TROPHIC LEVELS AND THE OBSERVATIONAL COMPLETENESS OF THE FOSSIL RECORD (*)

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ABSTRACT

Population density of benthic marine shelly species, as determined by their food requirements, seems to have an influence on the observational completeness of the fossil record of these potentially preservable faunas. Both comparisons made between life and death assemblages of bivalves and gastropods, and between Recent biocoenoses and Pleistocene molluscan faunas show that primary consumer species (filterers, browsers and detritivores) have a better chance of being incorporated into (and, subsequently, being sampled from) the fossil record than secondary consumer species (predators, scavengers and parasites). According to these results, it is suggested that the observational completeness of the fossil record of durably skeletonized species of invertebrates may be biased in favor of lower trophic level forms.

Keywords: Bivalves, gastropods, trophic levels, sampling biases, preservation potential, completeness of the fossil record.

RESUMEN

La densidad de población de las especies de invertebrados marinos bentónicos con concha, según viene determinada por sus requerimientos tróficos, parece influir en nuestro grado actual de conocimiento del registro fósil. Tanto las comparaciones efectuadas entre asociaciones vivas y muertas de moluscos bivalvos y gasterópodos, como entre las biocenosis actuales y la malacofauna pleistocénica, muestran que las especies de consumidores primarios (filtradores, herbívoros y detritívoros) tienen mayores oportunidades de incorporarse al registro fósil (y, posteriormente, ser muestreadas del mismo) que las de consumidores secundarios (predadores, necrófagos y parásitos). De acuerdo con estos resultados, se sugiere que la perfección aparente del registro fósil de las especies potencialmente conservables podría encontrarse sesgada en favor de las especies de nivel trófico más bajo.

Palabras clave: Bivalvos, gasterópodos, niveles tróficos, errores de muestreo, potencial de fosilización, perfección del registro fósil.

INTRODUCTION

The fossil record represents a non-random sample of the evolution of life on Earth through the geologic time: A relatively small number of the individuals and species that once existed in the past were finally preserved as fossils (taphonomic biases) and only few of them have been already collected from the geologic record (observational biases) (McKinney, 1991) (see Fig. 1). As a consequence, the record has traditionally been seen as highly incomplete.

A quantitative understanding of the completeness of the record is necessary for a proper undestanding of organic evolution (Anders *et al.*, 1987), but an appropriate measurement is still lacking, in part because different scales and categories of reference may be used to analyze palaeontologic completeness, such as ontogenetic, taxonomic or ecosystem completeness (for a review, see McKinney, 1991); it is also necessary to note that

completeness is in practice measured against some predetermined aim and therefore what matters is not that the fossil record is incomplete, but whether data incorporated in it are adequate to test theories (Paul, 1992).

If we consider only taxonomic completeness of potentially preservable marine species, the proportion recorded in the Phanerozoic fossil record may be up to 12 % (Valentine, 1989a): i.e., the group of reference is all durably skeletonized marine species, estimated in 2 million by Signor (1985), and the proportion of these species that was preserved is 12 % (McKinney, 1991).

Taphonomic (preservational) biases are due to 1) the intrinsic **fossilization potential** of organisms (i.e., presence of skeleton, mineralogical composition, size and shape of hard parts, life style and habit environment, etc.) and 2) to various **extrinsic factors** (i.e., mode of death, time of exposure of skeletal remains before burial, physicochemical weathering, bioerosion and encrusta-
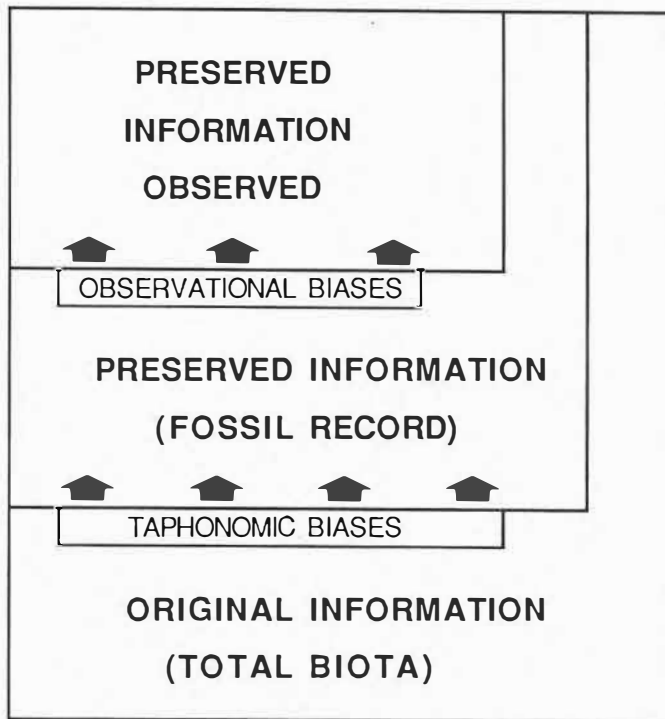
Figure 1. Completeness of the fossil record: Recorded and observed subsets of the original palaeobiological information. Based on an idea of Prof. Michael L. McKinney (pers. comm.).

tion, trampling, activity of carnivores and scavengers, dissolution, sorting, abrasion and breakage during transport, geochemical environment in the course of diagenesis, with textural, mineralogical and chemical changes of skeletal elements, selective solution and deformation, bioturbation and reworking, etc.) (Schopf, 1978; Müller, 1979; Shipman, 1981; Damuth, 1982; Staff et al., 1985, 1986; Kidwell and Bosence, 1991; Parsons and Brett, 1991; Tucker, 1991; Speyer and Brett, 1991).

Observational completeness in a subset of the preserved information locked in the fossil record (Fig. 1). Observational biases include: 1) **abundance** in the original palaeocommunities (i.e., population density) and **geographic range** of the fossil species (both favour their discovery); in addition, **stenotopic** species (which live in only one type of community and in limited environments) occur in palaeobiogeographically endemic conditions and tend to be more rare in the fossil record than **eurytopic** species (those adapted to a broader range of environmental conditions), which used to be more cosmopolitan (Boucot, 1990). 2) Their **age** (Cainozoic fossils have been more intensively studied than earlier ones). Outcrop areas of older sedimentary rocks are smaller than those of younger sediments, and sampling efficiency is therefore greater in the last ones, which explains in part the apparent trend of increase of diversity in marine invertebrates through the Phanerozoic; see Flessa and Sepkoski, 1978. Sediment ageing also causes information loss —by erosion, dissolution, etc.— of those fossils initially captured in the record. 3) Their **morphology** (big and elongate fossils are more

probably sampled from stratigraphic outcroppings, because a random cross-section or core will more probably intersect them, according to the laws of stereology); and 4) several rather **subjective factors** (palaeontologists have paid more attention to certain taxonomic groups, like molluscs; there are many geographic areas where the fossils are still relatively unstudied) (see the excellent discussion of McKinney, 1991, and references herein).

If we consider all together these potential biases, the mean percentage (87%) of durably shelly species (mainly bivalves and gastropods) of marine benthic communities that are also found dead at the thanatocoenoses (Kidwell and Bosence, 1991), and the slightly lower (but statistically significant) value of preservation (77%) that characterize Pleistocene molluscan assemblages in the Californian Province (Valentine, 1989b) seem both surprisingly high. These results should make us consider that deficiencies in the pre-Pleistocene fossil record of potentially preservable species would be caused by post-burial destruction (extreme diagenesis, erosion, tectonic activity and metamorphic processes) and not by an initial lack of shell accumulation in the early postmortem phase (Valentine, 1989b).

COMPILATION OF PRESERVABILITY PERCENTAGES

In this work I investigate the preservability potential of groups of marine shelly species (bivalves plus gastropods) that show different life strategies in order to obtain their trophic resources. Published data (Antia, 1977; Bosence, 1979; Cadée, 1968, 1984; Fresneda et al., 1984; Frey and Dörjes, 1988; Frey et al., 1987, 1988; Puig et al., 1984; Staff et al., 1985) on comparisons between live and dead assemblages (i.e., biocoenoses vs. thanatocoenoses) were used, and also between living and Pleistocene molluscan faunas (Kensley, 1985; Valentine, 1989b).

Species were arranged in two groups according to their feeding habits (if these aspects of their biology are known): primary consumers (including filter feeders, browsers and detritivores) and secondary consumers (predators, scavengers and parasites; i.e., carnivores). I use the historical trophic level concept, which has proved to be theoretically invalid (Cousins, 1987), only as a comprehensive way to refer to the food webs.

Preservability percentages of each trophic group were calculated from the number of potentially preservable species found in the living assemblages which were also recorded in Recent thanatocoenoses or in Pleistocene sediments, respectively. Given that most analyzed datasets are based on small sample sizes (less than thirty species), preservability percentages were calculated in both cases by first pooling all the studies together. I decided to pool among datasets obtained from diverse marine shelf habitats because many previous studies (summarized in Kidwell and Bosence, 1991) have shown no statistically significant differences among facies in the percentages of shelly species found live and also found dead at the same sites.

	Live biocoenoses vs. Dead thanatocoenoses	Recent biocoenoses vs. Pleistocene (fossil) faunas
Primary consumer species (filterers, browsers and detritivores) confidence intervals (p<0.05) of percentages	92.4% (452/489) {89.9% - 94.6%}	80.6% (386/479) {77.0% - 84.0%}
Secondary consumer species (predators, scavengers and parasites) confidence intervals (p<0.05) of percentages	86.7% (202/233) {82.1% - 90.8%}	72.0% (201/279) {66.6% - 77.1%}

Table 1. Preservability percentages of molluscan groups of shelly species (bivalves plus gastropods) established according to their trophic resources. Percentages were calculated pooling all analyzed datasets together.

RESULTS OF TROPHIC LEVELS COMPARISON

The results obtained are shown in Table 1. It must be stressed that this analysis considers only the molluscan shelled component of the benthic communities and not the total fauna. Comparison of live:dead assemblages of bivalve and gastropod species yields a somewhat higher global preservability percentage for primary consumers (92.4%) than that obtained for secondary consumers (86.7%); this difference is statistically significant ($p < 0.05$) according to a t-test.

Comparison between Recent molluscan faunas and Pleistocene ones provides in both trophic groups smaller preservation values than those of Recent thanatocoenoses, because taphonomic processes have operated (and biased) longer; mean preservation of lower trophic level species (80.6%) is again significantly different ($p < 0.01$) from the percentage of higher trophic level species (72.0%).

When bivalves and gastropolds are considered separately, or epifaunal species vs. infaunal ones, preservation values are similar in all cases (and not statistically different) if groups of the same food requirements are compared.

DISCUSSION AND CONCLUSIONS

The observed preservability differences between both trophic groups are congruent with those previously established using a smaller data set (Palmqvist, 1991) and are probably due to differences in the abundance of organisms in marine benthic communities related to their food requirements.

Primary consumer species exhibit higher population densities than secondary consumer ones, because the first group is located at the base of the energetic pyramid and the second at its top. According to exhaustive data compiled for land mammals in living ecosystems (Damuth, 1987; Peters, 1983), herbivores are from 4.8 to 6.9 times more abundant than predators of the same size (estimations obtained dividing the corresponding intercepts of log-log regressions for population density on body weight in both trophic levels); these values are similar to those considered for communities of benthic marine invertebrates (Stanton et al., 1981), although such detailed studies are still lacking in them.

Given that only a very small fraction of all produced shells will pass all taphonomic filters, the most abundant species will have more opportunities of undergoing fossilization, being sampled from sedimentary rocks by palaeontologists and then incorporated into the known fossil record. In addition, secondary consumer species are usually mobile, minute and have light shells (while primary consumers are sessile or not very vagile, large sized and with thicker shells to avoid predation) and many carnivorous gastropods have aragonitic shells which may be dissolved during diagenesis (Prof. Dr. Jordi Martinell, pers. comm.).

In the case of land mammals, the observational bias related to trophic levels appears to be similar to that calculated for marine shelly faunas: Only 17 out of 22 (77.3%) of European present-day living species of carnivores are known from the Pleistocene, while 61 out of 74 (82.4%) of the species of other orders were recorded (data on Pleistocene occurrences from Savaga and Russell, 1983). Nevertheless, in the terrestrial realm the taphonomic biases related to body size may be even greater (Behrensmeyer et al., 1979; Damuth, 1982; Palmqvist et al., 1992) and this is reflected in the percentages of preservation: 75.8% (47/62) for small species and 91.2% (31/34) for macromammals.

Therefore, the results obtained suggest that the observational completeness of the fossil record of potentially preservable species, such as bivalves and gastropods, may be relatively more deficient in the case of higher trophic level forms.

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