Almost 100 species of exotic marine invertebrates have been introduced into San Francisco Bay by man in the past 130 or more years. Primary mechanisms of introduction include transport of fouling, boring, and ballast-dwelling organisms by ships and epizoic and nestling invertebrates by commercial oysters. With the resolution of taxonomic problems and adequate exploration, many more introduced species may eventually be recognized from the Bay.

The impact of this exotic fauna can be assessed in economic terms (pestiferous species, including shipworms and other borers) and in geologic terms (an introduced boring isopod has modified extensive portions of the bay shoreline by weakening clay and mud banks). The greatest effect, however, may be biological and ecological: the establishment of an introduced fauna as numerical and biomass dominants in many regions of the Bay, as revealed in both short- and long-term quantitative and qualitative studies. The modern-day significance of introduced species in fouling, benthic, and mudflat ecosystems in portions of San Francisco Bay raises questions as to the role of invertebrates prior to the mid-19th century both in the organic matter budget of the Bay-Estuary system and in the support of large native shorebird populations.

Man’s extensive modifications of the Bay and concomitant creation of novel environmental conditions, the absence of a diverse native estuarine fauna, and competitive displacement have all played roles in the successful establishment of this impressively large and diverse introduced fauna.
INTRODUCED INVERTEBRATES OF SAN FRANCISCO BAY

JAMES T. CARLTON
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Almost 100 species of exotic marine invertebrates have been introduced into San Francisco Bay by man in the past 130 or more years. Primary mechanisms of introduction include transport of fouling, boring, and ballast-dwelling organisms by ships and epizoic and nestling invertebrates by commercial oysters. With the resolution of taxonomic problems and adequate exploration, many more introduced species may eventually be recognized from the Bay.

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In 1857, William Stimpson wrote that, “The Bay of San Francisco... is nearly barren of animal life except at its entrance.” Such is no longer the case. Of all the faunal modifications that have occurred in San Francisco Bay in the past 130 years, perhaps none has been more profound than the successful establishment of a large number of introduced invertebrates, transported accidentally by man to the Bay since the mid-19th century, from the western and southwestern Pacific and the Atlantic oceans. Unfortunately, the historical record of these introductions is largely an anecdotal one, attention having been focused upon a few of the larger, more conspicuous, or troublesome exotic species. Perhaps two-thirds of all known species of introduced invertebrates on the Pacific coast also occur in San Francisco Bay. The Bay may thus provide a model for the study of the biology of introduced faunas on the Pacific coast. Criteria for the recognition of introduced species are considered in detail by Carlton (1978). These criteria include evidence based upon paleontology, archeology, recent history, systematics, distributional ecology, transport mechanisms, and biogeography.

MECHANISMS OF INTRODUCTION

Two major mechanisms, and several of lesser importance, are responsible for the transport of exotic species into San Francisco Bay. These are (1) the introduction by ships of fouling, boring, and ballast-dwelling organisms, and (2) the introduction of epizoic and nestling invertebrates on and among commercial oysters imported from the western Atlantic and the western Pacific oceans.
There may have been some incidental ship introductions prior to the mid-19th century, but hard data are scanty. We know, for example, that in the fall of 1595, the ship San Agustín, four months out of Manila in the Philippines, and doubtless with a fouling and/or boring fauna on her wooden hull, sank in Drake's Bay (Fig. 1) near the entrance to San Francisco Bay (Wagner 1924; Heizer 1941). From the late 18th century until the mid-19th century, a few fur and hide ships, traveling between the Atlantic, western South America and the western and southwestern Pacific, operated along the California (and northwest American) coast, occasionally visiting San Francisco Bay. As Ewan (1955) has noted, "These vessels were the source of introduction of many organisms, some injurious: insects, weeds, and rodents," and there is no reason to suspect that these ships did not also carry fouling and boring faunas as well.

It was not, however, until the California Gold Rush of 1849 and subsequent years that shipping apparently became an important mechanism for the introduction of exotic invertebrates into the Bay. Indeed, there are no records of introduced species in San Francisco Bay prior to the Gold Rush years, but perhaps only because there is no biological record of the fauna of the Bay prior to the mid-19th century. From 1849 on, however, ships from many ports around the world, not only from both sides of the Atlantic, but also from China (Williams 1930), Australia and New Zealand (Monaghan 1966) and Chile and Peru (Monaghan 1973), arrived in increasing numbers. In the years 1849 and 1850, almost 48,000 persons, mostly gold seekers, arrived by ship at the port of San Francisco (Farwell 1891). By the early 1850's, passage from New York or Boston around Cape Horn to San Francisco Bay could be accomplished in 3 to 4 months (Rydell 1952). The ability of boring and fouling species to survive this journey from New England to California,
twice through tropical waters, appears certain: the transport of living ship-bottom biotic assemblages across comparable distances and temperature changes has been well documented (Pilsbry 1896; Chilton 1911; Hentschel 1923; Orton 1930; Bertelsen and Ussing 1936; Bishop 1951; Allen 1953; Skerman 1960). Indeed, many of the species concerned are overwhelmingly tolerant to euryhaline and eurythermal conditions. According to Rydell, more clipper ships passed through the Golden Gate in 1853 than in any other year of the Gold Rush; “on several occasions, three clippers stood in through the Golden Gate within twenty-four hours, and on two others, five arrived within forty-eight hours” (Rydell 1952:138). Coincidentally, the first record of an introduced species in San Francisco Bay is also 1853: the Atlantic barnacle, Balanus improvisus (Carlton and Zullo 1969).

An opportunity for both multiple and massive inoculations of exotic species occurred almost simultaneously: not only were hundreds of ships arriving within a period of a few years, compared to the few arrivals prior to the Gold Rush, but equal numbers were being abandoned in the Bay as ship’s crews left for the gold fields. In 1851, for example, more than 800 ships were at anchor or abandoned in Yerba Buena Cove in San Francisco (see Kemble 1957, for a series of contemporary photographs). Early introductions, besides Balanus improvisus, were likely hydroids (such as the Atlantic Tubularia crocea, present in the Bay by at least the late 1850’s), polychaetes (especially tubiculous species), cheilostome and ctenostome bryozoans, gammarid amphipods of the genera Jassa, Podocerus, Stenothoe, and Corophium, tunicates, and wood-boring organisms such as the gribble (isopod) Limnoria spp.. The anemone Metridium senile and the mussel Mytilus edulis were doubtless common components of this fouling fauna; while the former may have been and the latter was aboriginally present in the San Francisco Bay area, Atlantic stocks of both species were introduced and mixed with native populations. Indeed, it may be that morphometric analyses of fossil and archeological Mytilus edulis from the Bay region would reveal differences from present day local populations.

With the completion of the Transcontinental Railroad in 1869, shipping from the Atlantic declined, but increased again with the opening of the Panama Canal in 1914, although the fresh-water barrier of the canal now likely changed the composition of ship’s fouling faunas which successfully entered the Pacific Ocean. The last quarter of the 19th century saw considerable maritime activity in San Francisco Bay, the grain-trade figuring particularly prominently. In the peak year of the trade, 1880-1881, grain exports nearly equalled the mean annual exports for all dry cargo from San Francisco during the period 1925 to 1940 (Kemble 1957). The early decline of wooden sailing ships, the greatly increased efficacy of antifouling paints, and the increased speeds of ocean-going vessels may have led to a decrease in the transport of boring and fouling organisms. However, ship-borne introductions appear to continue, and a few species of western or south-western Pacific crustaceans recently noted in the Bay may be examples of present-day introductions; e.g., the isopods Dynoides dentisinus and Ianiropsis serricaudis and the amphipod Corophium sp. (E. Iverson and J. Chapman, pers. comm.).

Infaunal, semi-terrestrial, or relatively errant marine invertebrates may also be transported by ships, through water ballast (taking up and later discharging larvae or adults of benthic species), shingle ballast (taking up and discharging invertebrates among stones, rocks, and dried algal masses collected from beaches and used as ballast), and fouled sea-water systems.

The discharge of ship ballast in San Francisco Bay appears to have led to the introduction of at least two exotic maritime (semi-terrestrial) invertebrates. The Chilean or New Zealand shore-hopper (talitrid amphipod), Orchestia chilensis, redescribed as O. enigmatica from San Francisco Bay (see Bousfield and Carlton 1967) may have been transported to San Francisco Bay in either shingle ballast or round beach gravel. Beach gravel and debris are known to have been taken up for ballast, for example, at Chilean ports and discharged in such areas as the Oakland Estuary in San Francisco Bay, adjacent to Lake Merritt, in Oakland, where the only known California population
of this beachhopper exists. It is also probable that ballast has played a role in the introduction of the maritime earwig, *Anisolabis maritima* (Dermaptera), to the shores of San Francisco Bay, where the only established populations of this species in California, and perhaps on the Pacific coast, are known (see records in Langston 1974; Langston and Powell 1975; Langston and Miller 1977).

Newman (1963) has suggested that fouled sea-water systems were responsible for the accidental introduction of the western Pacific shrimp *Palaemon macrodactylus* into San Francisco Bay. This species was first found in the Bay in 1957, and Newman has compiled evidence that the introduction itself may have been about 1954. The synchrony of this introduction with the greatly increased military and cargo traffic between California and Japan and Korea immediately prior to 1954, associated with the Korean War, is striking. Despite the long history of ship traffic between both sides of the North Pacific Ocean, this appears to be a further example that intensified periods of shipping (also associated with the Gold Rush activity) are often concomitant with or immediately precede introductions. Similarly, the Australasian serpulid polychaete, *Mercierella enigmatica*, first appeared in San Francisco Bay about 1920, following increased world-wide shipping associated with the second decade of the 20th century.1

### Commercial Oyster Industries

Of equal or greater importance in the introduction of exotic invertebrates have been the commercial oyster industries. A single oyster shell may have upon it representatives of 10 or more invertebrate phyla, comprising dozens of species, and these numbers can be greatly increased when oysters are packed together for shipment with associated clumps of mud and algae, and with water pockets in empty valves used for cultch. Elton (1958) remarked that "...the greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture...". San Francisco Bay provides a thorough documentation of this. Beginning with the completion of the Transcontinental Railroad in 1869, hundreds of carloads of the Eastern (or Virginia) oyster, *Crassostrea virginica*, were transported to San Francisco Bay (and elsewhere on the Pacific Coast) from the Atlantic coast of the United States (Barrett 1963). Early shipments were heavily fouled, if one may judge from the introductions resulting from them, and little attempt was made to prevent the transport of the associated oyster bed fauna, although the relatively late appearance of the oyster drill, *Urosalpinx cinerea*, about 1890, suggests that some attention may have been given to deterring the introduction of potential pests. Throughout the latter half of the 19th century oysters were continually shipped from the east coast and planted throughout the Bay, providing extensive opportunity for the inoculation into the Bay of many common northwestern Atlantic bay and estuarine invertebrates. More than 100 years would pass before some of these introductions were to be recognized (such as the malaminid polychaete, *Asychis elongata*; see Light 1974).

Shortly after the turn of the century, the Atlantic oyster industry as a large scale endeavor in San Francisco Bay faded away for a variety of reasons, pollution appearing to be one of them. But the oysters had left a permanent legacy: many of the associated oyster epizoics had taken hold in vast numbers. Portions of the shallow bay waters are today carpeted almost solely with species introduced with Atlantic oysters. Among the mollusks, for example, are the ribbed mussel, *Ischadium demissum* (= *Modiolus demissus*), the soft-shell clam, *Mya arenaria*, the gem clam, *Gemma gemma*, and the mudsnail, *Ilyanassa obsoleta* (= *Nassarius obsoletus*).

In the early 20th century, oyster farmers on this coast turned their attention to the Japanese (or Pacific) oyster, *Crassostrea gigas*, an endeavor which largely involves bays and estuaries to the

1 Miller (1968), along similar lines, noted the apparent introduction by naval ships of the isopod *Paracerceis sculpta* from San Diego Bay to Hilo Harbor and Pearl Harbor, Hawaii, during World War II.
CARLTON: INTRODUCED INVERTEBRATES

north or south of San Francisco Bay (Barrett 1963). Throughout the 1930's plantings of Japanese oysters were made in San Francisco Bay, and these may have led to the introduction of a number of Japanese estuarine invertebrates. Two Japanese mollusks now abundant in the Bay, the rock-cockle, *Tapes japonica*, and the small mussel *Musculus senhousta*, were first collected in 1946, the date being perhaps more of an artifact associated with lack of intensive collecting in the Bay during the Second World War, rather than a close approximation of the date of introduction.

Other Mechanisms

Additional means of transport of foreign marine invertebrates into San Francisco Bay are known, but few established introductions have been traced to these.

A comparatively new mechanism appears to be algae (such as *Ascophyllum nodosum* and *Fucus* spp. received in shipments of Atlantic lobsters from New England by local restauranteurs and discarded into the Bay. Although the extent of this activity is probably limited, discarded algae have apparently served as the vehicle for the introduction of the Atlantic periwinkle *Littorina littorea* into the Bay since the late 1960's (Carlton 1969; Miller 1969). Adult *Littorina littorea*, now found nestled in rock crevices in several locations along the Bay's eastern shoreline, may provide a unique opportunity to observe the establishment, population increase, and dispersal of an introduced species in San Francisco Bay shortly after its introduction. Miller (1969) has listed additional species which are transported with algae shipped with lobsters.

Many exotic estuarine and fresh-water fishes have been introduced into the San Francisco Bay-Delta region (Moyle 1976a, b) by means of tank cars, and water associated with these introductions (Throckmorton 1874) may well have carried a wide variety of small planktonic or even benthic species. Little is known, however, of the establishment of any exotic species by this means, probably due to the limited knowledge, taxonomically and biogeographically, of candidate species which may have been transported by this means (such as protozoans, copepods, and rotifers). Hazel (1966), however, has suggested that the presence of the eastern American freshwater polychaete, *Manayunkia speciosa*, in the Sacramento-San Joaquin River Delta and in Oregon may be due to the transport of water associated with catfish introductions from the northeastern United States, including catfish and water directly from the type locality of *M. speciosa* in Pennsylvania.

THE INTRODUCED FAUNA

The result of 130 or more years of introductions has been the establishment in San Francisco Bay of about 96 species of exotic marine invertebrates (Table 1)\(^2\). The introduced fauna is largely restricted to the shallow estuarine rim of the Bay, and proportionately fewer introduced species are to be found as one approaches the Golden Gate. Somewhat more than half of the introduced fauna is composed of mollusks and crustaceans (21 and 32%, respectively). Polychaetes comprise about 15% of the fauna, and coelenterates about 14%. The introduced fauna is largely Atlantic in origin (66%), four times the number originating from the western Pacific (17%).\(^3\) Five percent of the Bay's exotic fauna derives from Australasia and Southeast Asia; 14% is of multiple or uncertain origin, and one species is from Chile.

The exact number of species introduced with each mechanism is difficult to determine because of extensive overlap in habitats of many species: that is, a number of species may have been

\(^{2}\) In discussions and tabulations, taxa indicated by "spp." in Table 1 are counted as two. The number of introduced species is taken as 96, excluding *Littorina littorea* and *Sabellaria spinulosa*, which are questionably established.

\(^{3}\) Includes species coded in Table 1 as A or A?; O or O?.
TABLE 1. INTRODUCED INVERTEBRATES OF SAN FRANCISCO BAY: A PRELIMINARY LIST (DATA FROM CARLTON, 1978 AND FROM NUMBERED REFERENCES, AS INDICATED.)

<table>
<thead>
<tr>
<th>Key:</th>
<th>Status:</th>
<th>Origin:</th>
<th>Mechanism:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>e?, t?</td>
<td>O, C, AA, SE, A, E</td>
<td>a, o, s</td>
</tr>
</tbody>
</table>

**Key:**
- e?, establishment (presence of reproducing populations) uncertain
- t?, specific taxonomy uncertain

**Origin:**
- O, Orient (Western Pacific: Japan and Korea)
- C, Chile
- AA, Australasia (Australia and New Zealand)
- SE, Southeast Asia
- A, Atlantic Ocean
- E, Europe (Northeastern Atlantic Ocean)

**Mechanism:**
- a, discarded algae
- o, commercial oysters
- s, shipping

### PORIFERA (1)
- *Haliclona* sp. (A, o, t?)
- *Microciona prolifera* (A, o)
- *Halichondria bowerbanki* (A, o)
- *Prosuberites* sp. (A, o, t?)
- *Tetilla* sp. (A, o, t?)

### COELENTERATA
#### Hydrozoa
- *Garveia franciscana* (A/AA, o/s) (2)
- *Clava leptostyla* (A, o/s)
- *Cordylophora lacustris* (A, o/s) (3)
- *Turritopsis nutricula* (A, o/s)
- *Syncoryne mirabilis* (A, o/s)
- *Corymorpha* sp. (A?, o?/s?, t?)
- *Tubularia crocea* (A, o/s)
- *Obelia* spp. (A/AA/O, o/s, t?)

### Anthozoa
- *Diadumene franciscana* (O?/AA?, s?) (4)
- *Diadumene leucolena* (A, o/s) (4)
- *Diadumene* sp. (E?, s?, t?)
- *Haliplanella luciae* (A, o/s) (4)

### PLATYHELMINTHES
- *Childia groenlandica* (A, o) (5)

### ANTHOZOAA: POLYCHAETA
- *Neanthes succinea* (A, o)
- *Neanthes* succinea (A, o) (7)

### ANNELIDA: POLYCHAETA
- *Marphysa sanguinea* (A?, o)
- *Boccardia ligerica* (E?, s?) (8)
- *Polydora ligni* (A, o) (8)
- *Polydora* spp. (A, o/s, t?)
- *Pseudopolydora kemi* (O, o) (8)
- *Pseudopolydora paucibranchiata* (O, o) (8)
- *Streblospio benedictii* (A, o) (8)
- *Capitella capitata* (A?, o/s, t?)
- *Heteromastus filiformis* (A, o)
- *Asychis elongata* (A, o) (9)
- *Sabellaria spinulosa* (A?, s?, e?)
- *Mercierella enigmatica* (AA, s)

### MOLLUSCA (10)
#### Gastropoda
- *Littorina littorea* (A, a, e?)
- *Crepidula convexa* (A, o)
- *Crepidula plana* (A, o)
- *Urosalpinx cinerea* (A, o)
- *Busycotypus canaliculatus* (A, o?)
- *Ilyanassa obsoleta* (A, o)
- *Ovatella myosotis* (A, s?)
- *Teneilla pallida* (E?, s?) (11)
- *Eubranchus misakiensis* (O, s?) (12)
- *Okenia plana* (o, s?) (11)
- *Trinchesia* sp. (O, s?) (13)
- *Odostomia bisuturalis* (A, o)
- *Musculus senhousia* (O, o)
- *Ischadionum demissum* (A, o)
- *Gemma gemma* (A, o)
- *Tapes japonica* (O, o)
- *Petricola pholadiformis* (A, o)
**MOLLUSCA (continued)**

- *Mya arenaria* (A, o)
- *Teredo navalis* (A?, s)
- *Lyrodus pedicellatus* (A?, s)

**ARTHROPODA: CRUSTACEA**

- **Ostracoda**
  - *Sarsiella zostericola* (A, o) (14)

- **Copepoda**
  - *Mytilicola orientalis* (O, o) (15)

- **Cirripedia**
  - *Balanus improvisus* (A, o/s) (17)
  - *Balanus amphitrite amphitrite* (AA, s)

- **Amphipoda**
  - *Ampithoe valida* (A, o)
  - *Ampelisca abdita* (A, o)
  - *Chelura terebrans* (A, s) (18)
  - *Corophium acherusicum* (A, o/s) (19)
  - *Corophium uenoi* (O, o/s)
  - *Corophium* sp. (SE, s) (20)

**ARTHROPODA (continued)**

- *Limnoria quadripunctata* (A?, s) (23)
- *Limnoria tripunctata* (A?, s) (23)
- *Dynoides dentisinus* (O, o/s)
- *Sphaeroma quoyanum* (AA, s) (24, 25)
- *Iais californica* (AA, s, with *Sphaeroma quoyanum*) (25)
- *Ianiropsis serricaudis* (O, o/s)

- **Chelifera**
  - *Tanais* sp. (O?, o/s, t?)

**Decapoda**

- *Palaemon macrodactylus* (O, s) (26)
- *Rhithropanopeus harrisii* (A, o) (27)

**ARTHROPODA: INSECTA**

- **Dermaptera**
  - *Anisolabis maritirna* (A?, s) (28)

**ENTROPROCTA**

- *Barentsia benedeni* (E, o/s) (29)

**ECTOPROCTA**

- *Alcyonidium* sp. (A, o/s, t?)
- *Victorella pavida* (A/O, o/s)
- *Bugula* spp. (AA/O, o/s, t?)
- *Conopeum* spp. (A, o/s, t?)
- *Schizoporella unicornis* (A/O, o/s)

**CHORDATA: TUNICATA**

- *Ciona intestinalis* (A, o/s)
- *Molgula manhattensis* (A, o/s)
- *Styela clava* (O, s) (30)

**SPECIES REFERENCES**


433
SAN FRANCISCO BAY

transported with either ships, or oysters, or both, and for many first recorded after 1869 we may nev-
er know exactly which of these three possible cases acted as transport mechanisms. Thirty-seven
percent of the introduced fauna appears to have been brought in with oysters, 19% with ships, and
46% may have come with either or both. The relatively close temporal proximity of the Gold Rush
(1849 and subsequent years) with the beginning of the oyster industry (1869 and the following
years), coupled with the scanty knowledge of the early Bay fauna compounds these difficulties.

It is further difficult to estimate the number of introduced species that have been overlook-
ed. Evidence from various sources indicates that the actual number of introduced species of
acoelomate and pseudocoelomate protostomes (acoel turbellarians, nemerteans, rotifers, nema-
todes, etc.), as well as protozoans, sponges, hydroids, smaller crustaceans (including pinnotherid
crabs, amphipods, and copepods), pycnogonids, oligochaetes, polychaetes, bryozoans, and tunic-
ates, may be quite large. With adequate exploration and taxonomy many more introduced species
than those now known from San Francisco Bay may be recognized. Many taxa are now only
marginally known and to discern native from exotic, or provincial from “cosmopolitan” is diffi-
cult. Confounding this situation is the fact that “cosmopolitan” taxa often reveal low degrees of
taxonomic resolution, suggesting that broad distributions may, in many species, be a taxonomic
artifact. The skeleton-shrimp (amphipod), Caprella equilibra, may be an excellent example: it is
known from San Francisco Bay, and it has also been recorded from virtually every coast line and
many islands of the world, from the surface to (questionably) 3000 m (McCain and Steinberg
1970). Concerning polychaetes, Day (1964) has remarked that, “. . .in the Polychaeta at any rate
more recent work suggests that many records of cosmopolitan species are due to misidentifica-
tions.” Hartman (1955:40) stated, in regard to the polychaete fauna of ocean basins off southern
California, “some species of cosmopolitan character . . .differ from typical representatives in more
distant parts of the world, in morphological characters which may have more than varietal or
trivial importance.” Fauchald (1977) also remarked “how exceedingly poorly known the group is
and how few generalizations can be made on the ecology and evolution of the polychaetes,” to
which, I believe, we may append on the biogeography of polychaetes as well. Bousfield (1973:38)
has made similar comments regarding the “sophistication” of amphipod taxonomy. I have remark-
ed elsewhere (Carlton 1975) on problems associated with treating species as “cosmopolitan.”

A related taxonomic consideration further obscures the number of introduced species. A
strong historical systematic tendency, which remains today, has been either (1) to attempt to
identify newly discovered estuarine taxa (which are in reality introduced) with species already
described from the Pacific coast, or (2) to describe them as new species. The small gammarid am-
hipod, Ampelisca milleri, abundant in parts of San Francisco Bay, provides an example of the
first kind: this is almost certainly the eastern American A. abdita. The true Ampelisca milleri is a
different, native eastern Pacific species. Table 2 lists several examples of the second kind. It may
be noted that more than 65 years passed before the synonymy of the isopod Sphaeroma pentodon
with the Australasian S. quoyanum was accepted by west American systematists (Rotramel 1972).
Other exotic species are doubtless present, masking as locally-described, and thus in the minds of
many biologists, native taxa. For example, the phyllodocid polychaete Eteone californica, de-
scribed from San Francisco Bay, may be identical with E. longa, having been perhaps introduced
with Atlantic oysters into the Bay. Not all populations that have been identified as E. californica,
however, may be identical with E. longa (such as those reported from open coast environments, or
from southern California). Similarly, evidence suggests that the anemone Diadumene franciscana
and the isopod Synidotea laticauda, while described from San Francisco Bay, are introduced

4 Includes species coded in Table 1 as o or o? s or s?
CARLTON: INTRODUCED INVERTEBRATES

(Carlton 1978).

The molluscan fauna is the best known invertebrate group in San Francisco Bay, and provides a detailed example of one group of introduced species. Seventy-five percent of the introduced mollusks are likely from the Atlantic; about 40% were already here by 1901 or earlier. By arranging the bivalves and prosobranch and pulmonate gastropods by year of discovery (early

### TABLE 2. INTRODUCED SPECIES REDESCRIBED AS NEW TAXA AFTER INTRODUCTION TO SAN FRANCISCO BAY (DATA FROM CARLTON 1978)

<table>
<thead>
<tr>
<th>Introduced Species</th>
<th>Redescribed as</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>COELENTERATA: HYDROZOA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Tubularia crocea</em> (Agassiz, 1862)</td>
<td><em>Parypha microcephala</em> Agassiz, 1865</td>
</tr>
<tr>
<td><strong>ANNELIDA: POLYCHAETA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Polydora ligni</em> Webster, 1879</td>
<td><em>Polydora amarincola</em> Hartman, 1936</td>
</tr>
<tr>
<td><em>Streblospio benedicti</em> Webster, 1879</td>
<td><em>Streblospio lutincola</em> Hartman, 1936</td>
</tr>
<tr>
<td><strong>MOLLUSCA: GASTROPODA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Ovatella myosotis</em> (Drapaud, 1801)</td>
<td><em>Alexia setifer</em> Cooper, 1872</td>
</tr>
<tr>
<td><strong>MOLLUSCA: BIVALVIA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Mya arenaria</em> Linnaeus, 1758</td>
<td><em>Mya hemphilli</em> Newcomb, 1875</td>
</tr>
<tr>
<td><em>Lyrodus pedicellatus</em> (Quatrefages, 1849)</td>
<td><em>Teredo townsendi</em> Bartsch, 1922</td>
</tr>
<tr>
<td><em>Teredo navalis</em> Linnaeus, 1758</td>
<td><em>Teredo beachi</em> Bartsch, 1921</td>
</tr>
<tr>
<td><strong>CRUSTACEA: OSTRACODA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Sarsiella zostericola</em> Cushman, 1906</td>
<td><em>Sarsiella tricostata</em> Jones, 1958</td>
</tr>
<tr>
<td><strong>CRUSTACEA: ISOPODA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Sphaeroma quoyanum</em> Milne-Edwards, 1840</td>
<td><em>Sphaeroma pentodon</em> Richardson, 1904</td>
</tr>
<tr>
<td><strong>CRUSTACEA: AMPHIPODA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Orchestia chiliensis</em> Milne-Edwards, 1840</td>
<td><em>Orchestia enigmatica</em> Bousfield and Carlton, 1967</td>
</tr>
<tr>
<td><strong>CRUSTACEA: CIRRIPEDIA</strong></td>
<td></td>
</tr>
<tr>
<td><em>Balanus amphitrite amphitrite</em> Darwin, 1854</td>
<td><em>Balanus amphitrite franciscanus</em> Rogers, 1949</td>
</tr>
</tbody>
</table>

collections of opisthobranchs are lacking) (Table 3), certain temporal patterns emerge: by shortly after the turn of the century, eight species had arrived with commercial oysters from the Atlantic; shipworms (*Teredo navalis* and *Lyrodus pedicellatus*) were discovered in the years bracketing World War I (reflecting the increased world-wide shipping throughout the second decade of the 20th century), and two Japanese mollusks were discovered within a decade of plantings of Japanese oysters in San Francisco Bay. Latest is the Atlantic periwinkle, *Littorina littorea*, synchronous with the relatively late development of shipping algae with living Atlantic lobsters to San Francisco. Not so easily explained was the discovery, one in the late 1920's and one in the late 1980's.

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5 Although dates in Table 3 are the dates of first collection, for some species a more precise timing of introduction can be established. Thus, the soft-shell clam, *Mya arenaria*, was introduced within a five-year period between 1869 and 1874, and accumulating evidence suggests that the mud snail, *Ilyanassa obsolete*, was introduced between 1904 and 1907.
TABLE 3. INTRODUCED MOLLUSKS (BIVALVES AND PULMONATE
AND PROSOBRANCH GASTROPODS) OF SAN FRANCISCO BAY
BY DATE OF DISCOVERY (DATA FROM CARLTON 1978)

COI = Commercial oyster industry

<table>
<thead>
<tr>
<th>Date of Discovery</th>
<th>Species</th>
<th>Mechanism of Introduction and Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>1871</td>
<td>Ovatella myosotis</td>
<td></td>
</tr>
<tr>
<td>1874</td>
<td>Mya arenaria</td>
<td></td>
</tr>
<tr>
<td>1890</td>
<td>Urosalpinx cinerea</td>
<td></td>
</tr>
<tr>
<td>1893</td>
<td>Gemma gemma</td>
<td></td>
</tr>
<tr>
<td>1894</td>
<td>Ischadium demissum</td>
<td></td>
</tr>
<tr>
<td>1898</td>
<td>Crepidula convexa</td>
<td></td>
</tr>
<tr>
<td>1901</td>
<td>Crepidula plana</td>
<td></td>
</tr>
<tr>
<td>1907</td>
<td>Ilyanassa obsoleta</td>
<td></td>
</tr>
<tr>
<td>1913</td>
<td>Teredo navalis</td>
<td></td>
</tr>
<tr>
<td>1920</td>
<td>Lyrodus pedicellatus</td>
<td></td>
</tr>
<tr>
<td>1927</td>
<td>Petricola pholadiformis</td>
<td></td>
</tr>
<tr>
<td>1938</td>
<td>Busycotypus canaliculatus</td>
<td></td>
</tr>
<tr>
<td>1946</td>
<td>Musculus senhousia</td>
<td></td>
</tr>
<tr>
<td>1946</td>
<td>Tapes japonica</td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>Littorina littorea</td>
<td></td>
</tr>
</tbody>
</table>

1930's, of two Atlantic mollusks, Petricola pholadiformis, a burrowing clam, and Busycotypus canaliculatus, a large predaceous whelk (one of the most spectacular introductions, and now the largest gastropod in San Francisco Bay), long after large-scale introductions of Atlantic oysters had ceased. The discovery in 1937 of the Atlantic mudsnail, Ilyanassa obsoleta, came a trematode parasite, which occasionally causes swimmer's itch (schistosome dermatitis) in San Francisco Bay (Table 1; Grodhaus and Keh 1958). Economically, the activities of shipworms, primarily Teredo navalis, and gribbles, such as the boring isopod Limnoria spp. have affected harbor and other installations throughout the Bay for many years, the gribble creating characteristic pencil-like pilings in its boring activities. The depredations of T. navalis

SOCIAL, ECONOMIC, AND GEOLOGIC IMPACTS OF THE INTRODUCED FAUNA

Certain pestiferous species exist among the introduced fauna. Along with the Atlantic mudsnail, Ilyanassa obsoleta, came a trematode parasite, which occasionally causes swimmer’s itch (schistosome dermatitis) in San Francisco Bay (Table 1; Grodhaus and Keh 1958). Economically, the activities of shipworms, primarily Teredo navalis, and gribbles, such as the boring isopod Limnoria spp. have affected harbor and other installations throughout the Bay for many years, the gribble creating characteristic pencil-like pilings in its boring activities. The depredations of T. navalis
shortly after its arrival about 1913 led to the formation, in 1920, of the “San Francisco Bay Marine Piling Committee,” of the American Wood Preservers’ Association, under the leadership of C. L. Hill and C. A. Kofoid, and to intensive studies of its biology and morphological variation. This culminated in the famous “Final Report” of 1927, one of the few scholarly “environmental impact” reports ever produced on San Francisco Bay. Modern methods of anti-borer treatments appear to have generally reduced the effects of shipworms and limnorias in San Francisco Bay.

The burrowing and boring isopod *Sphaeroma quoyanum*, long known as *S. pentodon* on the Pacific coast (Barrows 1919; Higgins 1956; Rotramel 1972) has had an important impact on the shoreline topography of the Bay since its introduction by ships from Australasia probably between the 1850’s and 1890’s. During the past 85 and more years, in several areas in north San Pablo Bay, and along the western and eastern shorelines of south San Francisco Bay, and in small central bay inlets such as Richardson Bay, many kilometers of shoreline have been eroded by the activities of this crustacean. Sections of shoreline on the eastern shore of south San Francisco Bay just north of the San Mateo Bridge typify what may be called “sphaeroma topography”: here, portions of the shore are shaped by the activities of this borer, which by weakening the clay banks, facilitates the removal of the banks by wave action. *Sphaeroma quoyanum* has also affected levees and dikes around the Bay, and in recent years this has been brought to public notice. The *Oakland Tribune* of 21 March 1976 reported one estimate that *S. quoyanum* could remove up to 30 ft of dike in one year! Unfortunately, no measurements appear to have been made of the general extent or rate of the erosional activity of this isopod along much of the Bay’s shoreline, although it may be estimated that in some areas this has involved the landward disappearance of many meters of shoreline.

### BIOLOGICAL AND ECOLOGICAL IMPACTS OF THE INTRODUCED FAUNA

The greatest impact of the introduced fauna must be measured in biological and ecological terms: in the large numbers of species which have been introduced, and in their establishment as numerical and biomass dominants in many areas of the Bay.

Lake Merritt (Fig. 1), a natural, shallow, brackish-water arm of the central east bay shore, connected to the Bay by a channel to the Oakland Estuary, provides one example. Here, the introduced fauna makes up an important component of the total fauna; indeed, almost all of the abundant species are introduced. In a 10-yr qualitative sampling study which I conducted from 1962 to 1972, 37 of the 46 recorded species of littoral, benthic, fouling, and boring macroscopic invertebrates were introduced species. The 20% native fauna consists largely of transient summer-invading species; a number of the introduced species are also present in the lake primarily in the summer. Abundant and comprising much of the macroscopic fauna in the lake are masses of the tubeworm *Mercierella enigmatica*, a gregarious polychaete introduced from Australasia about 1920 (but not described until 1923 from France). *Mercierella enigmatica* occurs throughout the lake on wharves, boat bottoms, retaining walls, rocks, wood, debris, and floating algae. Shortly after its introduction, local newspapers reported it as “coral” — a natural mistake for the coral-like masses which develop around rocks in the lake. Further, *M. enigmatica* has become a prominent organism in warm shallow manmade lagoons around the Bay, in such areas as Foster City, Belvedere, and Alameda. In the Alameda lagoons, it has caused almost complete blockage of some drainage pipes. Equally prominent are the Atlantic ribbed mussel, *Ischadium demissum*, which occurs in large beds along retaining walls all along the lake shoreline, the Japanese mussel, *Musculus senhousia*, found in dense mat-like beds on the lake bottom, and the Atlantic soft-shell clam, *Mya arenaria*, and the Japanese cockle, *Tapes japonica*. Common on all hard substrates in the lake are the bryozoans *Conopeum* sp., *Victorella pavida*, and *Barentsia benedeni*, and the barnacles *Balanus improvisus* and *Balanus amphitrite amphitrite*. On the lake shore is the Chilean or New Zealand beach-hopper,
**SAN FRANCISCO BAY**

*Orchestia chilensis*. In the algae and among the tubeworms, the amphipod crustaceans *Ampithoe valida*, *Corophium insidiosum*, *Grandidierella japonica*, and *Melita nitida*, (all introduced), and tanaids (the introduced *Tanaid sp.*) are seasonally abundant. The Asian anemone, *Haliphiella luciae*, and its small nudibranch predator, *Trinchesia sp.*, are sporadically common. Polychaetes abundant in the mud bottom include *Neanthes succinea*, *Polydora ligni*, *Streblospio benedicti*, and *Capitella capitata*, all introduced species. The only nemertean in the lake is the occasionally abundant *Lineus ruber*, whose tentative status as a native species in San Francisco Bay requires investigation. Seasonally present in Lake Merritt, coinciding with higher summer temperatures and salinities, are the introduced shrimp *Palaemon macrodactylus*, the anemone *Diadumene franciscana*, the hydroid *Tubularia crocea* and its nudibranch predator *Tenellia pallida*, the snails *Urosalpinx cinerea* and *Ilyanassa obsoleta*, the tunicates *Molgula manhattensis* and *Ciona intestinalis*, and among native species, the polychaetes *Harmothoe imbricata*, *Nereis vexillosa*, and *Eteone dilatae*, the sacoglossan slug *Aplysiopsis smithii*, and the mussel *Mytilus edulis*. The only relatively common native species in the lake on an annual basis is the mud crab, *Hemigrapsus oregonensis*. A predominantly exotic fauna in Lake Merritt appears to have existed since at least the 1930’s (Light 1941:188, 191).

In the nearby Oakland Estuary, Graham and Gay (1945) found that the dominant fouling fauna settling on experimental wooden panels is composed of the hydroid *Tubularia crocea*, the spionid polychaete *Polydora ligni*, the amphipod *Corophium insidiosum*, and the barnacle *Balanus improvisus*, all of which reach peak biomass in the summer months. All are introduced species. The only borers noted, in small numbers, was the introduced isopod identified as *Linnorina lignorum*, but probably *L. tripunctata*. Winter fouling was primarily composed of brown filamentous diatom mats and the brown alga *Ectocarpus sp.*; spring and summer algae include the green *Enteromorpha sp.* and the yellow-brown *Vaucheria sp.* Unfortunately, virtually nothing appears to be known about the probably large exotic algal flora of the Bay’s shallow estuarine margins.

Nichols’ (1977) study of the infaunal biomass and production of a mudflat near Palo Alto (Fig. 1) provides insight into the role of introduced species in the trophic structure of South Bay. Of the 16 taxa identified to species, two require brief discussion before the significance of exotic species to the biomass and secondary productivity of this mudflat invertebrate association can be assessed. One, the phyllodocid worm *Eteone californica* has already been mentioned: San Francisco Bay populations of this species may be the Atlantic *E. longa*. The other, the small tellinid clam *Macoma balthica*, may be (1) native, as a cold-water circumboreal species occurring regularly on the Pacific coast as far south as San Francisco Bay, but with bay and offshore records as far south as San Diego (Coan 1971; E. Coan pers. comm.); (2) introduced into San Francisco Bay between 1850 and 1869 with the native oyster, *Ostrea lurida*, from Willapa Bay, Washington, during an early trade in Pacific coast oysters (Barret 1963); or (3) introduced with Atlantic oysters after 1869. *Macoma balthica* has been reported by W. O. Addicott from sediments beneath the floor of southern San Francisco Bay that range in approximate age from 2000 to 6000 years (Atwater et al. 1977; B. Atwater pers. comm.). *Macoma balthica* in San Francisco Bay may thus represent native populations mixed with introduced stocks, through (2) and/or (3), above.

With the exception of *E. californica* and *M. balthica*, all of the species found by Nichols in the Palo Alto mudflat are introduced. At Nichols’ three stations, introduced species largely of the genera *Gemma, Mya, Streblospio, Heteromastus*, and *Ampelisca* comprise 20, 64, and 84% of the biomass (averaged for four seasons). In each case, however, *Macoma balthica* accounts for the greater amount of the remaining biomass: 77, 35, and 10% respectively. And, although represented by relatively few specimens, *M. balthica* tends to dominate biomass data because of the weight of single, large specimens (Nichols 1977). As a matter of fact, the overwhelming numerical dominants at the sites studied by Nichols were the tiny clam *Gemma gemma* and the spionid worm *Streblospio*.
CARLTON: INTRODUCED INVERTEBRATES

*benedicti* both of which because of sampling technique, were considered to be underestimated in numbers present (Nichols 1977). Not included directly in Nichols' study is an abundant epifaunal species, the mudsnail *Ilyanassa obsoleta*, which, "to the casual observer...is the only invertebrate of the mudflat. In fact, this species forms, in some areas, a pavement of shells on the mud surface." (Nichols 1977). Nichols noted that his observations that the total biomass is comprised largely of mollusks of the genera *Macoma, Mya,* and *Gemma,* along with nonquantified observations on the abundance of *Ilyanassa,* agree with similar observations in a Nova Scotia estuary by Burke and Mann (1974). Like Nichols, Burke and Mann found that mollusks of the genera *Mya* and *Macoma* were the chief primary consumers on intertidal sand and mud flats. In San Francisco Bay, this appears to be in no small part an artifact of man's introductions. Nichols concluded, in part, that the mudflat invertebrate association in south San Francisco Bay is an "important link in the cycling of organic matter of the San Francisco Bay estuary." The fact that this secondary productivity is tied up in large part in introduced species, especially so if *Macoma balthica* is an introduced form, raises questions as to the nature and role of mudflat invertebrates in the organic matter budget of the Bay estuary prior to the mid-19th century. Of interest also is that Nichols (1979) found that the introduced species of the genera *Streblospio, Ampelisca,* and *Gemma* are the important biological indicators of continuously physically-disturbed environments in south San Francisco Bay.

A further study on the trophic budget of San Francisco Bay is of interest here. Recher (1966) studied shorebird feeding ecology at Palo Alto, examining the stomach contents of plovers, avocets, dowitchers, sand-pipers, marbled godwits, knots, and willets. With the exception of 3% of the willet's diet, which consisted of the native mudcrab *Hemigrapsus oregonensis,* all identified prey items consumed by these birds (excluding *Macoma balthica*) are introduced species, including many of the species discussed by Nichols. Nichols (1977) has already pointed out that Recher's report of only *Neanthes succinea* and no other polychaetes may be due to the non-identifiability of some species of soft-bodied worms in stomach contents. Recher found that the prey items of greatest importance were *Neanthes succinea, Gemma gemma, Ilyanassa obsoleta,* and, for two bird species, unidentified ostracods (perhaps *Sarsiella zostericola*). *Mya arenaria* and *Macoma balthica* (combined in Recher's data) accounted for less than 7%, and generally less than 4% of any bird diet. How accurate a reflection this is of the reliance of migrating shorebirds on these introduced species in south San Francisco Bay is difficult to determine, although Nichols (1977) has also suggested the importance of shorebird predation on the invertebrates in his study area. There is no doubt, however, that shorebirds in south San Francisco Bay feed heavily on introduced invertebrate species, which arrived here a little more than 100 years ago, whereas the shorebirds have presumably visited the Bay, which lies along the Pacific Flyway, for thousands of years. In the Delta, introduced invertebrates are of occasional importance to both native and introduced fishes, although native mysids and native corophiid amphipods are often more significant. The Atlantic mudcrab, *Rhithropanopeus harrisii,* and several clams, including *Gemma gemma* and *Tapes japonica,* also are occasionally important in the diet of such species as white sturgeon (*Acipenser transmontanus*) (McKechnie and Fenner 1971).

Ecological interactions between native and introduced invertebrates in the Bay have been little studied. The ecological and spatial overlap among possibly competing species largely remains to be determined. Several pairs of potentially competing species readily suggest themselves however: (introduced indicated first) the shrimps *Palaemon macrodactylus* and *Cragon* spp.; the mud crabs *Rhithropanopeus harrisii* and *Hemigrapsus oregonensis*; the rock cockles *Tapes japonica* and *Protothaca staminea*; the marsh snails *Ovatella myosots* (= *Phytia setifer*) and *Assiminea californica,* and the mudsnails *Ilyanassa obsoleta* and *Cerithidea californica* (the interactions of the latter pair are now under investigation by Margaret Race of the University of California,
SAN FRANCISCO BAY

Berkeley). In certain areas of the Bay some of these species pairs do not co-occur; here, it may be that competition would be important only in essentially ecotonal habitats. In Lake Merritt, for example, where *Palaeomon macrodactylus* is seasonally abundant, *Crangon* spp. do not occur; *Tapes japonica* is common in the lake, but *Protophassa staminea* has never been found there; *Hemigrapsus oregonensis* is present, but *Rhithropanopeus harrissii*, first reported on the Pacific coast from Lake Merritt (Jones 1940), has not been found in the lake since my studies began in 1962, nor was it found in 1952 in another study of the lake.

In certain parts of the Bay, hermit crab populations may have responded to the increased variety and number of gastropod shells provided by introduced species of several genera, such as *Ilyanassa, Urosalpinx*, and *Busycotypus*. In south San Francisco Bay, at Coyote Point, Wicksten (1977) has noted that the population of the native hermit crab, *Pagurus hirsutiusculus*, is existing almost entirely in shells of either *Ilyanassa obsoleta* or *Urosalpinx cinerea*. Similar reliance on introduced shells by *P. hirsutiusculus* occurs in other areas of the Bay. It would appear that the hermit crabs have either switched to these exotic shells from native gastropod shells, which are not now common at Coyote Point, or have expanded their range or population sizes in the Bay.

The successful establishment of so many exotic species cannot be considered the result of any one cause, and in some cases reasons for establishment may be highly species-specific. Man’s extensive perturbations of the Bay, including major hydrological changes (through dredging, filling, sedimentation, diverting and damming of streams), installations of harbor and marina facilities (wharves, pilings, floats, dredged channels), and bay disposal of a wide variety of inorganic and organic pollutants, may have created novel environmental conditions to which only certain introduced species can adapt. More important, however, may be that the relatively young and island-like estuaries of the Pacific coast aboriginally supported, in terms of a number of species, a sparse native fauna (Jones 1940; Hedgpeth 1968; Carlton 1978); for many introductions there is no obvious native counterpart with which “competition” may have been necessary for establishment.

No native marine invertebrate is known to have become extinct in San Francisco Bay due to competition with an introduced species. However, portions of once-broader niches (*sensu lato*) of native species may have been acquired by introduced species, particularly by those exotics which occupy the brackish (up-estuary) ends of counterpart native species’ ecological ranges. Thus the introduced shrimp *Palaeomon macrodactylus* (compared to the native *Crangon* spp.), the introduced barnacle *Balanus improvisus* (compared to the native *Balanus glandula* and *Balanus crenatus*), and the introduced crab *Rhithropanopeus harrissii* (compared to the native *Hemigrapsus oregonensis*) all occur most abundantly in more brackish (or even fresh water) regions of San Francisco Bay, whereas the native species are most common in more saline areas. Investigations and experimental manipulative studies directed to dissecting out the relative importance of competition, of the absence of a diverse native fauna, and of the creation of modified and new environments, are needed, both to clarify the sequence of events that led to the successful establishment of introduced species in the past and to understand what types of introductions may be successful in the future.

I began by stating that the history of introduction in San Francisco Bay has largely been an anecdotal one, and an anecdote may serve to end this discussion. In the early 1890’s, the Atlantic mussel, *Ischadium demissum*, was introduced and has since become abundant throughout the Bay, where it may live with only its posterior end at the mud surface. In 1927, Dudley Sargent De

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6 That the established species are only a small percentage of those actually transported from foreign shores by ships and oysters is indicated by preliminary evidence summarized by Carlton (1978). Indeed, well-known fouling species introduced on other shores, such as the serpulid worm *Hydroides elegans* and the barnacle *Balanus eburneus*, have been found living on ships entering San Francisco Bay but have failed to become established.
CARLTON: INTRODUCED INVERTEBRATES

Groot of Stanford University, reporting on the biology of the California clapper rail (Rallus longirostris obsoletus) in San Francisco Bay, observed that the mussel had become an apparent danger to the rail, for as the birds walked through the marshes they would be trapped by a slightly opened Ischadium flush with the substrate. "It is our belief that at least seventy-five percent, and perhaps more, of the adult rail of the Redwood marsh area are minus toes from this cause," said De Groot, who further estimated, rather roughly, that approximately 25% of the chicks of hatched broods of the rail "meet an untimely end" by drowning at high tide while being held by the valves of the mussel. De Groot ranked Ischadium demissum as one of the causes of the demise of the California clapper rail in San Francisco Bay, a species now on the endangered list, although Moffit (1941) later showed that the detrimental effects, if any, of I. demissum may be outweighed by the fact that 57% of the total diet (and 66% of the animal protein in the diet) of clapper rails near Palo Alto consists of this mussel!

Introductions continue and these seem inevitable. In the San Francisco Bay area, introduced species of animals and plants predominate throughout much of the urban and agricultural terrestrial environment, and it seems only "natural" that man should contribute substantially to the exotic composition of the marine biota as well. We may expect that as man's methods of transportation in commerce and trade change and as our methods of traversing great distances on water with increasing speeds change, more and perhaps different exotic species will be introduced into San Francisco Bay and to the Pacific coast. Whether or not we will be able to detect an asymptotic situation relative to the numbers of introduced species in an environment such as San Francisco Bay, and whether or not we will observe the replacement or displacement of one introduced marine species by another introduced species -- not, to my knowledge, ever observed on this coast before, but so well documented among land plants and insects -- will require long and careful observation.

ACKNOWLEDGMENTS

I am indebted to a great many persons, acknowledged in Carlton (1978), who have contributed materially to the identification and resolution of the introduced fauna of San Francisco Bay. In particular, John Chapman, David Cross, Ernest Iverson, and Daphne Dunn graciously contributed unpublished records of gammarid amphipods, a caprellid, isopods, and an anemone, respectively, from San Francisco Bay. Debby Fishlyn and Steve O'Dell provided moral and logistic support in the preparation of this report for the San Francisco Bay Symposium in June 1977. I thank Frederic Nichols and John Chapman for reading the manuscript and for helpful criticisms. This paper is based, in part, on a thesis submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy at the University of California, Davis.

LITERATURE CITED

CARLTON: INTRODUCED INVERTEBRATES


SAN FRANCISCO BAY


