Use of bomb radiocarbon to validate otolith section ages of red snapper *Lutjanus campechanus* from the northern Gulf of Mexico

Abstract—The red snapper *Lutjanus campechanus* is an important recreational and commercial fish species in the northern Gulf of Mexico. Management approaches have varied in part because of uncertainty of their longevity. Snapper ages have been based on presumed otolith annuli; however, this methodology has not been validated for all age classes. A recent technique to validate otolith age utilizes the increase in oceanic ^{14}C resulting from atmospheric testing of nuclear bombs during the 1950s and 1960s. Analyses of annuli from living corals and fish otoliths from 1900 to the present have documented that elevated ^{14}C input has occurred throughout the world's oceans. We validated otolith section age estimates through accelerator mass spectrometry analysis of bomb-produced ^{14}C in red snapper (otoliths) hatched before, during, and after the nuclear testing periods. Delta ^{14}C data from the otoliths of red snapper with presumed birth dates between 1960 and 1973 clearly reflect the sharp increase in oceanic radiocarbon attributable to previous nuclear testing. Similarities between the otolith and nearby coral $\Delta^{14}C$ chronologies suggest that annulus-based age estimates of red snapper are valid on average to within 1–3 yr. In addition, this study provides the first carbonate bomb radiocarbon time series from the northern Gulf of Mexico.

The red snapper *Lutjanus campechanus* is one of the more important recreational and commercial fish species in the northern Gulf of Mexico (Shirripa and Legault 1999). Management approaches to all species are sensitive to various life history parameters, particularly longevity. Methods previously used to estimate ages of fishes include counts of annuli deposited on scales, whole otoliths, and otolith sections. These presumed annuli may or may not be deposited annually (Summerfelt and Hall 1987). Results from early red snapper age and growth studies have been inconsistent, but more recent work has resulted in increased estimates of longevity (Render 1995). Despite a lack of comprehensive otolith annulus validation studies, counts of annuli from sagittal otolith sections are now considered the best estimator of age for red snapper, as well as most fish species, from the northern Gulf of Mexico (Shirripa and Burns 1997; Wilson and Nieland in press). Despite the acceptance of this technique, a peer review report criticized the validity of red snapper age estimates from the Gulf of Mexico, mainly because of accounts of unusually old fish (MRAG Americas, Inc. 1997). Independent validation of the conventional otolith section technique used to age fish is critical for effective management strategies (Beamish and McFarlane 1983; Wilson and Nieland in press).

There are several accepted age validation methodologies available for teleosts, but all lack the ability to approach the task independently. Mark-recapture and tag-recapture studies have been used for many shallow-water fish species, but the low number of recaptures, the time involved, and possible errors associated with specimen measurement limit the usefulness of these techniques (Shirripa and Burns 1997). The most widely used method is the analysis of marginal increments (Beckman and Wilson 1995). Wilson and Nieland (in press) used increment analysis to validate otolith annulus formation in red snapper up to age 30 yr and reported that opaque zones were deposited between November and June. Marginal increment validation of red snapper age becomes problematic when dealing with the small sample sizes of older fish (>15 yr). For example, of the 3,757 red snapper randomly sampled from the Gulf of Mexico commercial fishery between March 1995 and February 1999, only 13 (0.3%) were older than age 15 yr, and only 5 (0.1%) were older than age 30 yr (D. L. Nieland pers. comm.). Radiometric age determination that uses the $^{210}Pb/^{226}Ra$ isotopic pair in otoliths has proved successful for several marine species, including three tropical lutjanids (Milton et al. 1995). Recent advances in $^{210}Pb/^{226}Ra$ determination technology have both enabled analysis of smaller otolith sample masses (<1 g) and increased precision in the measurement of extremely low levels of ^{226}Ra (Andrews et al. 1999). However, the relatively large errors associated with whole otolith (Bennett et al. 1982) and otolith core (Andrews et al. 1999) radiometric age estimates (in comparison to conventional otolith ageing) indicate that these techniques may be more suited to differentiating between extreme estimates of longevity.

Perhaps the latest and most promising approach to age validation uses a quantitative measurement of nuclear bomb-produced ^{14}C that is accumulated in carbon-containing hard parts of marine organisms over a known time period of unique atmospheric chemistry. The prerequisites for this technique are hard parts of organisms (i.e., otoliths, coral exoskeletons, bivalves, and calcareous algae) accreted during the atmospheric testing period of nuclear weapons (1958–1965). Elevated ^{14}C activity has been observed in hermatypic corals (Druffel 1980, 1989), and it is this dramatic increase in ^{14}C activity that has been used as a time-specific marker. More recently, analysis of bomb radiocarbon has been used to validate age estimates derived from hard parts in marine fishes (Kalish 1993; Campana and Jones 1998) and rhodoliths (Frantz et al. 2000). As had been expected, the general trend observed in the literature is that hard parts of living organisms accumulate bomb-produced ^{14}C at a rate similar to that of corals from the surrounding waters (Kalish 1993; Campana 1997; Frantz et al. 2000). Provided that archival otolith samples are available from the 1950s, 1960s, and 1970s, this age validation technique is relatively straightforward and is considered to be the most advanced and accurate method of fish age validation available today (Campana 1999).

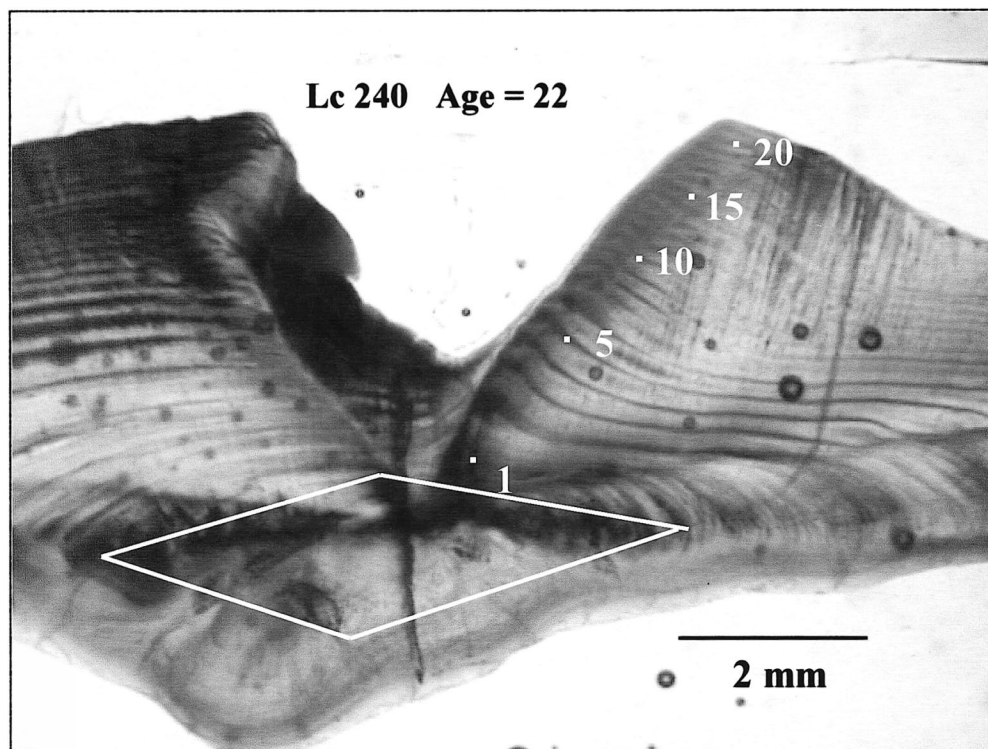This study was designed to determine whether ages de-

Fig. 1. Transverse section of an adult red snapper (ID = 240) presumed to be 22 yr old. The scale bar represents 2 mm. The white rectangle surrounding the otolith core depicts the period of growth (≤1 yr) extracted and analyzed for radiocarbon.

rived from sectioned sagittae indicate true (radiocarbon) age for red snapper from the northern Gulf of Mexico. We hypothesized that the radiocarbon chronology taken from the earliest formed portion (≤1 yr) of red snapper otoliths collected during the nuclear testing era of 1950s to 1960s would be similar to radiocarbon values observed in Caribbean Sea coral reference samples.

Methods—Red snapper ($n = 26$) were sampled from the commercial and recreational fisheries of the northern Gulf of Mexico between 1990 and 1998. For each specimen, one otolith was sectioned for aging purposes, and the other was prepared for radiocarbon dating. Otolith sections used for age estimation were examined with a compound microscope and transmitted light at 40× to 100× magnification (Fig. 1). Age estimates were based on annuli counted along the medial surface of the transverse section ventral to the sulcus (Wilson and Nieland in press).

To obtain the oldest portion of the otolith for radiocarbon analysis, otoliths were embedded in araldite epoxy and thin sectioned (~1 mm in thickness) through the otolith core with a low-speed diamond saw. The sections were then washed with water, dried, and placed under a dissecting microscope. The first year of growth on each otolith cross-section was identified and the outer boundaries marked with a felt-tip pen. The otolith core region targeted for removal was ~6 mm in width, 2–3 mm in height, and 1–2 mm wide. Extraction of the earliest formed portion of the otolith, hereafter referred to as the "otolith core," was modified from the

technique developed by Campana and Jones (1998). Otolith sections were mounted onto construction paper with masking tape to hold the section in place, and the core area was isolated with a high-speed, hand-held drill (Dremel tool) fitted with a carbide cutoff wheel. A new cutoff wheel was used for each otolith section, to minimize cross-contamination among samples. On several occasions, the core material would crack into several smaller pieces during extraction, rendering pieces that were literally too small (<3–5 mg) to withstand the acid-leaching necessary prior to accelerator mass spectrometry (AMS) submittal. In this event, two sections (from the same otolith) were needed to obtain the minimal otolith mass of 9–12 mg $CaCO_3$ necessary for AMS quantification of radiocarbon. The cores were then sonified (2×) in double distilled deionized water and allowed to air dry. Otolith samples were leached in a 10% HNO_3 solution to remove any contaminants that may have adhered to the otolith during the core extraction procedure. Cores were rinsed in double-distilled deionized water, allowed to air dry, weighed to the nearest 0.1 mg, and submitted to the AMS facility in acid-washed 20-ml glass scintillation vials. The mean sample weight submitted for AMS analysis was 10.7 mg.

At the AMS facility, otolith cores underwent acid hydrolysis with 85% phosphoric acid to yield CO_2, which was then made into graphite (pure C) by reduction at high temperature under vacuum. The graphite was pressed onto a target, loaded on the AMS unit, and analyzed for radiocarbon. Samples were also analyzed for ^{13}C, to correct for natural and ma-

Table 1. List of red snapper *Lutjanus campechanus* otoliths analyzed for stable carbon and bomb radiocarbon.

NOS-AMS number	I.D.	FL (mm)	Date caught	Otolith section age (yr)	Birth date	Otolith wt (mg)	AMS wt (mg)	$\delta^{13}C$ (‰)	$\Delta^{14}C$ (‰) (mean ± SD)	
OS-23901	56	829	1998	55	1943	4607.3	15.8	−3.0	−61.0	4.4
OS-23902	331	851	1995	48	1947	4576.5	17.8	−3.0	−47.6	3.9
OS-23904	21	900	1991	43	1948	4384.8	10.2	−3.3	−52.0	3.6
OS-23903	17	890	1991	41	1950	4594.0	12.5	−3.4	−64.3	3.3
OS-23905	65	810	1998	44	1954	4463.0	16.1	−3.7	−58.9	3.4
OS-23906	334	825	1995	41	1954	4234.2	13.0	−2.9	−75.2	3.1
OS-23907	16	840	1991	36	1955	3291.3	6.3	−2.6	−65.3	3.2
OS-23908	122	775	1990	30	1960	3298.6	12.9	−2.7	−3.1	3.8
OS-23909	640	862	1996	36	1960	3547.7	8.1	−3.6	−3.4	4.0
OS-23910	2656	820	1998	38	1960	3156.4	10.4	−3.3	−50.7	3.3
OS-23912	12	870	1991	30	1961	3686.0	9.1	−3.6	7.3	2.8
OS-23914	1353	870	1992	31	1961	3530.6	8.8	−3.0	−14.8	5.2
OS-23911	1381	836	1992	29	1963	3531.5	12.6	−2.8	61.6	3.1
OS-23917	2	840	1991	25	1966	3012.0	12.0	−2.0	112.4	3.5
OS-23913	24	870	1991	24	1967	4127.7	7.0	−3.2	99.0	3.7
OS-23918	20	850	1991	22	1969	2826.0	11.7	−3.2	151.5	3.7
OS-23916	14	890	1991	21	1970	2718.0	8.5	−3.8	107.9	4.7
OS-23915	15	900	1991	20	1971	3099.0	7.2	−2.9	150.3	3.7
OS-23919	1393	811	1992	20	1972	2694.4	9.6	−1.9	119.6	5.0
OS-23920	68	768	1998	25	1973	3120.1	10.4	−2.7	164.2	3.7
OS-23921	1477	890	1992	19	1973	2228.7	9.8	−2.6	140.5	5.2
OS-23922	240	810	1995	22	1973	3349.7	10.3	−2.6	164.1	5.5
OS-23923	19	820	1991	15	1976	2547.9	7.0	−2.3	143.6	4.6
OS-23924	8	750	1991	7	1984	1453.3	9.9	−3.6	122.5	3.6
OS-23925	3006	734	1998	9	1989	1528.0	12.1	−2.8	108.1	5.2
OS-23926	3121	274	1998	2	1996	201.1	9.2	−3.5	85.3	3.3
OS-23929*	1381	836	1992	29	1963	3531.5	12.6	−3.3	62.7	5.2
OS-23930*	12	871	1991	30	1961	3686.0	9.1	−2.9	−8.6	13.7
OS-23931*	240	810	1995	22	1973	3349.7	10.3	−2.9	177.4	9.1

AMS wt, the amount of otolith separated from the otolith section and submitted for accelerator mass spectrometry (AMS) radiocarbon analysis; FL, fork length.
* Blind duplicate samples used to test reproducibility of the AMS instrument used in this study.

chine fractionation effects. In addition to the 26 original samples submitted for radiocarbon analyses, 3 blind duplicates were analyzed to test the precision of the AMS instrument and methodology used in this study. Radiocarbon values from otolith cores were reported as $\Delta^{14}C$, the adjusted deviation from the radiocarbon activity of 19th century wood (Stuiver and Polach 1977).

Results—The red snapper used in this study ranged from estimated age 2 to 55 yr and were collected from the period 1990–1998 (Table 1). Otolith weight was a good indicator of age for fish age >15 yr ($n = 23$, $P = 0.0001$, $r^2 = 0.72$) (Fig. 2). As expected, there was no relationship between fork length and age for the same fish age >15 yr ($n = 23$, $P = 0.9539$, $r^2 = 0.0002$), which supports the concept that age length keys are not suitable for this species after age 15 yr, because most individuals have reached their approximate maximum size. Years of birth ranged from 1943 to 1996, which includes the time period of atmospheric testing of nuclear bombs.

Mean $\delta^{13}C$ values for red snapper otolith cores (mean ± SD = −3.00 ± 0.50) were similar to those reported in other fish age validation studies that used radiocarbon analyses. On the basis of the results of Quay et al. (1992) for the
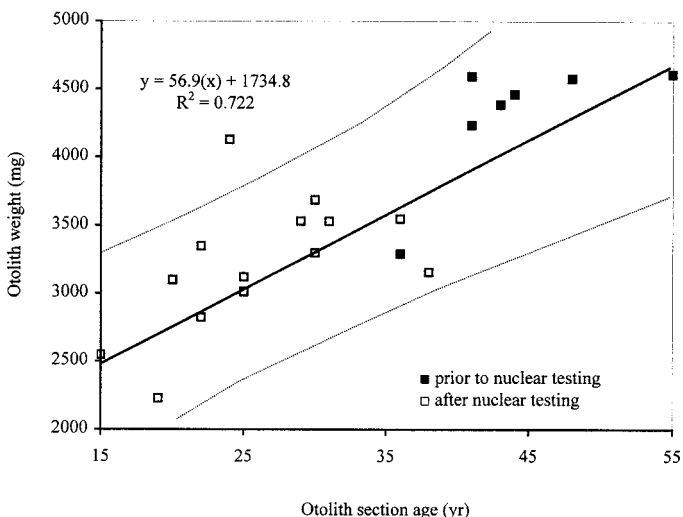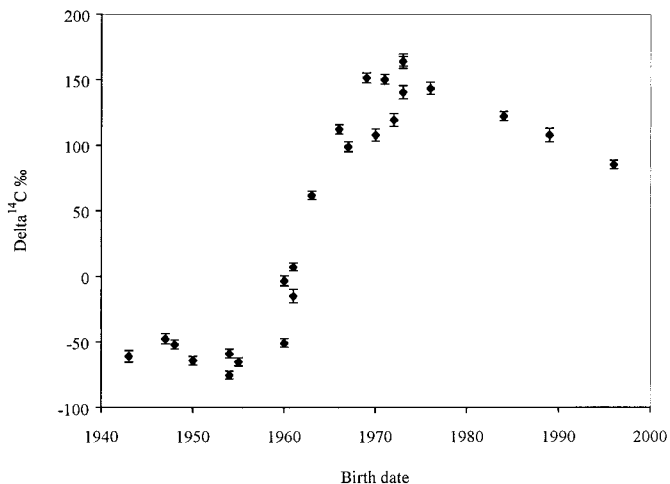

Fig. 2. Plot of otolith weight versus otolith section age for red snapper hatched prior to and after the atmospheric nuclear testing period. Dotted lines represent 95% confidence intervals.

Fig. 3. Δ^{14}C values (± 1 SD) of red snapper otolith cores plotted against birth date. Birth dates were estimated from otolith sections.

Fig. 4. Plot of Δ^{14}C values versus date of calcification for red snapper *L. campechanus* (this study) from the northern Gulf of Mexico and corals from Bermuda (Druffel 1989), South Florida (Druffel 1989), and Belize (Druffel 1980).

Pacific Ocean from 1970 to 1990, we would expect to see a 0.4‰ decrease in δ^{13}C during this time period in the Gulf of Mexico. We observed a slight but visible decrease in δ^{13}C between 1970 and 1990, but the slope was not significantly different from 0 ($b = 0.0042$, $P = 0.6049$, $r^2 = 0.01$).

In addition to the 26 samples submitted to the AMS facility for δ^{13}C and Δ^{14}C analyses, three additional otolith samples taken from the original otolith samples were submitted as blind duplicates. There was close agreement between original and duplicate samples in both δ^{13}C and Δ^{14}C values, which indicates that the AMS processing and analysis methodology used in this study was unbiased and accurately repeatable (Table 1).

Δ^{14}C values in the earliest formed portion of red snapper otolith cores sharply increased from the time period 1960 to 1973 and slowly decreased after that (Fig. 3). Fish with birth dates (estimated from annulus counts) prior to 1960 had no measurable Δ^{14}C. There was a significant linear relationship between birth date and Δ^{14}C for red snapper with birth dates between and including 1960 and 1973 ($n = 15$, $P = 0.0001$, $r^2 = 0.89$). After a peak in 1973, radiocarbon concentration in red snapper otoliths showed a slow but steady decline to a low in 1996, the most recent birth date used in this study.

The red snapper otolith Δ^{14}C chronology from 1943 to 1984 is remarkably similar to previously published Δ^{14}C coral chronologies from Bermuda, South Florida, and Belize (Druffel 1980, 1989) (Fig. 4). In all studies, the rate of increase was most dramatic between 1960 and the early to mid-1970s. A general linear test indicated that Δ^{14}C chronologies between 1960 and 1973 taken from this study and corals from Bermuda (Druffel 1989), South Florida (Druffel 1989), and Belize (Druffel 1980) were not significantly different (analysis of covariance [ANCOVA] test for homogeneity of slopes, $df = 1$, MS = 97.67, $F = 0.19$, $P = 0.9059$) (ANCOVA test for equal intercepts, $df = 3$, MS = 1808.97, $F = 3.43$, $P = 0.0244$).

The radiocarbon values obtained from red snapper otolith cores prior to, during, and after the period of atmospheric testing of nuclear weapons were comparable to those values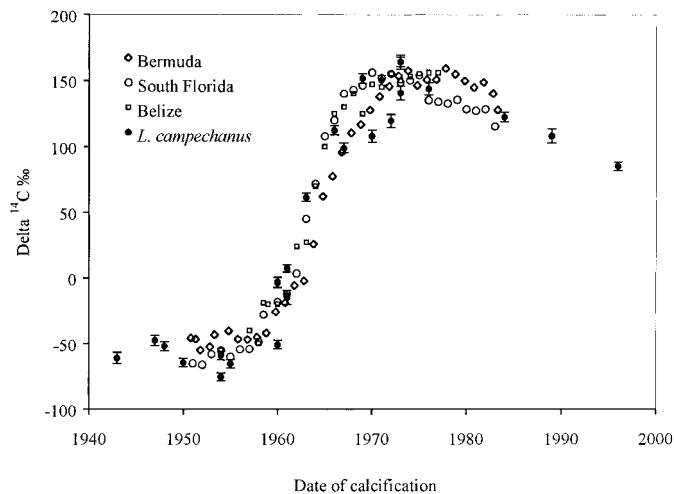 found in other radiocarbon-based age validation studies on marine teleosts (Kalish 1993; Campana 1997). The Δ^{14}C minimum (-75.2‰, 1954) observed in this study was similar to all other studies, because levels of natural ^{14}C > 0‰ in the world ocean did not exist prior to atmospheric testing of nuclear weapons.

Discussion—Radiocarbon chronologies based on AMS Δ^{14}C measurements of otoliths provide evidence that otolith section-based age estimates of red snapper from the northern Gulf of Mexico are valid. We are confident that red snapper live at least 55 yr. No measurable radiocarbon was detected in the cores of red snapper otoliths formed prior to the atmospheric testing period. Therefore, individuals with annulus-derived birth dates prior to ~1960 must be at least age 30–38 yr, irrespective of their date of capture. In addition, a positive linear relationship exists between otolith weight and otolith section age for red snapper at least age ≥15 yr, including those believed to have been hatched prior to atmospheric testing (Fig. 2). Unlike fish length and otolith size, otolith weight is a good indicator of fish age because it continues to increase throughout the life of the fish (Cardinale et al. 2000). Finally, the fact that variability between readers was so low for red snapper throughout all age classes indicates that age estimates derived from otolith sections of red snapper are valid throughout its life history (Wilson and Nieland in press). Radiocarbon-validated age estimates support the continued use of counting annuli on sagittal otolith sections as the most cost-effective age determination method for red snapper from the Gulf of Mexico.

Our results indicated that the pulse of radiocarbon in the northern Gulf of Mexico started around 1960, peaked around 1973, and has slowly declined until 1996, the most recent red snapper birth date examined. The fact that similar baseline Δ^{14}C values exist for red snapper and other corals, marine bivalves, and fishes studied from neighboring water bodies was not surprising. It is widely accepted that oceanic Δ^{14}C values > 0‰ did not exist prior to the onset of nuclear testing. Therefore, corals, bivalves, and fish otoliths with

Δ^{14}C values < 0‰ must have been formed prior to atmospheric testing.

The present study has provided the first radiocarbon chronology for the northern Gulf of Mexico. Δ^{14}C values observed in this study were similar to Δ^{14}C values recorded in living corals from Bermuda, South Florida, and Belize. Red snapper otoliths reached a Δ^{14}C maximum of 164.2‰ in 1973, which is consistent with post-bomb Δ^{14}C values reported for the world ocean (Broecker et al. 1985). The latitude of the general location of sample collection (28°N) coincides with the Δ^{14}C maximum observed for the northern hemisphere (Broecker et al. 1985). The Δ^{14}C maximum observed in red snapper from the Gulf of Mexico is exceeded only by the value observed in black drum *Pogonias cromis* from the temperate north Atlantic (Campana and Jones 1998). In that study, black drum year-of-birth Δ^{14}C values resembled the intermediate of surface oceanic (coral) and atmospheric values rather than those values observed at nearby coral reference sites. Campana and Jones (1998) speculated that the estuarine dependency of this species produced variable concentrations of radionuclides in individual fish. The clear, dramatic increase of Δ^{14}C in red snapper otolith cores from 1960 to 1973 and the fact that there are no significant differences between the slopes of red snapper and three coral Δ^{14}C time series during this period suggests that the radiocarbon levels in the northern Gulf of Mexico are similar to that predicted for the northern hemisphere (Broecker et al. 1985).

Radiocarbon dating has some sources of error and uncertainty that must be considered in every age validation study that is undertaken with use of that methodology. Failure to remove all portions of the otolith other than the earliest formed will undoubtedly lead to a faulty Δ^{14}C value. Grossly incorrect interpretation of otolith annuli would also have the same effect. If either one of these sources of error were present in these red snapper samples, the discrepancies would probably be seen in the Δ^{14}C time series, provided that the fish was hatched during the period of most rapid Δ^{14}C change (i.e., 1960–1973 in the northern Gulf of Mexico).

The use of bomb radiocarbon to validate fish age determination methodology has proven to be a precise, yet expensive, alternative to more conventional age validation techniques such as mark and tag-recapture, otolith increment analyses, and ^{210}Pb/^{226}Ra disequilibria analyses. Similarities between the otolith and nearby coral Δ^{14}C chronologies suggest that annulus-based age estimates of red snapper are valid on average to within 1–3 yr. The radiocarbon technique should prove suitable for other marine teleosts from the northern Gulf of Mexico, provided that these species occupy habitat similar to that of the red snapper. At present, the only drawbacks to the radiocarbon technique are the high costs involved (U.S. $275–$1,000 per sample) and the prerequisite that only fishes with birth dates in the 1960s and 1970s are suitable for age validation purposes. A carefully planned study could use as few as 10 fish hatched during the atmospheric testing period of 1960–1973, and the total cost would be much smaller than that spent on a typical age-validation study used by most laboratories. Despite the limitations of this technique, the analysis of bomb radiocarbon in otoliths is the simplest and most accurate approach to independent fish age validation available today.

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Mesozooplankton grazing effect on primary production: A global comparative analysis in marine ecosystems

Abstract—A comparative analysis of the importance of mesozooplankton (200–20,000 μm) as grazers of the phytoplanktonic primary production (PP) across a wide spectrum of marine ecosystems revealed mesozooplankton ingestion rates to increase nonlinearly with increasing PP. The slope of the log–log relationship between ingestion rates and PP was significantly <1, indicating a decline of relative importance of mesozooplankton grazing with increasing PP. The effect of mesozooplankton on PP (as the percent PP consumed per day) is moderate in most of the studies (mode 6%, mean 22.6%) and decreases exponentially with increasing productivity. Contrary to the common assumption, the size barrier imposed by dominant picoautotrophs does not always result in a lower grazing pressure in unproductive communities (we consider here those with PP < 250 mg C m^{-2} d^{-1}). Yet, the amount of phytoplanktonic carbon ingested per unit of mesozooplankton biomass is lower in unproductive than in moderate (250 to 1,000 mg C m^{-2} d^{-1}) and highly productive communities (>1,000 mg C m^{-2} d^{-1}). This observation, together with the generally low values of daily biomass-specific ingestions, suggests that alternative food sources (e.g., protozoans) must represent an important component of mesozooplankton diet in unproductive ecosystems. The relationships obtained in the study yield an estimate of 5.5 Gt phytoplanktonic C consumed per year in the global ocean, which represents ~12% of the oceanic PP.

Traditional views on the flow of carbon in planktonic food webs have been revised to assign an important role to microbial food webs (Azam et al. 1983) and to consider nonlinear effects, such as feedback and trophic cascade, as important structural factors (Pace et al. 1998; Calbet and Landry 1999). Similarly, copepods are no longer considered to be the main consumers of the phytoplanktonic primary production (PP) (Tsuda et al. 1989; Bradford-Grieve et al. 1998; Calbet and Landry 1999; Sautour et al. 2000) and apart from algae a sizable portion of their daily ration is also composed of heterotrophic flagellates and ciliates (Tiselius 1989; Fessenden and Cowles 1994; Calbet et al. 2000). Yet, mesozooplankton remain important consumers of phytoplankton carbon, particularly in productive ecosystems, where the classic linear food chain still appears to be the main path of carbon transfer. In productive ecosystems, sedimentation and advection are also important mechanisms of PP loss (Baines et al. 1994; Wassmann 1998). In contrast, these carbon losses appear to be low in unproductive ecosystems, where the efficient recycling of nutrients and organic matter minimizes carbon export. This recycling appears to be maintained largely by bacteria and small (<20 μm) protozoans (Azam et al. 1983; Sherr et al. 1988; Calbet et al. 2001). Moreover, picoplanktonic organisms, which are relatively unavailable to mesozooplankton predation are also responsible for an important proportion of the PP in these nutrient-poor systems (Agawin et al. 2000). As a result, mesozooplankton seem unlikely to efficiently exploit the primary production of unproductive ecosystems, except for some groups (e.g., tunicates and cladocerans), which may prey down to the picometer size fraction. Unfortunately, their abundance and effect have been traditionally neglected, and we lack knowledge on the relative importance of these groups in planktonic food webs (see review by Gorsky and Fenaux 1998).

Thus, the pattern depicted from the available information suggests an important removal of primary production by mesozooplankton in productive waters and a minor role in unproductive ecosystems. This view remains hypothetical and