A review of the fossil seabirds from the Tertiary of the North Pacific: plate tectonics, paleoceanography, and faunal change

Kenneth I. Warheit

Abstract.—Ecologists attempt to explain species diversity within Recent seabird communities in terms of Recent oceanographic and ecological phenomena. However, many of the principal oceanographic processes that are thought to structure Recent seabird systems are functions of geological processes operating at many temporal and spatial scales. For example, major oceanic currents, such as the North Pacific Gyre, are functions of the relative positions of continents and Antarctic glaciation, whereas regional air masses, submarine topography, and coastline shape affect local processes such as upwelling. I hypothesize that the long-term development of these abiotic processes has influenced the relative diversity and community composition of North Pacific seabirds. To explore this hypothesis, I divided the history of North Pacific seabirds into seven intervals of time. Using published descriptions, I summarized the tectonic and oceanographic events that occurred during each of these time intervals, and related changes in species diversity to changes in the physical environment. Over the past 95 years, at least 94 species of fossil seabirds have been described from marine deposits of the North Pacific. Most of these species are from Middle Miocene through Pliocene (16.0–1.6 Ma) sediments of southern California, although species from Eocene to Early Miocene (52.0–22.0 Ma) deposits are from Japan, British Columbia, Washington, and Oregon. During the history of the North Pacific seabirds, there were many widespread (global) and local (California Current) oceanographic events, but the underlying physical processes that affected the diversity of seabirds throughout the North Pacific were tectonic changes that led to sequential stages of thermal isolation and refrigeration of Antarctica. Besides these broad-scale phenomena, the uplift of the Isthmus of Panama and the initiation and intensification of coastal upwelling in the California Current directly affected the diversity of seabirds in southern California. For the most part, Middle to Late Miocene and Pliocene seabird faunas from California resembled Recent communities, but with several exceptions: (1) the extreme diversity and abundance, but subsequent extinction of gannets (Morus) and Flightless Alcids (mancallids); (2) the comparatively low abundance and diversity of cormorants and shags (Phalacrocoracidae) until the Late Pliocene; and (3) the absence of marine Laridae until the Late Pliocene. By affecting both the physical and biological environments, geological factors such as Antarctic glaciation, eustatic changes in sea levels, and local tectonic activities influenced and will continue to influence the structure of seabird systems in the North Pacific.


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Not only might community-level characteristics bear the stamp of events long past . . . but so also might the various properties of component species . . . . Yet such [past] events are surely no less real for having taken place before the ecologist arrives to observe their consequences; they are only less easily studied . . . .


Introduction

One goal in the study of ecological communities is to identify how and why particular species co-occur (see, e.g., Ricklefs 1973; Pianka 1983; Roughgarden 1989). To this purpose, ecologists study organisms and populations; predation, herbivory, species-level interactions, and Recent geographic distributions are frequently the kinds of data collected. The implicit assumption here is that species diversity within Recent ecological communities can be understood in toto through data collected on extant populations and environments. To be sure, many ecologists are now realizing that the temporal component of communities and ecosystems may extend beyond that of funding resources or even our own existences (as suggested by the epigraph). And the haunting sounds of the
“ghost of competition past” (Connell 1980) or the “ghost of extinction past” (Van Denber 1986) are frequently heard in studies of ecological communities. However, despite many exceptions (e.g., see papers in Diamond and Case 1986), the realization that history is important and the suggestion to incorporate paleontological data into studies of Recent communities and ecosystems (e.g., Fowler and MacMahon 1982; Janzen and Martin 1982), have inspired only a handful of ecologists to use geological data.

Although research on seabird communities has a history of long-term studies (e.g., Richdale 1957; Belopol’skii 1961; Ainley et al. 1983; Coulson and Thomas 1985; Ainley and Boelkeileide 1990), few studies have attempted to introduce data from the paleontological record. This is unfortunate because geological factors, such as changes in sea level and tectonic events, have directly affected Recent seabird systems through their effect on the geography, circulation patterns, and climate of the oceans. Although these geological processes may contribute to the structure of Recent seabird communities, they operate on a time-scale beyond that of human experience. Therefore, those aspects of Recent seabird communities that are affected by long-term geological events, either directly or through their effects on short-term ecological phenomena, cannot be explained adequately by studying only Recent communities.

The purpose of this paper is to associate temporal changes in seabird diversity in the North Pacific to changes in global geography, climate, and oceanography. To accomplish this, I provide a list of all species of fossil seabirds from the North Pacific, and group these species into faunas based on their relative temporal occurrences. I also relate the changes in seabird diversity between successive faunas to changes in continental configurations and physical features of the oceans. I describe geological events in terms of their scale effects. For example, large-scale events (e.g., Antarctic glaciation) can affect the entire North Pacific ecosystem, whereas other geological events can be more local in their impact (e.g., affecting only the California Current system). Differences in seabird communities measured temporally or spatially may be the result of a combination of these different scale effects. I discuss these scale effects using the California Current seabird communities as an example.

**Methods**

Seabirds Defined.—My definition of seabirds includes only the Procellariiformes (albatrosses, petrels, shearwaters, diving petrels, and storm-petrels), Pelecaniformes (pelicans, cormorants and anhingas, sulids, frigate-birds, and tropicbirds), Alcidae (auks), Laridae (gulls), and Sphenisciformes (penguins), the last of which is unknown in the North Pacific. I include in this analysis all taxa of fossil seabirds from the North Pacific that are described in the literature. Except for my work on the Sulidae (gannets and boobies), I do not include unpublished seabird material in these analyses. In addition to these seabird taxa, gaviiforms (loons), podicipediforms (grebes), and marine anseriforms (ducks) have been described from the eastern North Pacific. Because these taxa have freshwater or terrestrial habits, I did not include them in the following analyses (for listings of these taxa, see Howard 1983; Becker 1987).

Seabird Faunas.—Seabird fossils are usually found in marine deposits, and biostratigraphic time scales derived from marine plankton (e.g., diatoms, foraminifera, radiolarians) and molluscs are usually used to establish relative ages for the specimens. Typically, the stratigraphic information for the seabird-bearing formations are included by the authors in their fossil descriptions. However, because many of these descriptions are from the older literature, the stratigraphic data provided by these authors is out-of-date. Therefore, to establish seabird faunas, I used both biostratigraphic and radiometric data from the recent literature (see the Appendix for full discussion of literature and methods). Using these procedures, I described each fossil specimen in terms of its relative or absolute age. Specimens are considered isochronous if they occur within the same or close to the same strata within the same formation, or from another formation correlated in time to the first formation.
I recognized seven groups of seabird-bearing formations from the North Pacific, each produced during a single, but broadly defined interval of time (fig. 1, Appendix). I defined the assemblage of seabird fossils recovered from each group of isochronous formations as a seabird fauna. I therefore recognized seven seabird faunas from the North Pacific, each associated with one broadly defined time interval (fig. 1). The temporal sequences of these faunas in California were initially described in an earlier study (Warheit and Lindberg 1988: fig. 9.2), although that analysis was only a general introduction. In addition, that study did not define each fauna in terms of included formations (see the Appendix) and conducted the analyses at taxonomic levels higher than genus and species. Because I restricted my analysis here to the Tertiary, I did not include Fauna V (Warheit and Lindberg 1988).

Fossil Seabird Environments.—Paleoceanographers reconstruct the oceanographic conditions of ancient oceans from sedimentary remains of microfossils (typically diatoms, foraminifera, and radiolarians). Because the fossil remains of these plants and animals are abundant, and their taxonomies are well established, they provide refined indices of time (see, e.g., Woodruff et al. 1981). Sometimes the fossil sequences are so detailed that resolution can be in the order of tens and hundreds of thousands, instead of millions, of years (see, e.g., Bolli et al. 1985). These fossil taxa are also excellent indicators of environmental conditions, and provide detailed chronologies of oceanographic and climatic events (see Berger et al. 1989 and references therein). I used the published data on the biostratigraphy of deep-sea ocean cores (e.g., Barron and Keller 1982; Keller and Barron 1983, 1987; Barron and Larsen 1988), climatic affinities of diatoms and planktic foraminifera (e.g., Barron and Keller 1983), isotopic bottom-water temperatures (e.g., Savin et al. 1975; Woodruff et al. 1981; K. Miller et al. 1987; Woodruff and Savin 1989), and eustatic sea levels (e.g., Haq et al. 1987) as long-term and large-scale oceanographic indices. Because deep-ocean waters are formed at high latitudes, principally in the North Atlantic.
and Antarctica, “isotopic records provide both an estimate of the paleotemperatures of high-latitude surface waters, as well as an estimate of the amount of water stored in polar ice caps” (Barron and Baldauf 1989: p. 343). In addition, the development of polar ice contributes (with continental and oceanic configurations) to the pole-to-equator tempera-
ture gradient and therefore affects oceanic circulation patterns (for a brief discussion and example, see Rea et al. 1990). By recording the development of polar ice caps, the record of isotopic bottom-water temperatures also chronicles the development of global surface currents such as the North Pacific Gyre. Therefore, the record of bottom-water temperatures provides a history of not only the development of cold and nutrient-rich bottom waters, but also the evolution of large-scale phenomena such as oceanic currents, and local phenomena such as upwelling.

Spatial Distribution of Fossil Seabirds

Fossil seabird species from marine deposits of the North Pacific are listed in figure 2 (see table 1 for a listing of seabirds from non-marine deposits of western North America). This list includes only taxa that have been discussed in the literature and is subdivided into seabird faunas (see fig. 1) and geographic

<table>
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<tr>
<th>REGION / TAXON</th>
<th>FAUNA</th>
<th>References</th>
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<tbody>
<tr>
<td><strong>CALIFORNIA</strong></td>
<td><strong>PROCELLARIIFORMES</strong></td>
<td><strong>DIOMEDEIDAE</strong></td>
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<tr>
<td>Diomedea exulans</td>
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<td>Diomedea californica</td>
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<td>Diomedea (7?) californica</td>
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<td>Diomedea sp.</td>
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<td>Diomedea sp.</td>
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<td>Fulmarus miquelonensis</td>
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<td>Fulmarus hammeti</td>
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<td>Puffinus inceptor</td>
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<td>Puffinus michelli</td>
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<td>Puffinus prisca</td>
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<td>Puffinus barnesi</td>
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<td>Puffinus californicus</td>
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<td>Puffinus diomedea</td>
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<td>Puffinus fulgur</td>
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<td>Puffinus kanakoffi</td>
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<td>Puffinus sp.</td>
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<td>Oceanodroma sp.</td>
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<td>Oceanodroma hubbi</td>
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<td>Oceanodroma sp.</td>
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<td><strong>PELECANIFORMES</strong></td>
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<td>Morus vagabundus</td>
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<td>Morus new sp.</td>
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<tr>
<td>Morus sp.</td>
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<tr>
<td>Morus willari</td>
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<tr>
<td>Morus impoceanus</td>
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<td>Morus stocktoni</td>
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<td>Morus humerals</td>
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<td>Sula pohli</td>
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<td>Sula clarkei</td>
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<td>Sula sp.</td>
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**FIGURE 2.** Continued.
regions. The bulk of the known fossil seabirds from the North Pacific is from California, although our knowledge of early Tertiary seabirds is based mostly on material from Japan, British Columbia, Washington, and Oregon (fig. 2). Note that there is no known fossil material from latitudes north of Vancouver Island, British Columbia and Honshu, Japan in the eastern and western Pacific, respectively (figs. 2, 3). In fact, 88% of the fossil seabirds from the North Pacific were recovered from deposits between 32°N and 38°N latitude (fig. 3). Therefore, at best, the known history of seabirds from the North Pacific is very restricted geographically. Undoubtedly this narrow geographic distribution is an artifact of insufficient sampling rather than a historical fact.

All Tertiary fossil seabirds from California are from localities south of San Francisco, and
most of this material is from Los Angeles, Orange, and San Diego counties (fig. 4). Southern California is the only region in the North Pacific where seabird fossils are known from Faunas I through IV, as well as Fauna C (figs. 2, 4). Clearly, the known history of North Pacific seabirds is mostly the history of southern California seabirds, where the taxonomic and temporal coverage is extensive.

Table 1. Seabird taxa from nonmarine deposits of western North America. Data from Becker 1987.

<table>
<thead>
<tr>
<th>Fauna</th>
<th>Taxon</th>
<th>Locality</th>
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<tbody>
<tr>
<td>I</td>
<td>Laridae</td>
<td>San Bernardino Co., Calif.</td>
</tr>
<tr>
<td>II</td>
<td>Phalacrocorax leptopus</td>
<td>Malheur Co., Oreg.</td>
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<tr>
<td>III</td>
<td>Phalacrocorax idahensis</td>
<td>Owyhee Co., Idaho</td>
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<tr>
<td></td>
<td>Laridae</td>
<td>Mohave Co., Ariz.</td>
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<tr>
<td>IV</td>
<td>Pelecanus erythrorhynchos</td>
<td>Malheur Co., Oreg.</td>
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<td></td>
<td>Pelecanus halieus</td>
<td>Elmore, Owyhee, Twin Falls Co., Idaho</td>
</tr>
<tr>
<td></td>
<td>Phalacrocorax auritus</td>
<td>Malheur Co., Oreg.</td>
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<tr>
<td></td>
<td>Phalacrocorax atertus</td>
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<tr>
<td></td>
<td>Phalacrocorax idahensis</td>
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<td>Phalacrocorax macer</td>
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<tr>
<td></td>
<td>Phalacrocorax sp.</td>
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North Pacific Seabird Faunas

Fauna A (52–38 Ma; see the Appendix for dates).—All seabird taxa in Fauna A were recovered from localities in Oregon, and all but Hydrotherikornis oregonus were described by Goedert (1988, 1989; fig. 2, Appendix). A. Miller (1931) described H. oregonus as an alcid (similar to Ptychoramphus), but according to R. Chandler (personal communication 1990),...
the specimen is more closely related to petrels than to the Alcidae (for a contrary view, see Steadman, in Olson 1985: p. 183). I tentatively placed the species within the Procellariidae, but await Chandler’s publication for conclusive evidence.

The remaining species in Fauna A were members of either the Pelagornithidae or the Plotopteridae (extinct Pelecaniformes; fig. 2). The Pelagornithidae or pseudodontorns (=Odontopterygiformes in Howard [1957] and Harrison and Walker [1976]) were worldwide in distribution and are closely related either to the clade that includes the Sulidae, Phalacrocoracidae (cormorants), and Anhinga, or to the Pelecanidae (Warheit in preparation). The taxon consisted mostly of gigantic marine birds equipped with bony toothlike projections on the rostrum and mandible (see Olson 1985: fig. 9). Although the pseudodontorns varied considerably in size, most species were larger than the Wandering Albatross (Diomedea exulans), the largest extant seabird (wingspan of 2.5–3.5 m; Harrison 1983). An undescribed species from South Carolina had a wingspan of 5.5–6.0 m (Warheit and Olson in preparation). The structure of the wing and shoulder in these birds suggested that soaring rather than flapping flight was the primary mode of locomotion (Olson 1985). Furthermore, Zusi and Warheit (1992) suggest that pseudodontorns obtained their food (probably fish or squid) in a manner similar to frigatebirds (dipping) or albatrosses (surface seizing). Goedert (1989) described two taxa of pseudodontorns from the Late Eocene (40.5–39 Ma) beds of northwestern Oregon and tentatively referred one of these specimens to Argillornis, an eastern Atlantic taxon.

Olson and Hasegawa (1979: p. 688) described the Plotopteridae as “giant, flightless penguinlike birds” whose “hindlimb and pelvic morphology is most similar to that of Recent anhingas, but the wing is paddlelike
and remarkably convergent toward penguins and flightless auks." Unquestionably these marine birds were wing-propelled divers, as are penguins, but many were larger than penguins, possibly twice the height of the largest extant penguin, the Emperor Penguin (Aptenodytes forsteri) (length of femora: gigantic plotopterid from Japan = 225 mm, Olson 1985; A. forsteri = 118.5 mm, mean of 30 specimens, Livezey 1989). Phocavis maritimus was described from a single specimen (tarsometatarsus) recovered from the same formation in northwestern Oregon as Argillornis sp. (see above; Goedert 1988), and is the oldest known member of this taxon. In addition, P. maritimus and the two species of pseudodontorns described by Goedert (1989) are the oldest known seabirds in the North Pacific.

Fauna B (31[?]-22.8 Ma).—Only three seabird taxa are definitively known from Fauna B, and similar to Fauna A, these taxa are members of either the Pelagornithidae or Plotopteridae. Fauna B is the first in which fossil seabirds are known from Japan (see the Appendix). Although the plotopterid material from Japan was not described to species, Olson and Hasegawa (1979) considered at least four species present. Also from Japan is an incomplete humerus from northern Kyushu, described by Okazaki (1989) as an Odontopterygiformes (Pelagornithidae). The third taxon from this fauna is Tonsala hildegardae, a plotopterid from northern Washington state (Olson 1980).

Cyphornis magnus is a pseudodontorn (Olson 1985; Warheit and Olson in preparation) from Vancouver Island, British Columbia (Cope 1895), and the northernmost member of this taxon in the North Pacific. The age of C. magnus is in doubt and has been described alternatively as Late Eocene (Fauna A), Oligocene (Fauna B), and Early Miocene (Fauna C). I listed this species here for convenience only (see the Appendix: Fauna B, Carmanah Point). Drummond (1979) stated that Late Eocene to Early Miocene sediments off southern and western Vancouver Island were deposited onto a steep continental slope in an area without a significant continental shelf. Therefore, despite its age, I presumed that C. magnus frequented an oceanic environment with little or no continental shelf, and a steep continental slope.

Fauna C (24 [?]–18 Ma).—Although plotopterids were present in the eastern Pacific as early as the Late Eocene (Fauna A; figs. 1, 2), Fauna C is the first in which a plotopterid was recovered from a California deposit. In addition, Plotopterum joquinensis, from the Pyramid Hill local fauna (Howard 1969; 22–21 Ma, Woodburne 1987) is the only known plotopterid and the oldest known marine seabird from California (fig. 2).

The remaining seabirds from this fauna are pelagornithids from central Oregon. Olson (1985) considered these specimens to be part of the genus Osteodontornis, initially described from Late Miocene (Fauna II) deposits of southern California (Howard 1957).

Fauna I (18 [or 15]–13 [or 12] Ma).—Of the 102 fossil seabirds in the North Pacific (black bars in fig. 2), 91 are members of Faunas I through IV, and 89 of these 91 are from the eastern Pacific. A summary of the taxonomic diversity of these eastern North Pacific seabirds is shown in figure 5. Except for Hydrotherikornis oregonus (see above; Fauna A), Fauna I is the first in which extant seabird taxa are present (Alcidae, Sulidae, Procellaridae [petrels and shearwaters], and Diomedeidae [albatrosses]) (figs. 2, 5). In addition to these extant taxa, Osteodontornis sp. was also present and widespread, found from localities in Japan, Oregon, and California. Although the specific identity of the pseudodontorn from Japan is uncertain (Ono 1989), the Oregon and California specimens were probably conspecific (O. orri; Warheit and Olson in preparation).

Plotopterids also remained extant in Japan during the time of Fauna I. But unlike the earlier plotopterids from the western Pacific, these specimens were relatively small and similar in size to Plotopterum joquinensis from Fauna C (see above) and the Recent Brandt’s Cormorant (Phalacrocorax penicillatus) (Olson and Hasegawa 1979, 1985). Sulids also existed on both sides of the Pacific during this time, although the material from the eastern North Pacific is far more abundant and diverse than that from Japan (fig. 2).

The taxonomic diversity of Fauna I was
dominated by the Sulidae and the Procellariidae (fig. 2). In addition, two species each of Alcidae and Diomedeidae were also present. One of the two species of Alcidae (Alcides aff. A. ulnulus) is considered closely related to the mancallids (Praemancalla and Mancalla; Howard 1968; Howard and Barnes 1987), an extinct group of flightless auks, similar in morphology to the Great Auk (Pinguinus impennis; Lucas 1901a,b; for morphometric comparisons, see Livezey 1988). It is not clear from the morphology of Alcides sp., however, if the individuals in this taxon were flightless, although Howard (1968: p. 19) maintained that the species "was progressing towards flightlessness." In summary, Fauna I can be characterized by the pan-North Pacific distribution of the pseudodontorns, and the initial radiation of extant families of seabirds in the North Pacific, in particular, the Sulidae and Procellariidae.

*Fauna II (13–8 [6] Ma).—*If Fauna I is considered important in the North Pacific radi-ation of gannets and shearwaters, Fauna II must be characterized as "the age of the Alcidae." The number of alcid taxa in the eastern North Pacific increased dramatically during this time, when 11 sympatric species occurred in California (fig. 5). At least seven alcid genera were also present, including Alca and Aethia (fig. 2), known in the Recent from only the North Atlantic and North Pacific/Bering Sea, respectively. Besides these volant alcids, mancallids were also represented in this fauna; two species of the flightless *Praemancalla* and *Alcides ulnulus* (fig. 2).

Sulids and procellariids continued their relatively high diversity, while cormorants and storm-petrels (Oceanitidae) made their first appearances in the eastern North Pacific at this time (fig. 5). Although there was considerable taxonomic turnover within the Sulidae and Procellariidae between Faunas I and II (fig. 2), their total taxonomic diversity remained relatively constant (fig. 5). In addition, the diversity curves for the sulids and

![Figure 5. Histograms showing the number of seabird species per higher taxon in each fauna (includes only those specimens from the eastern North Pacific, but does not include *Cyphornis magnus* because of the uncertainty in its age; see the text). Flightless Alcidae are the mancallids. *Hydrotherikornis oregonus* is the Procellariidae in Fauna A. The question mark signifies taxonomic uncertainty (see the text).](image-url)
procellariids remained remarkably similar to each other throughout Faunas I–IV (fig. 5). Despite their relatively constant taxonomic diversity, the morphologic diversity of the Sulidae increased in Fauna II. For example, although *Morus (Miosula) media* and *Morus (Paleosula) stocktoni* are easily identified as sulids (Miller 1925, 1935), the structure of their legs and wings revealed morphologies similar to those in cormorants and wing-propelled divers, respectively (Miller 1925; Warheit 1990). This suggested convergent locomotory habits between these species of *Morus* and the Phalacrocoracidae and Alcidae.

In summary, the most distinctive characteristic of Fauna II is the dramatic increase in diversity of both volant and flightless alcids. Other important events that occurred during the time of this fauna were the initial radiation of the cormorants and storm-petrels, and the continued high diversity of the sulids and shearwaters. Morphologic diversity of the sulids also increased during this period.

**Fauna III (7 [6–4 Ma]).**—Fauna III is unlike the other faunas in that declining diversity was the general theme for all taxonomic groups except the mancallids (figs. 2, 5). Although there was a decline in diversity and extinction of *Praemancalla* and *Alcoides*, respectively, from Fauna II to Fauna III, *Mancalla* increased in diversity (see figs. 2, 5). *Mancalla* is more advanced in its development of a penguinlike wing than either *Praemancalla* or *Alcoides* (Howard 1966b, 1968). The number of volant species of alcids decreased from eight in Fauna II to five in Fauna III (figs. 2, 5). If the Cedros Island, Mexico species were not included in figure 5, the drop in volant Alcidae diversity would be more dramatic (i.e., two of the five species of volant alcids were indigenous to Cedros Island, while the one species of mancallid found on Cedros Island also occurred in southern California; fig. 2). Therefore, while other taxa of Alcidae declined in diversity in Fauna III, the mancallids diversified.

A decline in diversity was also apparent in both the Pelecaniformes and Procellariiformes. The Sulidae and Procellariidae declined to one species each from southern California and Cedros Island, Mexico, while the number of albatross species decreased to one in California and none in Mexico (figs. 2, 5). Missing from this fauna are the Phalacrocoracidae and Pelagornithidae. The pseudodontorns apparently became extinct in the eastern North Pacific at this time, but were still present in Japan, and remained extant into the Pliocene in both the South Pacific (New Zealand) and North Atlantic (North Carolina) (Howard and Warter 1969; Olson 1985; Warheit and Olson in preparation).

(I am aware of additional, unpublished seabird material from deposits in Santa Cruz County, California [Purisima Formation; F. Perry in preparation]. Although additional species of Alcidae, Procellariidae, and Sulidae are known from this unpublished locality [Perry in preparation], the number of taxa present does not drastically alter the diversity curves, including the local extinction of the pseudodontorns [fig. 5].)

In summary, the general theme for Fauna III is declining diversity for all taxa except the mancallids. In addition, Fauna III is the first fauna since Fauna C where the pseudodontorn, *Osteodontornis sp.*, was not present in California. It appears that the pseudodontorns became extinct in the eastern North Pacific before the time of Fauna III, but remained extant in Japan into Fauna III.

**Fauna IV (3–1.5 Ma).**—Fauna IV consists of abundant fossil remains from the San Diego Formation, San Diego, California. Chandler (1990) reviewed this material, and the taxonomic listing for this fauna in figure 2 is a summary of his work. The transition from Fauna III to Fauna IV was essentially a mirror image of the transition from Fauna II to Fauna III. That is, all taxa, except *Mancalla* sp., experienced an increase in taxonomic diversity. Volant alcids increased from five species in Fauna III (three species from California) to six species in Fauna IV (fig. 5). In addition, this increase was due primarily to the radiation of small alcids in the genera *Brachyramphus*, *Ptychoramphus*, and *Synthliboramphus* (fig. 2). Although *Mancalla* decreased in diversity from five species in Fauna III to three species in Fauna IV, their numerical dominance in this fauna was evident, with most of the 2000 plus specimens from the San Diego Forma-
tion identified as maccallids (R. Chandler personal communication).

Although the Laridae had been known from nonmarine deposits in western North America from at least the time of Fauna I (table 1), Fauna IV includes the first appearance of gulls or terns in marine deposits from the North Pacific (figs. 2, 5). Chandler (1990) identified only one larid to species (Rissa estesi; fig. 2), and considered it most similar to the Recent Black-legged Kittiwake (R. tridactyla). Chandler also identified Larus sp. as a species of gull intermediate in size between the Recent Ring-billed Gull (L. delawarensis) and the Recent California Gull (L. californicus), and Sterna sp. as a tern similar in size to the Recent Royal Tern (S. maxima).

Among the Pelecaniformes, there was an increase in the number of sulids from the time of Fauna III to that of Fauna IV (fig. 5), and for the first time in the North Pacific, the diversity of Sula equaled that of Morus (fig. 2). The diversity of Phalacrocoracidae also increased during this time interval. Before Fauna IV, the only specimen of cormorant or shag to be recorded from marine deposits in the North Pacific was Phalacrocorax femoralis. Chandler (1990) listed at least a dozen specimens from at least four different species of Phalacrocoracidae from the San Diego Formation. Chandler followed Siegel-Causey (1988) in placing the Recent Pelagic and Red-faced Cormorants (=Shag in the sense of Siegel-Causey) in the genus Stictocarbo (S. pelagicus and S. urile, respectively), and described a new species of shag (S. kumeyaay), similar in morphology to the Red-faced Shag. The second phalacrocoracid species from Fauna IV is Phalacrocorax kennelli, originally described by Howard (1949: p. 189) as a cormorant intermediate in “size between [Phalacrocorax pelagicus] Pelagic Shag] and [Phalacrocorax penicillatus [Brandt’s Cormorant].” Chandler (1990) left undescribed the remainder of the cormorant and shag material from the San Diego Formation, although he explicitly stated that there were at least two more species in the formation, and that one of these was larger and more robust than P. kennelli.

The Procellariiformes also increased in diversity from the time of Fauna III to that of Fauna IV (fig. 5). Three species of albatross were discussed by Chandler (1990), although only one species was named. Chandler described Diomeda howardi as a medium-sized albatross about the same size as the Recent White-capped Albatross (D. cauta) of the Southern Hemisphere. This species was therefore intermediate in size between the large D. californica and the very small D. milleri, both from Fauna I (fig. 2). The two other species of albatross described by Chandler were identified only to genus (Diomeda). Chandler considered species “A” similar in size and possibly closely related to D. californica (size comparable to the Recent Short-tailed Albatross [D. albatrus]; Miller 1962; Howard 1966a), whereas species “B” was similar in size to the small D. milleri (smaller than the Recent Black-footed Albatross [D. nigripes]; Howard 1966a). Finally, Chandler described an unidentified species of storm-petrel (Oceanodroma sp.) from the San Diego Formation (fig. 2).

In summary, there was an increase in diversity of all seabird taxa, except the maccallids, in Fauna IV. This was a reversal of the trend set in Fauna III. Although the maccallids declined in diversity, they were still, perhaps, the most abundant taxon on the California coast. Among the notable radiations during this time, was the increase in the larid, phalacrocoracid, and diomedaid diversities. Except for the presence of sulids and flightless alcids (maccallids), the seabird diversity of Fauna IV closely resembled that of the Recent California Current seabird communities (see Briggs et al. 1987).

Plate Tectonics and Paleoceanography: Mechanisms for Change in the Diversity of North Pacific Seabirds

Large-scale oceanographic processes of the Recent North Pacific are, in part, functions of the anticyclonic North Pacific Gyre. Physical factors that disrupt or alter the North Pacific Gyre can affect biological characteristics in a wide geographic area. For example, during El Niño-Southern Oscillations (ENSO), global climatic and oceanographic patterns are altered, thereby affecting the thermocline and
upwelling regimes in the eastern boundary systems of both the North and South Pacific Gyres (California and Peru Currents, respectively; for details see Glantz and Thompson 1981; Ainley and Boekelheide 1990). By reducing the availability of nutrients upwelled into the euphotic zone, ENSOs disrupt entire food chains (Glynn 1988). The complete reproductive failure and disappearance of a seabird community on Christmas Island, central Pacific Ocean, and increased adult mortality and nesting failure of seabirds in Peru, South Africa, and the eastern North Pacific are examples of the effects of ENSOs on Recent seabird populations (see Schreiber and Schreiber 1984; Hodder and Graybill 1985; Ainley et al. 1986; Duffy et al. 1986; Hatch 1987).

The availability of nutrient-rich waters, and the occurrence and timing of particular oceanic currents and local upwelling, are important factors in understanding the behaviors and distributions of Recent seabirds (see, e.g., Ainley 1977; Pocklington 1979; Brown 1980; Ainley and Boekelheide 1984, 1990; Haney 1986, 1987; Briggs et al. 1987). These factors are also assumed to have been important in extinct seabird systems. In other words, as in Recent seabird systems, the availability of food for extinct seabirds in the North Pacific depended, in part, on the occurrences and timing of oceanic currents and upwelling. From a geological perspective, ENSOs are short in duration, and although they may eliminate entire cohorts from seabird populations (and therefore affect population structure), they do not appear to alter the long-term diversity or structure in seabird communities (i.e., long-term species composition in Peruvian seabird colonies and at Southeast Farallon Island, California do not appear to have been affected by ENSOs occurring during the past century; see Ainley and Lewis 1974; Duffy 1983; Ainley and Boekelheide 1990). However, geological events operating on a long temporal time scale alter the structure of large-scale oceanographic systems and may, in turn, affect radiations and extinctions of particular species of seabirds. Because the Recent circulation patterns of the oceans are functions of continental position, and because the relative positions of land masses have changed during the history of the North Pacific seabirds, tectonic events may have influenced the diversity of seabirds in the North Pacific (for the effects of tectonic events on Paleocene-Eocene non-seabird diversity, see Rea et al. 1990). I will summarize these tectonic events, and their influences on global and California oceanography in terms of their affects on North Pacific seabird diversity (for a summary of physical events, see fig. 6). Although I present the following results as if the temporal correspondence between tectonic events (and their affects on oceanographic features) and changes in the diversity of North Pacific seabirds is a causal relationship, I am aware that to claim causality is to assume that the physical factors were, in part, responsible for changes in seabird diversity. Therefore, the following results are hypotheses and not statements of fact.

Before the time of Fauna A (>52 Ma) the world’s oceans were warm, and global climate was a function of equatorial waters (Savin et al. 1975; Barron and Baldauf 1989). At this time, the Arctic Ocean was isolated from the remainder of the world’s oceans, and the southerly position of both Australia and India inhibited surface and deep-water circulation around Antarctica (Barron and Baldauf 1989). Although there are no seabirds recorded from the North Pacific at this time, I am unable to determine if this was the result of the oceanographic and climatic conditions or the vagaries of the fossil record.

The evolution of the North Pacific ecosystem and the development of its seabird faunas proceeded through five broadly defined oceanographic stages. The first stage began with a major oceanic cooling event at about 52 Ma, following the initial opening of the Norwegian Sea (fig. 6; Barron and Baldauf 1989). The appearance of the first North Pacific seabirds (Fauna A) coincided with these events, and suggest that the shift from a warm to cool oceanic environment was important in the initial radiation of pteropods and pelagornithids. At about 36 Ma, two tectonic events—the initial northward movement of Australia and India, and the widening of a previously narrow Atlantic-Arctic Ocean connection—led to further cooling of the
world’s oceans. More importantly, these tectonic events resulted in the initial refrigeration of Antarctica, bringing glaciers to East Antarctica and a weak Circum-Antarctic Current (fig. 6; Savin et al. 1975; K. Miller et al. 1987; Barron and Larsen 1988; Barron and Baldauf 1989).

Building on the oceanographic effects of the first stage, the second stage in the development of the North Pacific seabird faunas involved continued glaciation in Antarctica. The dramatic cooling of Antarctica around 31–28 Ma contributed to an enhanced latitudinal thermal gradient, with the atmosphere and oceans near the equator remaining warm, while that of the high latitudes becoming increasingly cool (Fauna B, fig. 6). In addition, the opening of Drake Passage at about 24–20 Ma resulted in a strong Circum-Antarctic Current that helped establish the basic oceanic circulation patterns of today (Keller and Barron 1983; Barron and Baldauf...
1989; Fauna C, fig. 6). During these two time periods, the radiation of plotopterids and pelagornithids continued in both Japan and the eastern North Pacific (figs. 2, 5, 6).

Although the Recent oceanic circulation patterns were established by 20 Ma, areas of oceanic productivity were still restricted to equatorial regions (Keller and Barron 1983, 1987; fig. 6). In addition, following the steady decline in ocean temperatures that began at 52 Ma, a sharp rise in ocean temperatures occurred from 22 Ma to 16.3 Ma, with maximum temperatures occurring 16.5-14.5 Ma (Woodruff et al. 1981; K. Miller et al. 1987; Woodruff and Savin 1989).

Although some authors (Olson and Hasegawa 1979; Warheit and Lindberg 1988) have suggested that the plotopterid extinction in the Early Miocene resulted from the radiation of cetaceans and gregarious pinnipeds, respectively, plotopterid extinction also coincided with this sharp rise in ocean temperatures. Goedert (1988) proposed that this warming event was a better explanation for the extinction of the plotopterids than the radiation of marine mammals. The last occurrences of a plotopterid species was 22–21 Ma and 18–15 Ma in the eastern and western North Pacific, respectively (fig. 2; Appendix). Because warm water persisted in the North Pacific from 22 Ma to 14.5 Ma, the extinction of the plotopterids in both the eastern and western North Pacific occurred during this time interval, suggesting support for Goedert’s hypothesis. However, although the plotopterid extinction in the western North Pacific occurred later than that in the eastern North Pacific, the first occurrence of gregarious pinnipeds in the western North Pacific also occurred later than that in the eastern North Pacific (Fauna I; for pinniped data, see Dubrovo 1984; Takeyama and Ozawa 1984).

In other words, there is good temporal correspondence between the extinction of the plotopterids and the radiation of pinnipeds in both the eastern and western North Pacific. This supports the hypothesis (Warheit and Lindberg 1988) that the extinction of the plotopterids was, in part, the result of competition for terrestrial habitat. It is conceivable that both warm water (and a reduction in food, similar to that seen during ENSOs) and pinniped radiations (and a reduction in breeding habitat) played roles in the extinction of the plotopterids.

Following the high ocean temperatures at 16.5-14.5 Ma, there was a precipitous decline in bottom-water temperature (Woodruff et al. 1981; Keller and Barron 1983; K. Miller et al. 1987; Woodruff and Savin 1989; fig. 6), and a shift in areas of high oceanic productivity from the equator to the coastal margins of the North Pacific. At the same time, tectonic activity increased within the panamic portal, and “central american” waters between the Atlantic and Pacific Oceans began to shallow (Duque-Caro 1990; fig. 6). Between 15 and 13 Ma, a permanent ice cap in East Antarctica formed, enhancing the latitudinal thermal gradient (fig. 6).

These oceanographic and tectonic events produced smaller-scale oceanographic changes to the waters of coastal California. The steepened latitudinal thermal gradient intensified the gyral circulation of surface currents, and strengthened the coastal and trade winds that promote upwelling (Barron and Baldauf 1989). Beginning at 13.4 Ma, the planktonic flora and fauna in California switched from subtropical and temperate assemblages to those typical of a cool California Current (fig. 6; Barron and Baldauf 1989). In Recent seabird systems, prey is more easily located, abundant, and predictable in cold-water than in warm-water environments (Ainley 1977; Ainley and Boekelheide 1984). Therefore, I assume that seabird prey during the time of Fauna I switched from a patchy and unpredictable resource typical of Recent subtropical regions to a seasonal but predictably abundant resource similar to that seen in Recent temperate to polar regions.

This third stage in the development of the North Pacific ocean produced the most dramatic changes in seabird faunas to date. While the cool California Current became established and food became abundant and predictable, seabird diversity dramatically increased and shifted from a fauna dominated by archaic Pelecaniformes to a diverse system with extant representatives of both the Pelecaniformes and Procellariiformes (see Fauna
I in figs. 2, 5). Although the genera representing these higher taxa in this fauna are commonly found today in temperate waters, the first of these “extantlike” faunas (Fauna I) bore little resemblance to the Recent seabird communities of the North Pacific.

At least two related tectonic events are perhaps responsible for the fourth stage in the development of the North Pacific ecosystem. The Middle Miocene collision between Australia and Indonesia narrowed the Indo-Pacific seaway and caused a deflection of equatorial waters northward along the western margin of the North Pacific (Keller and Barron 1983). In the eastern Pacific, the Isthmus of Panama began to emerge at 13–12 Ma, limiting the Atlantic-Pacific connection to shallow water (Duque-Caro 1990). At this time, sea levels dropped, and deep-sea circulation and phytoplankton productivity patterns typical of today became established (Keller and Barron 1983; fig. 6). The increasing latitudinal thermal gradient of the third stage, and restricted equatorial flow in both the eastern and western Pacific in this fourth stage caused intense upwelling of nutrient-rich bottom water in California at about 12.4–11.1 Ma (Barron and Keller 1983; Barron 1986b; fig. 6). The diversity of Alcidae dramatically increased during this time period (Fauna II; figs. 1, 2, 5).

Alcids are wing-propelled diving seabirds restricted to cold to temperate water regions of the Northern Hemisphere (Storer 1960; Ainley 1977; Harrison 1983; Olson 1985). Ainley (1977) showed that in Recent seabird systems 40%–80% of the seabirds nesting in polar and subpolar regions are birds that obtain their food by either wing-propelled or foot-propelled diving. He also showed that the incidence of diving birds is highly correlated with water temperature, increasing in number as water temperature decreases (Ainley 1977: fig. 1; see also Ainley and Boekelheide 1984). In addition, Briggs et al. (1987: p. 66) observed that alcids in California are intimately associated with the upwelling zone of the California Current system, and that the Recent “California seabird fauna is dominated in numbers and biomass by species that reach greatest abundance in cool waters of the upwelling zone.” During warm-water events in California, and especially during the 1983 ENSO when upwelling ceased, reproductive success for alcids on Southeast Farallon Island was extremely low (Ainley and Boekelheide 1990). Apparently the success of the Alcidae in the California Current is strongly tied to the evolution and maintenance of the upwelling system, and the dramatic rise in alcid diversity in Fauna II is related to the increase in productivity and the proliferation of predictable and local food resources. In addition to the growth in alcid diversity, the increase in the morphologic diversity of the Sulidae during this time (see Fauna II above) suggests that they expanded their foraging habits from plunging (Ashmole 1971; Ainley 1977) to wing-propelled or foot-propelled diving (Warheit 1990). According to Ainley (1977), for seabirds foraging in Recent cold upwelling regions, diving is a more successful strategy than plunging, and the move toward this habit in the Sulidae suggests that they too are taking advantage of an increase in food supply.

Although the oceanographic conditions that led to an increase in seabird diversity in Fauna II were similar to the conditions of today, they were not identical. The California Current itself was narrower and closer to shore at 10 and 8 Ma than today’s current (Domack 1986). A narrower, inshore California Current would establish a more sharply defined east-west gradient from the cold nearshore environment to the warmer offshore environment of the North Pacific Gyre (Domack 1986). Because the foraging habits of today’s California Current seabirds are largely determined by the character of the current (Briggs et al. 1987), foraging habits and habitats of seabirds in these extinct communities probably differed from those of the Recent system.

The decrease in seabird diversity in Fauna III is associated with a drop in sea level (fig. 6; Barron 1986b) and a broad and offshore California Current (Domack 1986). In addition, Barron and Keller (1983: fig. 12, table 8) showed frequent warm-water events of short duration between 8 and 5 Ma (see also Woodruff and Savin 1989). Although Faunas I, II, and III experienced both warm- and cold-wa-
ter events, the fluctuations in global water temperatures during Faunas I and III were more frequent and intense than those of Fauna II (Barron and Keller 1983). Whereas the more constant cold-water environment of Fauna II may have been important in the radiation of eastern North Pacific seabird taxa, the resumption of a more variable and possibly warmer (and therefore less productive) environment during Fauna III may have contributed to the extinction of some seabird taxa from Fauna II. In addition, Vermeij (1989) showed that several molluscan taxa endemic to the western North Pacific had representatives in the eastern North Pacific that became extinct during the time of Fauna III. (Vermeij 1989: p. 338) stated that the last appearances of these eastern North Pacific taxa occurred in the Empire Formation of Coos Bay. Armentrout et al. (1983) showed this formation to be approximately 10-6 Ma, putting the last appearances of these molluscs in seabird Fauna II. Vermeij (1989) attributed the extinction of the eastern North Pacific molluscs and the survival of their western North Pacific counterparts to the interruption of productivity in the eastern Pacific only. Although the poor fossil record of seabirds from the western North Pacific from this time period does not permit an analysis similar to that of Vermeij, the fact that pseudodontontors remained extant in the western North Pacific but became extinct in the eastern North Pacific during the time of Fauna III is consistent with the pattern of molluscan geographical restriction uncovered by Vermeij (1989). However, the increase in maccalid diversity in this fauna is inexplicable.

An alternative hypothesis is that the decline in seabird diversity during Fauna III is an artifact of the fossil record. It is possible that seabird taxa were diverse and abundant during Fauna III but not preserved, or, that material was preserved and has yet to be collected. Evidence to support this alternative hypothesis was suggested by the unpublished Purisima Formation material discussed above. In addition, rocks deposited in California during the time of Fauna III are more enriched in detrital components than those deposited during the time of Fauna II (Barron 1986b). This suggests that animals or plants that occurred during the time of Fauna III had a lower probability of being preserved as fossils than those that occurred during the time of Fauna II (Barron 1986b). At this time, it is difficult to choose between these alternative hypotheses.

The well-resolved paleotemperature curves of Woodruff et al. (1981), Barron and Keller (1983), and others do not include data for the Pleocene (Fauna IV; see fig. 1). However, Savin et al. (1975) stated that isotopic temperatures dropped rapidly during the Pliocene, bringing the bottom-water temperatures to today's levels. Savin et al. (1975: fig. 6) showed that the drop in bottom-water temperatures occurred within the Planktonic Foraminiferal Biochronozone N21 (roughly 3 Ma; Haq et al. 1987 and references therein) or during the time of Fauna IV. Savin et al. (1975: p. 1505) attributed this final drop in ocean bottom temperatures to the continued "expansion of [the Antarctic] ice sheets, large-scale delivery of ice to the seas, and formation of sea ice." In addition, Barron and Baldauf (1989) reported a high thermal gradient and the onset of Northern Hemisphere glaciation around 2.5 Ma.

The seabirds of Fauna IV experienced rapid fluctuations in eustatic sea levels (see Haq et al. 1987) associated with polar glaciation and intensified tectonic activity, as well as decreasing water temperatures (for effects of mountain uplift on coastal upwelling in the eastern North Pacific, see Ruddiman and Kutzbach 1989). I considered these oceanographic and geographic events to be the fifth stage in the development of the Recent North Pacific ecosystem. In addition, this stage most likely extended into the Pleistocene, and may continue to affect Recent seabird systems. Although changes in the eustatic sea level are global, their regional or local effects depend on local geography and topography and behavior of the seabird taxa. Thus, the effects of eustatic sea-level changes on the California Current system may be different from those in Japan and depend on the local ocean-bottom and terrestrial topography (see Warheit and Lindberg 1988). Because there are no published accounts of seabirds from the west-
ern North Pacific during the time of Fauna IV, I am unable to compare the seabird community composition and diversity in eastern North Pacific with that of the western North Pacific. Nevertheless, fluctuations in sea level in California during Fauna IV time and into the Pleistocene may have rapidly changed the amount and quality of available seabird and pinniped breeding (or haul-out) space (Warheit and Lindberg 1988). Seabird taxa that are morphologically and behaviorally equipped to cope with these rapid changes in habitat would have higher probabilities of survival than taxa that are unable to alter their breeding habitat preferences.

Vrba and Gould (1986 and references therein) discussed the interaction among organism-level characters (e.g., breeding-habitat preference) and the environment (e.g., availability of breeding space), and speciation and extinction. They hypothesized (p. 224) that “the probability that organisms will perceive environmental changes as deterioration of habitat is greater in the case of certain specialists than in generalists. Thus, such stenotopes [specialists] should be subject more frequently to directional selection at the level of genotypes and phenotypes, and consequently to fragmentation and divergence of populations, speciation, and extinction.” The rapid rise of marine Laridae in Fauna IV (especially between Fauna IV and the Recent) and the Pleistocene extinction of the Sulidae in the California Current system may have been related to their relative abilities to cope with the environmental fluctuations (see Warheit and Lindberg 1988). The taxonomic decline of the flightless mancullids between Fauna III and IV and their Pleistocene extinction may be related to local changes in sea level and the synchronous diversification of pinnipeds (Warheit and Lindberg 1988). As with the flightless plotopterids, mancullid extinction may have resulted from competition for breeding space with gregarious pinnipeds rather than from changes in food resources (Warheit and Lindberg 1988). Because mancullids and sulids were among the most diverse and ubiquitous taxa in the California Current seabird communities (figs. 2, 5), the ecological and geological factors that contributed to their radiations and extinctions were important structuring agents in these fossil faunas. In addition, because the composition of Recent seabird communities is contingent upon historical events (e.g., radiations and extinctions), factors governing these historical events (e.g., Antarctic glaciation) are, in themselves, structuring agents of the Recent communities.

Conclusion

Changes in the relative geographic positions of Antarctica, Australia, Central and South America, and India during the Tertiary produced profound effects on the paleoceanography of the North Pacific. Large-scale phenomena, such as events in the Southern Hemisphere, affected the North Pacific on several temporal and spatial scales. The continued breakup of the Antarctic/Australian continent, and the widening of the East Indian Antarctic Basin in the Late Eocene resulted in a worldwide decline of ocean-bottom temperatures (stage 1). The decline in temperatures in the North Pacific coincided with the evolution of plotopterids and pseudodontornans in both the western and eastern North Pacific. The widening of Drake Passage between Antarctica and South America during the Early Miocene intensified the thermal isolation of Antarctica and provided near-freezing ocean-bottom waters to the North Pacific (stages 2 and 3). These events coincided with the rise of seabird faunas more typical of Recent seabird systems (Fauna I). Because these physical events were global in nature, they affected the North Pacific as a whole, producing similar changes in the avifauna of both Japan and the eastern Pacific.

The increase in the latitudinal thermal gradient during the Middle and Late Miocene (stage 4; Fauna II) was also related to tectonic events in the Southern Hemisphere and glaciation on Antarctica. Nevertheless, its combined effect with the contemporaneous rise of the Isthmus of Panama, and the presence of an eastern boundary current off California produced local, small-scale changes in the oceanographic properties particular to the California Current. The dramatic rise of the Alcidae and the morphological diversifica-

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tion of the Sulidae in California coincided with these local changes in bottom temperature and upwelling. Rapid changes in eustatic sea level and the evolution of gregarious pinnipeds in the eastern North Pacific (stage 5) are other examples of local, small-scale phenomena that may have influenced seabird diversity in California during the time of Fauna IV.

Structure and diversity of seabird communities in the North Pacific today are, in part, functions of historical events operating at several temporal and spatial scales. Similarities among seabird communities within the North Pacific and between the North Pacific and the North Atlantic may be more the product of long-term, large-scale geological events than convergent similarities resulting from similar environmental conditions today. Conversely, seabird communities within the North Pacific may differ in composition as a result of smaller-scale, regional phenomena. The interactions among the differently scaled geologic and ecologic factors produced the structure in today’s seabird systems. I urge seabird biologists to use all available data, including the fossil record and oceanographic histories, to test hypotheses concerning the structure of seabird systems throughout the world.

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Literature Cited


Appendix

The following is a list of formations included in each seabird fauna. Following the formation name and location are reference numbers (in parentheses) corresponding to the references listed in figure 2.

FAUNA A (52-38 Ma)


a) 40-39 Ma in Armentrout et al 1983

b) Goedert (1988, 1989) considered the formation correlated with the Pliobronchian Chronostratigraphic Stage (40-36 Ma in Berggren et al 1985).
FAUNA B (31 [7−22.8 Ma)

1. Pyaht Formation of Twin River Group, Clallam Co., Wash. (38)
   31(7−24 Ma in Armentrout et al. 1983

2. Hatazu, Asagai, and Ashiya Formations, Honshu and northern Kyushu, Japan (35, 36, 47)
   a) According to Hasegawa (1977), the Hatazu and Asagai Formations are correlated with the Chattian Chronostratigraphic Stage (30−23.7 Ma in Berggren et al. 1985), and the Ashiya Formation is correlated with the Aquitanian Chronostratigraphic Stage (23.7−22.8 Ma in Berggren et al. 1985).
   b) Although Berggren et al. (1985) placed the beginning of the Chattian at 30 Ma (Magnetic Polarity Anomaly 10 in Chron 10), Swisher and Prothero (1990) placed this anomaly at about 28 Ma.

3. Carmanah Point, Vancouver Island, British Columbia, Canada (1, 16, 46)
   Becker (1987) summarized the debate concerning the age of this locality. The only seabird fossil from this locality is *Cyprornis magnus*, described by Cope (1895: p. 451) as “not older than Eocene nor later than Oligocene.” However, Wetmore (1928) considered the fossil Miocene in age, whereas Ray (personal communication in Becker 1987) believed this locality to be Oligocene. Finally, Goedert (1989) provided data suggesting that the Carmanah Point rocks are Late Eocene to Early Oligocene in age. I listed this locality here, and considered *C. magnus* to be in Fauna B for convenience only.

FAUNA C (24−18 Ma)

1. Pyramid Hill Local Fauna of Jewett Sand, Kern Co., Calif. (24, 27, 36)
   Tedford et al. (1987) placed this local fauna at 22−21 Ma. Considered late Arikareean North American (N.A.) Land-Mammal Age

2. Nye Formation or Mudstone, Lincoln Co., Oregon (40)
   24−18 Ma in Armentrout et al. (1983)

FAUNA I (18 [or 15]-13 [or 12] Ma)

The first three formations listed in this fauna are in California and northern Baja California and between 15 and 13 Ma. The last two localities are in Japan or Oregon and slightly older (possibly as old as 18 Ma). Unfortunately most of the fossil material in this fauna is from the first three formations, with only a few specimens from the latter two localities. When additional fossil and stratigraphic data are obtained, it may be possible to divide this fauna into two faunas, with the older two localities being referred to as Fauna D.

1. Sharktooth Hill Local Fauna, Round Mountain Silt, Kern Co., Calif. (12, 13, 17, 21, 32, 40, 44, 49, 50)
   Tedford et al. (1987) placed this local fauna at 15−13 Ma. Considered late Barstovian N.A. Land-Mammal Age and Lusitan Benthic Foraminiferal Stage

2. La Misión Local Fauna, Rosarito Beach Formation, northwestern Baja California, Mexico (44)
   According to Deméré et al. (1984) this local fauna also includes silicoflagellates indicative of the *Corbisena trisacantha* Zone dated at 14−15 Ma. Potassium-argon radiometric dates for basalts located above and below the local fauna are 14.3 ± 2.6 Ma and 16.1 ± 2.1 Ma, respectively (Deméré et al. 1984).

3. Upper Oso Dam assemblage, Topanga Formation, Orange Co., Calif. (33)
   Based on the shark, and marine and land mammal fossils, Howard and Barnes (1987) and Rashcke (1984) considered this assemblage to be of the same age as the Sharktooth Hill local fauna.

4. Astoria Formation, Lincoln Co., Oreg. (40)
   a) 18−17 Ma in Armentrout et al. (1983)
   b) Goedert (1989) stated that this formation is correlated with the Newportian and not the Pillar surgeon Stage, as reported by Becker (1987). Armentrout showed the Newportian Molluscan Stage as being 20−13 Ma.

5. Nagura Formation, Chichibu, Saitama Prefecture, Japan, and Akeyo Formation, Mizunami, Gifu Prefecture, Japan (37, 42, 43, 47)
   Correlations with North American ages and formations are not well understood. Olson and Hasegawa (1985: p. 138) stated that the Akeyo Formation is a correlative of the Na-taki Formation in Japan and “approximately correlative with the Astoria Formation of Oregon some 15 to 18 million years ago.” Ono (1989) stated that the Nagura Formation and fossil from the Mizunami Basin (~Akeyo Formation) are Middle Miocene (approximately 17−12 Ma in Berggren et al. 1985).

FAUNA II (13−8 Ma)

1. Laguna Hills (Leisure World locality): Monterey Formation, Orange Co., Calif. (22, 23)
   The age of this locality was discussed by Howard (1976, 1978). Based on vertebrate fossil correlations, the age is estimated to be Clarendonian N.A. Land-Mammal Age (12−9 Ma in Tedford et al. 1987, but slightly older than Laguna Niguel.

2. Laguna Niguel: Monterey Formation, Orange Co., Calif. (28, 29)
   The age of this locality was discussed by Howard (1976, 1978). Based on vertebrate fossil correlations, the age is estimated to be Clarendonian (12−9 Ma in Tedford et al. 1987), but slightly younger than Laguna Hills locality.

3. Flagstone Quarry (Tepusquet Creek): Monterey Formation, Santa Barbara Co., Calif. (19)
   Howard (1983) stated, without explanation, that Tepusquet Canyon is correlated with the Clarendonian N.A. Land-Mammal Age (12−9 Ma in Tedford et al. 1987).

4. Taylor Quarry: Santa Margarita Formation, Santa Cruz Co., Calif. (49, 50)
   This formation was figured by Barron (1986a) and considered by Repenning and Tedford (1977) to be 12−9 Ma.

5. Valmonte (Lomita) Diatomite: Monterey Formation, Los Angeles Co., Calif. (8)
   a) Obradovich and Naeser (1981) placed the Valmonte Diatomite at 13 (12−8 Ma, but discussed an ash deposit 38 m from top of diatomite that has a fission-track date of 6.9 ± 0.6 Ma.
   b) Barron (1986a) showed the Valmonte Diatomite to be roughly 12−7.5 Ma.

6. Modelo Formation, El Sereno, Studio City, and Calabasas, Los Angeles Co., Calif. (5, 20)
   a) Obradovich and Naeser (1981) showed two fission-track dates of 7.8 ± 0.8 and 11.5 ± 1.2 within the Modelo Formation. According to their figure 4, these dates are from the middle to lower portions of the formation, respectively. No seabird publication indicated the place in the formation from which the fossils were recovered.
   b) Barron (1986a) provided biostratigraphic age estimates (based on Benthic Foraminiferal Zones) for the dates listed by Obradovich and Naeser (1981). These ages are 8.6−6.5 Ma and 13.9−13.3 Ma, respectively.

7. Lompoc Diatomite: Sisquoc/Monterey Formation, Santa Barbara Co., Calif. (4, 30)
   The exact location of this locality is not known. All microfossil evidence discussed below assumes that the seabirds (and marine mammals) were recovered from the Johns-
Manville diatomite Quarry (Barron personal communication 1990). Barnes (personal communication 1990) suggested that the marine mammals and birds from Lompoc were not from that quarry, but from a quarry to the west of Johns-Manville.

a) Biostratigraphy of marine vertebrates (see, e.g., Repenning and Tedford 1977) strongly suggests that this locality is Clarendonian N.A. Land-Mammal Age, Mohonian Benthic Foraminiferal Stage, and about 12–10 Ma. The Greco Quarry is to the east of Lompoc and is roughly 11–9 Ma (Barron personal communication 1991).

b) Obradovich and Naeser (1981) dated an ash bed 165 m above the footwall of the Johns-Manville Quarry at 7.6 ± 1.3 Ma. These authors also considered this locality to be within the Monterey Formation.

c) Barron (1986a, personal communication 1990) also placed the Johns-Manville Quarry within the Monterey Formation and showed it to be roughly 8–6 Ma.

Therefore, there are two estimates for the age of this locality: 12–10 Ma and 8 (8.9)–6 Ma.

### FAUNA III (7[6]–4 Ma)

1. San Mateo Formation, Oceanside, San Diego Co., Calif. (31, 41)

   Barnes (1976) stated that the San Mateo, Purisima, Capistrano, and Almejas Formations are correlated with each other, and may be correlated with the Jacalitos and Etche-goin Formations, making these formations correlated with the “Jacalitos” and “Etche-goin” Provincial Molluscan Stages. Barnes (1976: p. 331) added that the formations are “less directly” correlated with the Hemphillian N.A. Land-Mam-mal Age and the late Delmontian, Repettian, and Venturian Foraminiferal Stages. Barnes did not explicitly specify how these formations were correlated, but were presumably based on the fossil cetaceans.

2. Almejas Formation, Isla Cedros, Baja California, Mexico (26)

   a) Howard (1971) considered this formation Early Pliocene.

   b) Barnes (1976) considered this formation correlated with the San Mateo Formation (see above).

   c) Repenning and Tedford (1977) estimated the age of otarioid seals from this formation at 8–6 Ma.

3. Purisima Formation, Santa Cruz Co. and San Mateo Co., Calif. (49, 40; F. Perry in preparation)

   a) Repenning and Tedford (1977) estimated the age of otarioid seals from this formation in Santa Cruz County at 6.7–4 Ma.

   b) Based on diatom biostratigraphy Barron (1986a) estimated the age to roughly 6–4.5 Ma.

   c) Based on magnetic stratigraphy Madrid et al. (in Barron 1986a) showed that the lower part of the Purisima extends from the upper part of polarity Chron 6 to the lower part of the Gilbert Reversed polarity Chron (6–5 Ma in Berggren et al. 1985)

4. Capistrano Formation, Orange Co., Calif. (11)

   a) Miller (1951) described this formation as Middle Miocene, whereas Howard (1983) listed Oceanodroma hubbsi (the only seabird from this formation) as being Late Miocene-Early Pliocene, or Hemphillian N.A. Land-Mammal Age. Tedford et al. (1987) placed the Hemphillian at 9–4.5 Ma.

   b) Barron (1986a) figured the Capistrano Formation from Newport Beach, California as correlated with the Purisima Formation. He also showed the boundary between the older Monterey Formation and younger Capistrano Formation at 5.5 Ma.

5. Dainichi Sand of Kakegawa Group, Kakegawa, Shizuoka Prefecture, Japan (47)

   Okazaki (1989) listed two seabird localities from the Pliocene of Japan: Maesawa, Iwate Prefecture and Kakegawa, Shizuoka Prefecture. Ono (1980) considered the Kakegawa, Shizuoka Prefecture locality Middle Pliocene. According to Berggren et al. (1985) the Pliocene ranges from about 5.3 to 1.6 Ma, the middle of which is 3.7 Ma (there is no formal “middle Pliocene” epoch).

   Based on the correlations of Barnes (1976) and Barron (1986a) I estimated the age of Fauna III to be about 7 (6)–4 Ma.

### FAUNA IV (3–1.5 Ma)

1. San Diego Formation, San Diego Co., Calif. (9, 14, 15, 18, 25, 26, 39, 48)

   a) Barnes (1976: p. 332) stated that the San Diego Formation is “younger than the vertebrate-bearing levels in the lower part of the Almejas Formation . . . and therefore judged indirectly to be younger than the bulk of the Purisima, Capistrano, and Drakes Bay Formations, may be broadly correlative with the Blancon North American [Land Mammal Age], the Wheelerian foraminiferal stage, the ‘San Joaquin’ provincial molluscan stage.”

   b) Deméré (1983) considered the San Diego Formation no older than Planktonic Foraminiferal Zone N21 (3–2 Ma in Berggren et al. 1985) and at least as young as the Emiliania annula Subzone, dated at approximately 1.5 Ma.

   c) Repenning and Tedford (1977) estimated the age of the otarioid seals from this formation at 4–2 Ma.