O$	Nucleus	14.89	26	< 0.001	Lagoon > Ocean
		Edge	9.60	27	< 0.001	Lagoon > Ocean
	$\delta^{13}C$	Nucleus	-1.92	26	NS	
		Edge	3.16	27	< 0.01	Lagoon > Ocean
1994 vs 2006						
Lagoon	$\delta^{18}O$	Nucleus	-0.09	51	NS	
		Edge	1.12	60	NS	
	$\delta^{13}C$	Nucleus	-0.99	51	NS	
		Edge	-1.05	60	NS	
Ocean	$\delta^{18}O$	Nucleus	-2.80	27	< 0.01	1994 < 2006
		Edge	-5.74	24	< 0.001	1994 < 2006
	$\delta^{13}C$	Nucleus	3.22	27	< 0.01	1994 > 2006
		Edge	3.03	24	< 0.01	1994 > 2006

Table V. – Results of student t-test comparison between isotopic signatures of nucleus and edge of otoliths from fish captured in lagoon and in ocean for both years. NS = Non significant

Table VI.– Mean values of the stable isotope signatures (in ‰ PDB) of reef fish otoliths (nucleus and edge) from the ocean and the lagoon in Taiaro Atoll (1994 and 2006), and of the values of the isotopic signatures of the water (in ‰ SMOW). The temperatures were calculated from these values.

		N	δ^{18}Ooto	δ^{18}Ow	Temperature (°C)
Ocean 1994	Nucleus	10	-1.30	0.78	29.0
	Edge	7	-1.04	0.78	27.8
Lagoon 1994	Nucleus	18	-0.23	1.82	28.9
	Edge	22	-0.11	1.82	28.3
Ocean 2006	Nucleus	19	-1.10	0.97	29.0
	Edge	19	-0.80	0.97	26.5
Lagoon 2006	Nucleus	35	-0.24	1.82	28.9
	Edge	40	-0.04	1.82	28.0

–2.75) and –4.84 ± 1.26 ‰ PDB (–7.94; –0.94), respectively. $\delta^{18}O$ and $\delta^{13}C$ values corresponding to the nucleus exhibited lower values than those of the edge mainly in the $\delta^{13}C$ values. The isotopic signatures showed significant differences for the nucleus and the edge between both areas and years studied. The $\delta^{18}O$ of the nucleus and of the edge were higher in the lagoon than in the ocean for both years.

Comparison 1994/2006

$\delta^{18}O$ values

Regarding the $\delta^{18}O$ values of otoliths from the lagoon, no significant difference was recorded between the two years for the δ^{18}Ooto mean values for the nucleus and for the edge (Table V). The range of variations of δ^{18}Ooto values of all the reef fish in the lagoon was very similar, –0.66 to 0.24 ‰ and –0.87 to 0.52 ‰ PDB, respectively in 1994 and 2006. Isotopic temperatures calculated from δ^{18}Ooto and δ^{18}Ow give undistinguishable values at 28.6 and 28.8 °C (both ± 1 °C) respectively for 1994 and 2006 showing stability over the decade (Table VI).

In the ocean, the δ^{18}Ooto values of reef fish ranged from –1.47 to –0.96 and –1.55 to –0.58 ‰ PDB in 1994 and in 2006, respectively. Moreover, the δ^{18}Ooto mean (SD) values (nucleus and edge) in the ocean were significantly different in 1994 (1.20 ± 0.17 ‰) and in 2006 (–0.94 ± 0.22 ‰). The difference of the edge of otoliths 1994 *vs* 2006 was about 0.25 ‰ PDB in $\delta^{18}O$ (Tables IV and V).

$\delta^{13}C$ values

The $\delta^{13}C$ of the nucleus was slightly higher in the ocean than in the lagoon in 1994. $\delta^{13}C$ oto values of the fish from the lagoon were –5.00 ± 1.00 ‰ and –5.39 ± 1.56 ‰

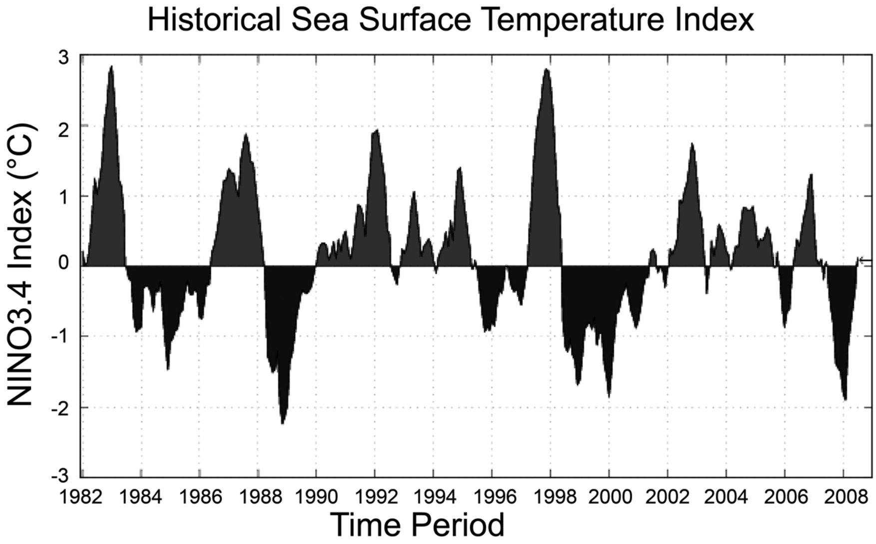

Fig. 3. – Variations of the Sea Surface Temperature Index from 1982 to 2009 (data from the IRI data library).

PDB in 1994 and 2006 respectively (Table III); and δ^{13}C oto values of the open ocean were –3.70 ± 2.39 ‰ and –5.67 ± 1.60 ‰ in 1994 and 2006, respectively (Table V).

δ^{13}C increased through life whatever the site and the year (Table IV). Nuclei δ^{13}C were lower than corresponding values obtained from the edge. In both cases (Table V), the differences were statistically significant ($p < 0.001$).

DISCUSSION

The stable isotope analysis of coral fish otoliths provided information on the ambient environmental conditions that fish experienced in and around Taiaro Atoll throughout their life history and between two different periods of time. Numerous studies suggest that otoliths (*sagittae*) reach or are close to the O-isotope equilibrium during their formation (Devereux 1967, Campana 1999). This implies that O-isotope compositions of reef fish otoliths can be used as palaeo-thermometer whenever δ^{18}O value of seawater is known (Kalish 1991, Iacumin *et al.* 1992, Thorrold *et al.* 1997), with the underlying assumptions that the O-isotope records are continuous through time. Otolith isotopic values vary on both a spatial and temporal basis.

δ^{18}O and temperature

δ^{18}O values of otoliths and waters from the lagoon suggested stable conditions during the last decade whereas their counterparts from the ocean indicated more variable environmental conditions. This result is reinforced by the shape analysis study on the same sample batch used for geochemistry (Anonymous 2006). These results indicated different morphological patterns between ocean and lagoon otoliths, but no significant difference between the years 1994 and 2006 in the lagoon, whereas a slight separation was observed for the ocean. This confirmed that the fish from the lagoon achieved their complete life cycle in the lagoon.

In 1994 temperature estimates derived by combining δ^{18}Ooto values of the ocean reef fish and corresponding water indicated a temperature in the range of 28.9 ± 0.5 °C. For the fish from the lagoon, a temperature in the range of 28.9 to 28.3 was calculated. These temperature estimates are not significantly different and both temperatures, within the analytical errors, are in good agreement either with those measured by other studies (Dufour *et al.* 1998, Blamart *et al.* 2002) and those given by the Levitus & Boyer data base (1994).

In 2006, a difference of 0.25 ‰ in the δ^{18}Ooto values of the ocean reef fish, compared to 1994, is in favor of a change of the variables (temperature and/or salinity) of the ocean waters. Two hypotheses could be proposed to understand this variability i) global change; ii) fish growth.

i) The expected temperature driven variation of δ^{18}O of aragonite should be about 0.2 ‰ per °C and vary inversely with T °C (e.g., Grossman & Ku 1986, Thorrold *et al.* 1997). The δ^{18}Ow signature of the ambient sea water correlates positively with salinity from 0.27 ‰ to 0.42 ‰ per unit of salinity (Corrège 2006). The δ^{18}Ow does not vary much, or at least not enough to overwhelm the seasonal temperature effect on the otolith isotopic composition. Change in salinity in the Pacific is less than 0.5. Consequently, temperature should dominate the mean otolith δ^{18}O composition observed for the ocean fish in 2006 (–0.94 ± 0.22 ‰). This value is in favor of a decrease of temperature in contrast to the global warming observed in the past 30 years, shown by Delcroix & Cravatte (2009). Sea surface temperature has warmed over about the past

30 years (0.4 °C) significantly as global climate has warmed over the past century (Jones *et al.* 2001). However, the major source of inter-annual climate variability is the ENSO phenomenon. ENSO has two phases: during El Nino phase the surface of the water is warmer whereas it is colder during La Nina phase. The record of SST index shows inter-annual variations characterized by negative SST index (Fig. 3) from 1998 to 2002 and in 2006 (Delcroix & Cravatte 2009), in accordance with the higher otolith $\delta^{18}O$ value observed in ocean fish in 2006.

ii) However, each otolith records the specific SST conditions under which the fish grew. Moreover, the fish are not sessile and their profiles reflect a mean of the local waters in which they develop. In our study, fish are 6 to 9 years old. They had experienced cooler conditions in their early years of life, between 1998 and 2002, when growth was at a maximum, suggesting that the increase in the otolith $\delta^{18}O$ composition observed did not only reflect the recent habitat temperature conditions, but the previous ones under which they have grown. The similarity in $\delta^{18}O$ in ocean otolith nuclei (2006) and edge (1994) suggests that larvae and adult fish live in similar ocean conditions, whereas the differences in $\delta^{18}O$ in ocean otolith edge (1994 *vs* 2006) indicates that fishes experienced different environmental water conditions between years (Table V, Fig. 2). Thus, the O-isotope composition of ocean fish seemed to record the variability of the ocean system. Another explanation for the drop of temperature calculated between 1994 and 2006 from fish otolith is that fish are recent migrants from cooler environments (such as deeper areas).

The lagoonal waters showed uniformity between 1994 (data from Dufour *et al.* 1998) and 2006, consistent with a lack of notable input of ocean waters. The $\delta^{18}O$oto values of the lagoon reef fish were not significantly different in 2006 compared to 1994, and a temperature not very different from 1994 may be calculated for 2006 (29 °C). No difference appeared between the two years, showing stability in time for the temperature and salinity consistent with the isolation of the lagoon waters from the ocean. Combining the $\delta^{18}O$ values of the nuclei of otoliths from the lagoon with the $\delta^{18}O$ of the lagoon water, a temperature of 29.2 ± 1.5 °C is found (Table VI). This temperature is indistinguishable from the temperature measured in the lagoon and implies that the fishes currently found in the lagoon have spent their larval stage in the lagoon.

$\delta^{13}C$

The $\delta^{13}C$ values of the otoliths (nuclei or outer parts), either from the ocean or from the lagoon, appear too depleted to be at the isotopic equilibrium. This disequilibrium can reach 6 to 7 ‰ in our case and cannot be explained either by a variation of the temperature during the formation of the otoliths or a change in the $\delta^{13}C$ values of the surface waters that are too small to account for such $\delta^{13}C$ depletion. Experimental studies (Fritz & Poplawski 1974, Iacumin *et al.* 1992, Schwarcz *et al.* 1998, Solomon *et al.* 2006) suggest a link between the metabolic activity and the $\delta^{13}C$ values of the carbonates. More specifically, Kalish (1991) determined that the proportion of carbon derived from the metabolism ($-15 > \delta^{13}C > -25$ ‰) is mainly a function of the dietary regime and the oxygen consumption. The remainder of the otolith carbon came from the dissolved inorganic carbon (Solomon *et al.* 2006). High metabolic activity, as in the case of reef fishes, induces depleted $\delta^{13}C$ values of the carbonates. This can be amplified by the food source which changes from plankton ($\delta^{13}C$ at –20 to –25 ‰) at the larval stage to a specific dietary regime at the adult stage. These changes are recorded in the $\delta^{13}C$ values of the otoliths.

Differences in $\delta^{13}C$ measured in nuclei between lagoon and ocean reflected changes in the food eaten. The lagoon is poorer in zooplankton than the ocean and three taxa (decapods larvae, ostracods and copepods) accounted for 90 % of the zooplankton (Carleton & Doherty 1998). So this low plankton diversity in the lagoon restricts the choice of food for larval fishes, represented here through the restricted $\delta^{13}C$ values of the nuclei. The relationship between $\delta^{13}C$ of plankton and well defined water masses may be explained because each water mass is characterized by its specific temperature and distribution of planktonic species (Fontugne & Duplessy 1981).

Differences exist between species and between life stages in the ocean. During larval life, all $\delta^{13}C$ values of the otoliths in both the ocean and the lagoon are in favour of food essentially based on various groups of zooplankton (various zooplankters). During adult life in the open ocean, all $\delta^{13}C$ values of the outer parts of the otoliths differ between species because fish became herbivore (*Acanthurus triostegus*), carnivore (*Epinephelus merra*) or they graze on sessile invertebrates (*Chaetodon ulietensis*). In the lagoon, if differences exist between herbivorous fishes and other consumers, it remains difficult to separate carnivorous species from grazers on invertebrates.

In conclusion, on the basis of stable isotope compositions of the otoliths recorded on coral reef fish species collected respectively in 1994 and in 2006 in and around Taiaro lagoon (Tuamotu Archipelago of French Polynesia), the change in oceanic sea surface temperature (SST) in twelve years has been tested. Our results demonstrate the potential of otolith isotope records to serve as indicators of climatic change in ocean waters. Nevertheless, interpreting scale isotope data is complicated by the fact that the pattern of isotope composition in otoliths varies when fish grow. Nuclei (larval stage) of fish otoliths from the lagoon or the ocean are at O-isotopic equilibrium with the surrounding waters. The $\delta^{18}O$ values of reef fish otoliths from the lagoon are enriched by 1 ‰ compared to the otoliths from the ocean. This difference also corresponds to the O-isotopic variation between lagoon and ocean water. This attests that the lagoonal populations achieved a complete biological cycle without migration at the larval stage to the open ocean. The outer parts of fish otoliths from the two populations showed a slight departure (> 0.2 ‰) from O-equilibrium which may be related to changes in habitat and diet between larval and adult stages.

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