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Nassariid gastropods as destructive agents in preservation and fossilization of marine fishes

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Abstract. Experimental investigations on the feeding activity of the gastropod *Nassarius moestus* in intertidal environments in the Sea of Cortez (Gulf of California) show them to be effective agents influencing processes of marine fish taphonomy. Time-lapse documentation reveals that potential whole-body preservation of fish carcasses is largely prevented through the rapid destruction of soft tissues, muscles, and ligaments, followed by disarticulation and subsequent disassociation of skeletal elements. Dissociated bones are subject to differential dispersal through hydrodynamic transport and physical wear through abrasion. Transformation of whole-body carcasses into thoroughly defleshed and disarticulated skeletons by large groups of scavenging snails was commonly observed to take place within one tidal cycle. The loss of information during taphonomic processes via destructive biological agents may ultimately bias the fossil record in a significant way and thus have implications for the paleoecological interpretation of fossil teleost assemblages.
Key words. Taphonomy; teleosts; gastropods; intertidal; Sea of Cortez; Nassarius; fossil record.

Exceptionally preserved fishes are well-documented from many Cenozoic freshwater deposits, but whole-body preservation is comparatively rare in marine sediments. Marine localities, notably the Eocene shales of Monte Bolca, Italy, and the Miocene diatomites and diatomitic shales of southern California, represent exceptional depositional environments where physical, chemical, and biological destructive forces were absent or had little effect on the preservation of whole fish carcasses[1,2]. The majority of Cenozoic fish fossils, however, are isolated elements from disarticulated skeletons deposited in nearshore marine environments. Taphonomy, the study of the complex processes that lead to deposition and ultimately fossilization of organisms, has been a crucial tool to understanding the ecologies of the past. While taphonomy of whole-body preservation in freshwater fishes has been studied[3-5], few studies have examined how pre-depositional mechanical and biological forces influence the preservation of fishes in nearshore marine facies.

Post-mortem scavenging by marine organisms may alter or greatly influence the likelihood of preservation of fish remains, destroy paleoecological information about the organism and ultimately bias the fossil record. Nassariid gastropods are well known opportunistic intertidal scavengers[6-8]. Scavenging behavior of some species has been studied[9,10], but almost no mention has ever been made regarding their potential as biasing agents in marine taphonomy. Schafer[11] reported on nassariid gastropods occasionally disarticulating crustacean exoskeletons, but did not mention other potential taphonomic roles nassariid gastropods played in marine environments. This study reports on taphonomic experiments conducted with fish carcasses in intertidal environments in the northwestern Sea of Cortez (Gulf of California, fig. 1A), and documents the potential influence of the snail *Nassarius moestus* (Hinds, 1844) on the preservation of marine teleosts. Time-lapse sequences illustrate phases of carcass destruction and subsequent taphonomic alteration.

Materials and methods

Fish carcass taphonomy experiments were conducted at two localities in the northwestern Sea of Cortez (Gulf of California, fig. 1A), in late March, 1993. The first locality was at San Felipe, and the second at Laguna Percebu about 11 km to the south (fig. 1B). Observations were made at low tide. The San Felipe locality was on a flat, sandy mud intertidal beach near a fishing encampment. The Laguna Percebu locality was a sandy to sandy mud intertidal area interspersed with large cobbles. Both localities are populated by the intertidal gastropod *Nassarius moestus*. Fresh fish carcasses were placed on the shore just after the tide receded in the morning, and watched intermittently throughout daylight hours as individual *Nassarius moestus* arrived and began feeding on them. A total of 14 carcasses were observed; 10 at San Felipe and four at Laguna Percebu. The beaches at San Felipe and Laguna Percebu have large sand dunes that absorb sea water during high tides, and as the tides recede, water slowly drains from them across the intertidal flats thus keeping them wet. When fish carcasses were placed on the intertidal flats, the seawater draining from the dunes carried the scent of dead fish across the flat and into the surf (fig. 2A).

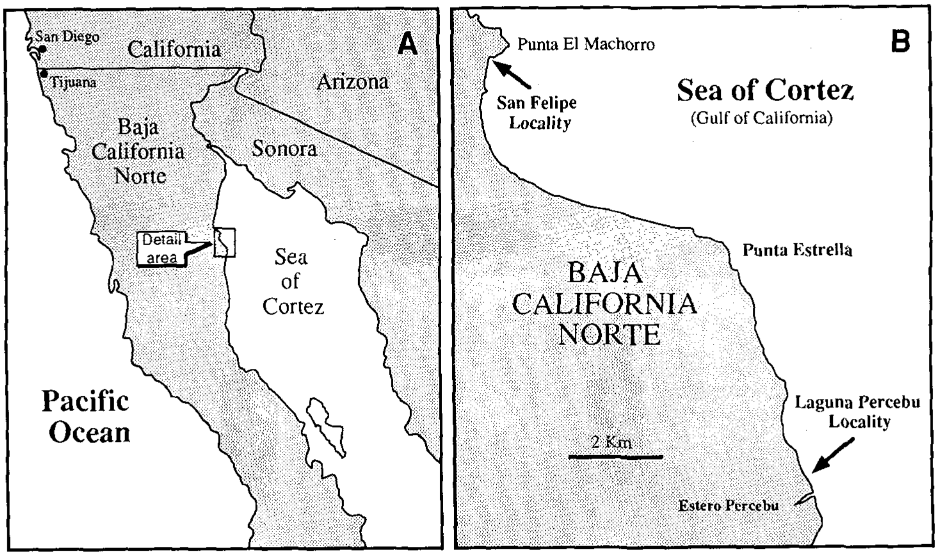

Figure 1. *A* Schematic map of Mexico showing area where observations were made. *B* enlargement of inset showing location of the study sites referred to in this paper.

Observations were noted and time-lapse photographs were taken as the gastropods fed on the carcasses. For each fish carcass, the number of nassariid gastropods present was recorded and the length of time it took for the gastropods to consume the soft tissue on the fish carcass were measured. The carcasses were observed for 24 h and at least one complete tidal cycle to observe any other post mortem scavenging and destruction.

Results

Within five to ten minutes after placing the fish carcass, *Nassarius moestus* emerged from the exposed tidal flat or moved up from the surf-line following the scent plume to its source, often following small rivulets created by salt water draining from the dune front to the ocean (fig. 2A). Over the entire observation period *Nassarius moestus* was the only nassariid gastropod species seen on the intertidal flats at these localities, and was the only species observed feeding on fish carcasses. The snails first fed on the fish's slime coating, and then entered the body cavity through the mouth, the eyes, the anus, or through other small holes (figs 2B-D). Once inside, the snails rasped away organs and skin with their radula, rapidly enlarging previous holes and making new ones (figs 2C-D). Eventually, they ate all the soft tissue on the carcass and left behind bones and scales (figs 2E-F). Over 300 *N. moestus* were seen feeding on a single carcass at one time, but the number of snails present at individual carcasses ranged from approximately 40 to 200. Some snails left the carcass and others arrived at the carcass at different times throughout the cycle, so the exact total number of individuals that fed on a single carcass is unknown.

The snails transformed a whole carcass into a cleaned skeleton in 8 to 24 h, depending on the locality and the number of snails present. At the San Felipe locality, snails remained on the carcass for about 20 to 40 minutes with about 50 to 300 snails on a carcass at any one time, and fish carcasses were cleaned of all soft tissue in 8 to 10 h. At the Laguna Percebu locality, there were usually 40 to 100 individual snails on the carcass at any one time. Most snails remained on the carcass for about 40 to 70 min and it took about 24 h for the snails to remove all the soft tissue from the carcass. The number of snails on a carcass at a given time declined in relation to the amount of flesh still present on a carcass. After the carcass was fully cleaned, the advancing tide scattered and transported disarticulated fish bones (fig. 2F). In some cases, snails returned to feed on the remaining tissues on the same carcass at the next low tide.

Only adult snails fed on carcasses, and no specimens smaller than 10 mm were ever noted. Feeding *N. moestus* ranged in size from 10.69 mm to 15.56 mm, with an average shell length of 13.24 mm. Upon close examination, over a third of the snails (12 out of 32 specimens examined) carried eggs on their operculum. Brooding snails measured from 12.95 mm to 15.27 mm, averaging 14.22 mm.

Discussion

Investigations on the preservation potential of fish carcasses at the two intertidal localities in Baja California clearly demonstrate the direct taphonomic impact of scavenging nassariid gastropods. Although these snails may not be the only biasing agent to fish in intertidal environments, they were the most abundant and efficient

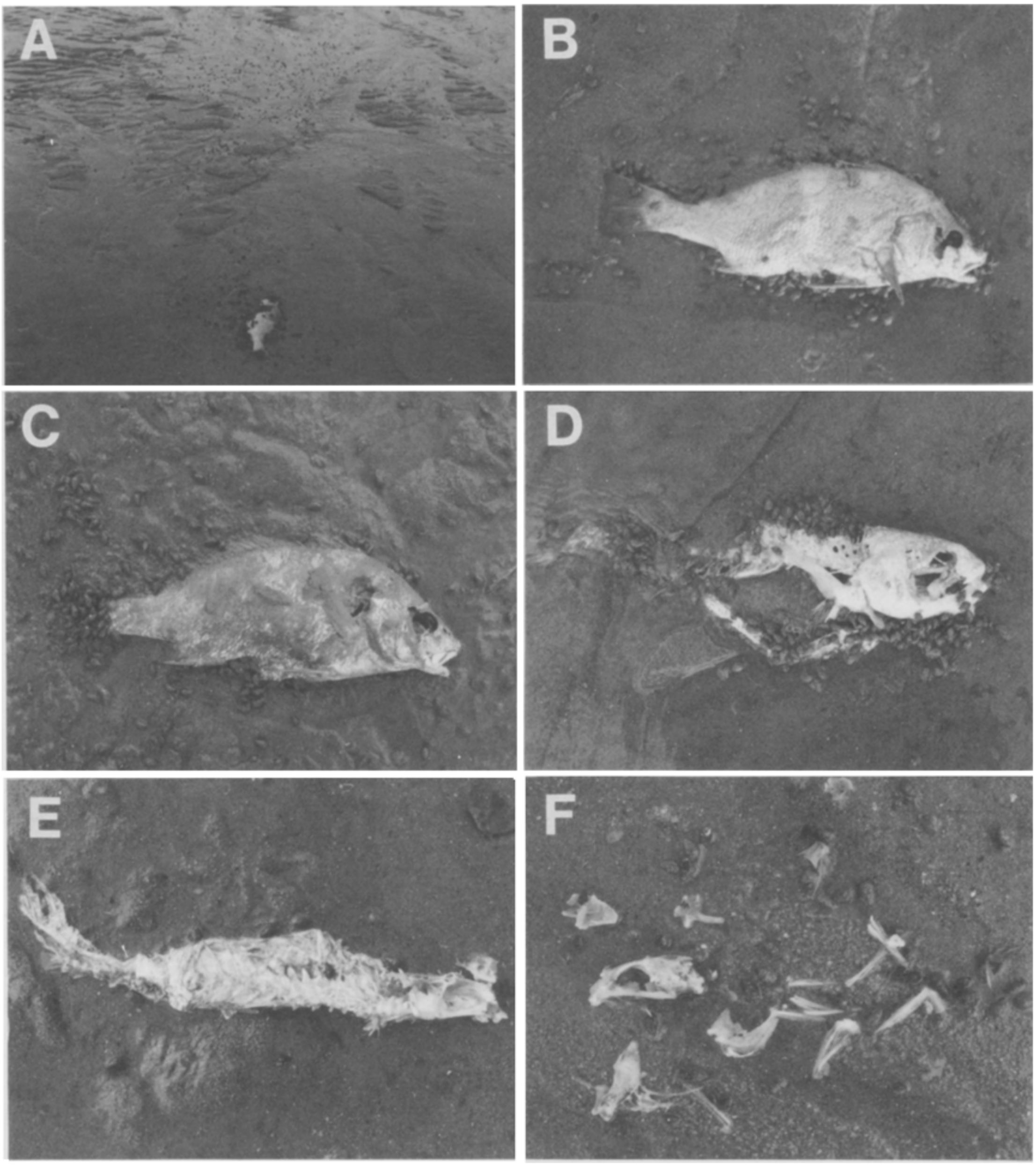

Figure 2. Time-lapse composite photographs of *Nassarius moestus* scavenging on fish carcasses over a 24 h period (total length of the fish is approx. 30 cm).
A Photograph of tidal flat showing hundreds of *Nassarius moestus*, many following the scent plume and heading toward the fish carcass in the foreground.
B Snails arriving at a fish carcass and entering through holes in the body (after 2 h).
C The carcass is muddied by mud and feces of snails climbing on it, and shows new holes made by snails rasping from inside the body (after 4 h).
D The carcass showing the majority of soft tissue removed and skeleton exposed (after 8 h).
E The carcass after one tide with snails still feeding on remaining flesh (after 16 h).
F Skeletal remains of the carcass after a second tide showing all soft tissue removed, disarticulation of the skeleton, and differential transport of skeletal elements due to waves from the second tide (after 24 h).

scavengers in this intertidal setting. Morton[10] showed that the intertidal scavenger *Nassarius festivus* eats about 15.33% of its wet tissue weight per day. The speed and efficiency with which *N. moestus* cleans fish carcasses of nearly all soft tissue demonstrates that these organisms are destructive and biasing agents to the preservation potential of marine fishes. Scavenging by these snails is not directly a destructive force on the skeletons, but is an initiating force for subsequent phases of skeletal disarticulation and differential transport executed mainly by tidal currents. This destruction precludes the possibility of preservation of fin rays, scale patterns, coloration, or soft organs. Scales and fin rays are relatively hard structures that are themselves not eaten by the snails, but removal of skin and connective tissue frees them from the body of the fish. Although preservation of soft tissues is rare in most depositional environments[2], scavenging by these snails completely rules out the possibility of such preservation, and hence reduces the amount of potentially preservable biological information.

More importantly, removal of connective tissue disarticulates and frees the bones within the skeletal framework, and they become disassociated and displaced from their original context. Consumption of soft tissues in conjunction with subsequent phases of disarticulation and disassociation of skeletal elements prevents whole-body transport of the carcass. Because of this, all carcasses observed in this study could neither be preserved as a whole in situ nor transported as a whole to another depositional environment. Some depositional environments preserve entire bodies of neritic and nearshore fishes carried by currents and tides from coastal environments into deeper basins[1]. Evidently, this type of whole-body transport into a more favorable preservational environment cannot occur if carcasses have been previously disassociated and disarticulated.

Bones freed from connective tissues are under the influence of post-mortem hydrodynamic and other physical forces. Behrensmeyer[12] and others noted that bones of terrestrial vertebrates travel at differential rates in moving water depending largely on their size, shape, weight, and density. Fish bones of different sizes, shapes, and densities can be expected to be sorted and transported at different rates and distances depending on tide and wave action. Elder and Smith[4] noted that bones of fish carcasses disarticulated by scavengers were not displaced with respect to the hydrodynamic character of the bone. Their experiments, however, were not performed in a high-energy intertidal area, and all of our observations confirmed otherwise.

Advancing tide and waves sorted and moved small bones (ribs), light weight fin rays and scales first. Large but thin bones, such as the caracoid and basipterygium, were also carried off. Smaller dense bones, such as vertebrae, stayed closer to the original site of disarticulation, as did larger, denser bones such as the dentary and ceratohyal. The skull often remained fully articulated and was often the last series of elements to be transported from the original site of disarticulation. Increased or prolonged hydrodynamic transport, in this case wave action and longshore transport, decreases spatial proximity of disarticulated skeletal elements and lessens the likelihood of burial together. Without the protection of soft tissues, hydrodynamic forces, sediment abrasion, biotic and abiotic factors additionally may break, erode, and dissolve bones before they are deposited. Wave action pounds the bones against the substrate and longshore transport abrades them against sand. Physical wear of bones due to abrasion against substrate may vary greatly[12], but any degree of abrasion is a negative effect on the overall preservation of the specimen. These destructive factors not only lessen the preservation potential of the fish carcasses, but may also bias the fossil record. Additionally, an inaccurate identification based on fragmentary and incomplete material may lead to faulty comparisons with living analogs, and may provide comparatively less ecological and environmental information than whole-preserved carcasses. Taphonomic loss affects other areas of paleoecology, such as species presence/absence, relative abundance, community structure, age and sex ratios, seasonal variation, depth, and distance from shore[12–14].

Nassariid gastropods live worldwide in tropical, subtropical, and temperate coastal marine habitats, and nearly all appear to scavenge to some degree[6–8]. *Nassarius* is diverse and widespread by the Miocene[15]. In addition, several other related genera of scavenging gastropods (e.g. *Babylonia* and *Bullia*) also have cosmopolitan distributions[10,16]. Although nassariid gastropods may have fed on fish carcasses throughout most of the Cenozoic, it is difficult to assess the direct association between nassariid gastropods and fishes in a fossil deposit.

Much is known about taphonomic processes of terrestrial vertebrates[12], yet little is known about taphonomy of their marine counterparts. This study demonstrates the potential and destructive power of the scavenging intertidal gastropod *Nassarius moestus* and its effectiveness as biasing agent in marine fish taphonomy. Scavenging intertidal gastropods may affect the preservation potential of many marine vertebrates through destruction of soft tissues, prevention of whole-body transport, disarticulation of the skeletal elements, and ultimately may bias the fossil record in a significant way. As a modern analog, this example illustrates processes that may have happened globally throughout most of the Cenozoic in many intertidal environments.

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