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FRESHWATER MOLLUSKS OF CALIFORNIA: A DISTRIBUTIONAL CHECKLIST¹

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The principal focus of this list is the freshwater fauna. In addition, species of inland saline habitat and some coastal brackish-water to intertidal forms are included. Introduced species are listed only when known to occur in the wild. The state fauna consists of 91 described forms: 24 bivalves (1 introduced); 29 prosobranch gastropods (5 introduced); and 38 pulmonate gastropods (3 introduced).

INTRODUCTION

Data for each species in this checklist include (1) type locality; (2) range, with emphasis on California; and (3) habitat. As appropriate, other information includes (4) status (narrowly localized, possibly extinct, or exotic); (5) threats; (6) synonyms; and (7) earliest record of exotic species in California. Habitat applies to California; widespread species may be found in different situations elsewhere. Synonyms listed are only those based on specimens from California. Type localities have been modernized by correction of place names and addition of current political units as appropriate.

The sequence of families, subfamilies, genera, subgenera, and species listed is alphabetical within superfamilies except that the typical group is listed first.

Few if any species listed are rare, in the sense of low density of individuals throughout the entire geographic range. A number are narrowly localized—restricted to one or a few lakes, springs, or streams, where they may be locally abundant. Threats to the habitat are threats to the very existence of such species. Those forms that are narrowly localized and restricted to a narrow range of habitat are those most likely to be eradicated by human activities.

Most of the literature on the fauna, including references to original descriptions and illustrations, is accessible through a bibliography by Taylor (1975). For non-specialists, Table 1 will be helpful in showing correspondence between the names used herein and those in the standard work by Edmondson (1959).

This list includes only the described species. Anyone attempting to identify aquatic mollusks in California should be aware that there are numerous undescribed species and even some genera, especially among small and inconspicuous forms.

TABLE 1. Comparison of Molluscan Generic Names Used in This List With Those Used by Edmondson (1959).

	<i>This List</i>	<i>Edmondson (1959)</i>
Unionidae	<i>Anodonta</i>	<i>Anodonta</i>
	<i>Gonidea</i>	<i>Gonidea</i>
Margaritiferidae	<i>Margaritifera</i>	<i>Margaritifera</i>
Corbiculidae.....	<i>Corbicula</i>	<i>Corbicula</i>

¹ Accepted for publication October 1980.

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Sphaeriidae	<i>Sphaerium</i>	<i>Sphaerium</i>
	<i>Musculium</i>	<i>Musculium</i>
	<i>Pisidium</i>	<i>Pisidium</i>
Valvatidae	<i>Valvata</i>	<i>Valvata</i>
Pleuroceridae	<i>Juga</i>	<i>Goniobasis</i> , part
Potamididae	<i>Batillaria</i>	Not listed
	<i>Cerithidea</i>	Not listed
Thiaridae	<i>Thiara (Melanoides)</i>	Not listed
	<i>Thiara (Tarebia)</i>	<i>Tarebia</i>
Viviparidae	<i>Bellamva</i>	<i>Viviparus</i> , part
	<i>Cipangopaludina</i>	<i>Viviparus</i> , part
Littorinidae	<i>Littorina</i>	Not listed
Assimineidae	<i>Assiminea</i>	Not listed
Hydrobiidae	<i>Fonticella</i>	Not listed
	<i>Pyrgulopsis</i>	<i>Pyrgulopsis</i>
	<i>Savaginius</i>	Not listed
	<i>Lithoglyphus</i>	<i>Fluminicola</i>
Littoridinidae	<i>Tryonia</i>	<i>Tryonia</i>
Pomatiopsidae	<i>Pomatiopsis</i>	<i>Pomatiopsis</i>
Lymnaeidae	<i>Lymnaea</i> (s. s.)	<i>Lymnaea</i> (s. s.)
	<i>Lymnaea (Hinkleyia)</i>	Not listed
	<i>Lymnaea (Stagnicola)</i>	<i>Lymnaea (Stagnicola)</i>
	<i>Bakerilymnaea</i>	Not listed
	<i>Fossaria</i>	<i>Lymnaea (Galba)</i>
	<i>Pseudosuccinea</i>	<i>Lymnaea (Pseudosuccinea)</i>
	<i>Radix</i>	<i>Lymnaea (Radix)</i>
Lancidae	<i>Lanx</i>	<i>Lanx</i>
Ancylidae	<i>Ferrissia</i>	<i>Ferrissia</i>
Planorbidae	<i>Gyraulus</i> (s. s.)	<i>Gyraulus</i> (s. s.)
	<i>Gyraulus (Armiger)</i>	<i>Armiger</i>
	<i>Biomphalaria</i>	<i>Tropicorbis</i>
	<i>Helisoma</i> (s. s.)	<i>Helisoma</i> , part
	<i>Helisoma (Carinifex)</i>	<i>Carinifex</i>
	<i>Planorbella (Pierosoma)</i>	<i>Helisoma</i> , part
	<i>Planorbella (Seminolina)</i>	<i>Helisoma</i> , part
	<i>Vorticifex</i>	<i>Parapholys</i>
	<i>Micromenetus</i>	Not listed
	<i>Menetus</i>	<i>Menetus</i>
	<i>Promenetus</i>	<i>Promenetus</i>
Physidae	<i>Physa</i>	<i>Physa</i>

Class Pelecypoda
Order Naiadoidea
Superfamily Unionacea

FAMILY UNIONIDAE

Freshwater mussels have parasitic larvae that develop on the gill or fins of freshwater fishes. The preferred host is commonly a group of closely related species. Distribution of the mussels is therefore determined by suitable habitat for the nearly sedentary adults, by availability of suitable fish hosts, and by dispersion of larvae on the fishes. Summary of ranges of the mussels is given below according to the drainages outlined by Moyle (1976), for comparison with fish distribution data.

Anodonta californiensis Lea, 1852

Type locality: "Rio Colorado," actually a former distributary of the river, approximately New River, Imperial County, California.

Southern British Columbia to northernmost Baja California, eastward to western Wyoming, eastern Arizona, and Chihuahua. The species in this broad sense is probably composite, but shell characters are poorly marked. Originally widespread in California in the following drainages; Lower Klamath (Shasta River only); Pit River; Central Valley; north coast streams; Pajaro-Salinas system; Lahontan system; Owens River; Mojave River; San Diego region (Santa Margarita River only); Los Angeles basin (Los Angeles and Santa Ana Rivers); south-central coastal drainages (near San Luis Obispo only); Salton Sea (New River only). Probably extinct in most of the Central Valley and southern California.

Habitat: Lakes, reservoirs, perennial streams.

Status: Probably most natural populations in the state have been eradicated.

Threats: Pollution; lowering of water-table through agricultural development; changes in stream flow through damming or increased flooding due to overgrazing or logging; elimination of natural fish hosts on which life cycle depends.

Synonym: *Anodon micans* Anthony, 1865; type locality "Texas" in error; probably from former course of New River near mouth of Carrizo Creek, Imperial County, California.

Anodonta oregonensis Lea, 1838

Type locality: Near mouth of Willamette River, Columbia County, Oregon.

Southernmost Alaska to northern California, eastward to eastern Washington. Northeastern California only, in the following drainages: Lower Klamath River (above Shasta River only); upper Klamath River and Lost River; Central Valley (only in Middle Fork of Feather River, Sierra Valley, Plumas County).

Habitat: Lakes and slow rivers.

Anodonta wahlamatensis Lea, 1838

Type locality: Near mouth of Willamette River, Columbia County, Oregon.

Lower Columbia River, Oregon-Washington. In California in the following drainages: Pit River; Central Valley, in the larger, slow streams only, as far south as the northern San Joaquin Valley, and in Crystal Springs Reservoir, San Mateo County; Clear Lake (including nearby Blue Lakes).

Habitat: Lakes and slow rivers.

Status: Probably eradicated in most of original range.

Threats: Pollution.

Synonyms: *Anodonta rotundovata* Trask, 1855; type locality lagoons of Sacramento Valley. *A. triangularis* Trask, 1855; type locality Sacramento River below mouth of American River.

Gonidea angulata (Lea, 1838)

Type locality: "Lewis's River", i.e., Snake River, Idaho (no specific locality).

Southern British Columbia to southern California, eastward to southern Idaho and northern Nevada. In California formerly throughout most of the State, in the following drainages: Lower Klamath; 1b, upper Klamath River and Lost River; Pit

River; Central Valley; north coast streams (lower Eel River and lower Russian River); Clear Lake (including Blue Lakes); Pajaro-Salinas system (Pajaro River drainage only); Los Angeles Basin (Ballona Creek and Santa Ana River). Probably extinct in most of the Central Valley and southern California.

Habitat: Creeks and rivers, less often in lakes.

Status: Probably eradicated in much or most of original range in California.

Threats: Pollution; lowering of water-table through agricultural development; changes in stream flow through damming or increased flooding due to overgrazing or logging; elimination of natural fish hosts on which life cycle depends.

Synonyms: *Anodonta randalli* Trask, 1855; type locality Sacramento and San Joaquin rivers (no specific locality). *Gonidea angulata haroldiana* Dall, 1908; type locality Coyote Creek, between San Jose and San Francisco Bay, Santa Clara County.

FAMILY MARGARITIFERIDAE

Margaritifera falcata (Gould, 1850)

Type locality: Fort Walla Walla, Walla Walla County, Washington.

Southern Alaska to central California, eastward to western Montana, western Wyoming, and northern Utah. In California in the following drainages: Lower Klamath River (including Smith River); Goose Lake; Pit River; Central Valley; north coast streams; Clear Lake; Pajaro-Salinas system (only in streams of the southern Santa Cruz Mountains); Upper Kern River; Lahontan system.

Habitat: Trout streams.

Status: Probably extinct in San Lorenzo River, Santa Cruz Mountains.

Threats: Pollution; silting of habitat by rapid runoff; elimination of stream habitat by damming.

Synonym: *Alasmodon yubaensis* Trask, 1855; type locality Yuba River about 40 miles above mouth, Yuba County.

Order Veneroidea

Superfamily Corbiculacea

FAMILY CORBICULIDAE

Corbicula fluminea (Müller, 1774)

Type locality: China (no specific locality).

Widely established in the United States and northern Mexico. Earliest record in California: 1945, Sacramento River north of Pittsburg (Hanna 1966). Widespread in the state in reservoirs and canals.

Habitat: Principally in artificial water bodies such as canals and reservoirs. It appears to occur in artificial or disturbed situations; does not thrive in natural water bodies that are unmodified by human activity.

Status: Exotic; probably not a primary threat to native fauna in California. An extensive series of studies is summarized by Britton (1979).

FAMILY SPHAERIIDAE

Sphaerium (s. s.) *patella* (Gould, 1850)

Type locality: Fort Vancouver and Walla Walla, Washington.

Southwestern British Columbia to northernmost California, eastward to southeastern Washington. In California in the Klamath and Lost River drainages,

known from four populations: Shasta River and adjacent Klamath River, two spring-fed tributaries of Lower Klamath Lake, and Clear Lake Reservoir of the Lost River drainage, Modoc County.

Habitat: Perennial rivers, larger creeks, and lakes.

Status: Narrowly localized in California; only four populations known. As the species is restricted to the Klamath and Lost River drainages, no significant additions to range are expected.

Sphaerium (Amesoda) striatinum (Lamarck, 1818)

Type locality: Lake George, Warren County, New York.

Widespread over northern North America; in most of the United States except for the extreme southwest. Northern California only. Widespread in the Sacramento and lower San Joaquin drainages, but presumed to be locally extinct through much of its former range; Salmon Creek, Sonoma County, and interior drainages in the northeastern part of the State.

Habitat: Perennial rivers and creeks, in mud, sand, gravel, or among sand and gravel beneath cobbles or boulders.

Musculium raymondi (J. G. Cooper, in Raymond and Cooper, 1890)

Type locality: Soda Springs, Tuolumne Meadows, Tuolumne County, California.

Widespread over northern North America, southward at higher elevations to southern California, Utah, Colorado. In California across the northernmost part of the state, but to the south only on either side of the Central Valley: along the coast south to the Santa Cruz Mountains, and through the Sierra Nevada; isolated in the San Bernardino Mountains.

Habitat: Marshes, ponds, and lakes subject to seasonal fluctuation, drying partly or entirely.

Musculium securis (Prime, 1852)

Type locality: Fresh Pond and Cambridge Meadows, Middlesex County, Massachusetts.

Widespread over northern North America; in most of the United States except for the arid and semi-arid Southwest. Northeastern California only, from Siskiyou County to Lake Tahoe area, where it is known from only five localities.

Habitat: Ponds and small lakes that do not dry entirely.

Status: Sporadic in California; only five populations known. Others are likely to be found in the northeastern part of the state.

Musculium truncatum (Gould, 1848)

Type locality: Connecticut (no specific locality).

Widespread over northern North America; in virtually all of the United States. Throughout nearly all of California except for the southernmost and southeastern regions.

Habitat: Irrigation ditches, streams, ponds, and lakes, often in situations subject to seasonal fluctuations. Rarely found with *M. raymondi*; more often in running water or ponds at lower elevation than that species.

Psidium (s. s.) *idahoense* Roper, 1890

Type locality: Near Cataldo Mission, Kootenai County, Idaho.

Circumboreal; in far northern North America in creeks and ponds as well as larger lakes, but southward becoming sporadic and restricted especially to the deeper water of larger lakes in the northern United States. In California there

were two natural populations in the San Francisco Bay region; both are presumed extinct: Mountain Lake in San Francisco and near Alvarado, Alameda County. The two present known occurrences are Hat Creek, Shasta County; and upper Willow Creek and its tributary springbrooks, Lassen County.

Habitat: Cool-water outflow of large springs.

Status: Narrowly localized in California; only two populations known. Others may occur in outflow of large springs in the northeastern part of the state.

Pisidium (Cyclocalyx) casertanum (Poli, 1791)

Type locality: Caserta, Italy.

Nearly world-wide, the most widely distributed species of freshwater mollusk. Throughout the United States and general in California; the most common *Pisidium* in the state.

Habitat: Seasonal to perennial water bodies, flowing or standing. Found in small seasonal streams and ponds, seepages, creeks, and rivers to deeper water of lakes and high-altitude ponds.

Synonyms: *Pisidium occidentale* Newcomb, 1861; type locality Ocean House, formerly near the northeastern corner of Lake Merced, San Francisco. *P. rowelli* Sterki, 1903; type locality near Sisson (now the town of Mt. Shasta), Siskiyou County. *P. nevadense* Sterki, 1913; type locality Nevada County (no specific locality).

Pisidium (Cyclocalyx) compressum Prime, 1852

Type locality: Fresh Pond, near Cambridge, Middlesex County, Massachusetts.

Widespread over most of North America, relatively sporadic in the arid and semi-arid Southwest. In California common in the northern part of the state; in the south recorded only in the Los Angeles River and San Gabriel River drainages, where now presumably rare or extinct.

Habitat: Perennial creeks or rivers.

Pisidium (Cyclocalyx) contortum Prime, 1854

Type locality: Pittsfield, Berkshire County, Massachusetts; subfossil.

Widespread over northern North America; in most of the United States except for the arid and semi-arid Southwest. Northern California only, on either side of the Sacramento Valley. The southernmost natural population was in Mountain Lake in San Francisco, where now presumed extinct.

Habitat: Perennial ponds and lakes, characteristically in those with water lilies.

Pisidium (Cyclocalyx) lilljeborgi Clessin, in Esmark and Hoyer, 1886

Type locality: Arctic Norway.

Circumboreal; widespread over northernmost North America, but southward becoming sporadic and restricted to higher elevations. In California known only from three lakes in the Trinity Alps.

Habitat: High-altitude lakes.

Status: Narrowly localized in California; only three populations known. Many others might occur in the less accessible ponds and lakes in glaciated parts of mountains.

Pisidium (Cyclocalyx) milium Held, 1836

Type locality: Bavaria, Germany.

Circumboreal; widespread over northernmost North America, but southward

becoming sporadic; as far as California and Utah. Northern California only, on the northwestern coast and in the northeastern part of the state, where known at seven localities.

Habitat: Ponds, creeks, or rivers, always in especially favorable habitats, i.e., where mollusk diversity is high.

Status: Sporadic in California; only seven populations known.

Pisidium (Cyclocalyx) pauperculum Sterki, 1896

Type locality: Not specified.

Widespread in southern Canada and the United States, but rare and sporadic in the arid and semi-arid Southwest. Northeastern California only, where known from three populations: Pit River and tributary Crystal Lake, Shasta County; and Willow Creek, Lassen County.

Habitat: Perennial rivers and larger spring-fed creeks.

Status: Narrowly localized in California; only three populations known. As it is rare throughout the western United States, few additional populations are expected in California.

Pisidium (Cyclocalyx) ultramontanum Prime, 1865

Type locality: Canoe Creek (now Hat Creek), probably at Rising River, Shasta County, California.

Southwestern Oregon and northeastern California, in only four drainages. In California in the Klamath River as far downstream as Shasta River, and perhaps formerly in Lower Klamath Lake; formerly in Tule Lake of the Lost River drainage, now extinct; Pit River and lower part of its tributary Hat Creek; and Eagle Lake, Lassen County.

Habitat: lakes and large streams.

Status: Narrowly localized in California; only three populations known. As the species is restricted to larger perennial water bodies, additional populations are unlikely to be found.

Pisidium (Cyclocalyx) variable Prime, 1852

Type locality: Fresh Pond, Middlesex County, Massachusetts.

Widespread over northern North America; in most of the United States except for the arid and semi-arid Southwest. Northeastern California only, from Pit River and upper Sacramento Valley to the Lake Tahoe area.

Habitat: Perennial flowing water, from spring-fed rivulets to creeks and rivers.

Pisidium (Cyclocalyx) ventricosum Prime, 1851

Type locality: Stream running out of Fresh Pond, Cambridge, Middlesex County, Massachusetts.

Widespread over northern North America, southward at higher elevations to southern California, Utah, Colorado. In California sporadic in the northeastern part of the state, central Sierra Nevada, and isolated in the San Bernardino Mountains.

Habitat: Marshes, ponds, and lakes subject to seasonal fluctuation, but not drying entirely.

Synonym: *Corneocyclas tremperi* Hannibal, 1912; type locality Bluff Lake, San Bernardino Mountains.

Pisidium (Neopisidium) insigne Gabb, 1868

Type locality: Spring at Fort Tejon, Kern County, California.

Widespread in the western United States and adjacent parts of Canada and Mexico; eastward rare and sporadic as far as the Great Lakes region. In California widespread except for the southeastern part.

Habitat: Seepages and spring-fed rivulets, often small, but always with perennial flowing water. It may be found in fine organic mud or among thick vegetation such as watercress or mosses.

Pisidium (Neopisidium) punctatum Sterki, 1895

Type locality: Ohio; no one of three original localities specified.

Western United States in California, Oregon, Idaho, and Nevada; southeastern Canada south to the central-eastern states. Northeastern California only, in three drainages: Klamath River drainage in tributaries of Lower Klamath Lake to Shasta River; Pit River and lower part of its tributary Hat Creek; upper Willow Creek, Lassen County. The known localities represent three to five populations.

Habitat: Fine substratum in perennial flowing water where not subject to flood scour, thus restricted to low-gradient rivers and the outflow of large springs. The habitats are always especially favorable, i.e., mollusk diversity is high.

Status: Narrowly localized in California and uncommon where found; only three to five populations known. As it is rare throughout its total range, few additional localities are to be expected.

Pisidium (Neopisidium)ingleyi Sterki, 1898

Type locality: Guadalupe River, Comal County, Texas.

Southernmost United States southward through Central America and Greater Antilles. In California known from only two localities in the Los Angeles River system; last collected in the Rio Hondo in 1924.

Habitat: Perennial stream.

Status: Probably extinct in California.

Class Gastropoda
Subclass Prosobranchia
Order Ectobranchia
Superfamily Valvatacea

FAMILY VALVATIDAE

Valvata humeralis Say, 1829

Type locality: Vicinity of Mexico City, Mexico.

Southern British Columbia to western Wyoming, southward to southern Utah and Colorado; isolated in coastal or high altitude colonies to the south, in southern California; White Mountains, Arizona; and southern plateau of Mexico. Widespread in northern California on either side of Central Valley; in southern California isolated in the San Bernardino Mountains, and formerly in the Los Angeles River where presumably extinct. Northern and eastern limits of range uncertain; possibly synonymous with some species named from eastern North America.

Habitat: Lakes, ponds, marshes, and slow perennial streams on mud bottom, commonly in dense vegetation.

Synonym: *Valvata humeralis californica* Pilsbry, 1908; type locality Big Bear Lake, San Bernardino County.

Valvata virens Tryon, 1863

Type locality: Clear Lake, Lake County, California.

Clear Lake, probably extinct; also a pond near Watsonville (which one unknown), but not collected since the early part of the century and possibly extinct.

Habitat: One lake, one pond.

Status: Narrowly localized and possibly extinct.

Threats: Pollution by pesticides; introduced fishes. Hopkirk (1973) thought the species was extinct in Clear Lake because of predation by carp.

Order Ctenobranchia
Superfamily Cerithiacea

FAMILY PLEUROCERIDAE

The Pleuroceridae of the Pacific Northwest were classified as *Goniobasis* for many years, as the shells show no significant differences from that eastern American genus. With study of the reproductive system and egg mass, it appears that in these features *Juga* is more distinctive than all the various genera in the eastern United States.

Juga (s. s.) *silicula shastaensis* (Lea, 1856)

Type locality: "Shasta and Scott Rivers, California."

Southwestern Washington west of the Cascade Range southward to Klamath River, California. In the Klamath drainage from the Shasta River downstream, and in the lowest Trinity River. Smith River and its tributary Mill Creek, Del Norte County.

Habitat: Large creeks and rivers.

Synonyms: *Goniobasis circumlineata* Tryon, 1865; cited from a number of localities in California, all wrong. *Goniobasis yrekaensis* Henderson, 1935; type locality Shasta River about 4 miles above mouth, Siskiyou County.

Juga (*Calibasis*) *acutifilosa* (Stearns, 1890)

Type locality: "Eagle Lake," actually the nearby head of Willow Creek, Lassen County, California.

Northeastern California and adjacent Oregon, known from eight isolated colonies: Shoa Springs, Jackson County, Oregon (tributary to Jenny Creek, part of Klamath drainage); Big Spring, Siskiyou County, California (tributary to Shasta River, part of Klamath drainage); Ash Creek, Lassen County (tributary to Pit River); Fall River, Shasta County (tributary to Pit River); Crystal Lake, Shasta County (tributary to Pit River); headwaters of Willow Creek, Sellicks Springs, and Tiptons Springs, all in Lassen County (tributary to Honey Lake, interior drainage).

Habitat: Large springs and their outflows, often narrowly restricted to the source area.

Status: Narrowly localized in California, where only seven populations known. The information on range and status given by Clarke (1977) is misleading. As the species is restricted to relatively large springs, few if any additional colonies are likely to be discovered.

Threats: Pollution; ponding of springs with elimination of flowing-water habitat.

Synonym: *Goniobasis acutifilosa siskiyouensis* Pilsbry, 1899; type locality head of Fall River, Shasta County.

Juga (Calibasis) occata (Hinds, 1844)

Type locality: Sacramento River, California (between American River and mouth).

Northern California, in the Sacramento River, and Pit River below the falls.

Habitat: Large river.

Status: Surviving in the lower Pit River, but status in the Sacramento River unknown—no records in the present century. Changes in the riverbed due to extensive placer-mining in the last century might have eliminated it in most of the Sacramento River.

Threats: Pollution; impoundment of river.

Synonym: *Goniobasis acutifilosa pittensis* Henderson, 1935; type locality Fall River Mills, Shasta County.

Juga (Oreobasis) chacei (Henderson, 1935)

Type locality: Small tributary of Smith River, Adams Station, Del Norte County, California.

Drainage of Smith River and adjacent Lake Earl, Del Norte County.

Habitat: Rivulets and small creeks. It is rarely found with *Juga silicula shastaensis*, which lives in larger streams.

Juga (Oreobasis) nigrina (Lea, 1856)

Type locality: Clear Creek, Shasta County, California.

Northern California and adjacent parts of Oregon and Nevada. Common in tributaries of the Sacramento River, and interior drainages in the northeastern part of California; locally in upper part of Klamath River drainage. West of the Sacramento River drainage in uppermost Eel River drainage; Napa River; and coastal streams from Mendocino County (Big River, Noyo River) south to Sonoma County (Russian River drainage). The southernmost population in Salmon Creek, Sonoma County, is thought to be extinct.

Habitat: Seepages, springs, and creeks, in perennial flowing water.

Synonym: *Melania californica* Clessin, 1882; type locality "California".

Juga (Oreobasis) orickensis (Henderson, 1935)

Type locality: Redwood Creek, Orick, Humboldt County, California.

Coastal drainages of extreme southwestern Oregon south to drainage of the Mad River, Humboldt County; eastward in the Trinity River drainage, Trinity County.

Habitat: Small spring-fed rivulets to creeks. In drainages where *Juga silicula shastaensis* occurs also, the two are not associated, *J. orickensis* living in smaller streams.

FAMILY POTAMIDIDAE

Batillaria attramentaria (Sowerby, 1855)

Type locality: Unknown.

Native in eastern Asia, the precise range uncertain. Introduced at various localities along the Pacific Coast, in bays and estuaries. In California in Elkhorn Slough, Monterey County, and Tomales Bay, Marin County. First record in California: 1930, from boxes of Japanese seed oysters at Elkhorn Slough (Bonnot 1935, as *Potamides multiformis*).

Habitat: Tidal marine to brackish water, ranging up to about mid-tide level,

thus not so high as *Cerithidea*. In Bennett Slough (the northern arm of Elkhorn Slough) it overlaps the range of the characteristic brackish water species, *Tryonia imitator*.

Status: Exotic; perhaps displacing *Cerithidea* to some extent in the intertidal range where the two overlap.

Cerithidea californica californica (Haldeman, 1840)

Type locality: Santa Barbara, Santa Barbara County, California.

Bays along the coast of southern California, from Morro Bay, San Luis Obispo County, southward to Scammons Lagoon, Baja California; it intergrades with and is replaced southward by *C. californica albonodosa* Carpenter, in Gould and Carpenter, 1857; type locality Guaymas, Sonora, Mexico.

Habitat: Tidal marine to brackish water, ranging into the upper intertidal zone and often found in *Salicornia* marshes. In upper Newport Bay, Orange County, it overlaps the range of the characteristic brackish water species, *Tryonia imitator*.

Synonym: *Potamis pullatus* Gould, 1855; type locality San Diego, California.

Cerithidea californica sacrata (Gould, 1849)

Type locality: Sacramento River, California; presumably near the upper limit of brackish water.

San Francisco Bay region, where thought to be general in *Salicornia* marshes before filling and pollution largely eliminated it. Known in upper Tomales Bay, Schooner Bay, and Bolinas Lagoon, Marin County; nearly extinct in San Francisco Bay, where it survives only in local colonies.

Habitat: Tidal marine to brackish water, ranging into the upper intertidal zone and often found in *Salicornia* marshes.

Status: Extinct in most of original range. Populations in bays on the outer coast are probably in nearly natural state, but the total range is probably less than 10% of its original extent because of alteration in San Francisco Bay.

Threats: Pollution of bays, dredging, and land fill.

Cerithidea fuscata Gould, in Gould and Carpenter, 1857

Type locality: San Diego, California.

Eastern San Diego Bay.

Habitat: No precise details recorded; presumably on intertidal mudflats or in *Salicornia* marshes.

Status: Narrowly localized; possibly extinct. Formerly abundant, but last collected in 1935.

Threats: Pollution, dredging, and land fill.

Synonym: *Cerithidea sacrata hyporhyssa* S. S. Berry, 1906; type locality San Diego, California.

FAMILY THIARIDAE

The two species listed here are sometimes classified in different genera. These groups are ranked as only subgenera of *Thiara*, following the precedent by Pace (1973) and references therein.

Thiara (Melanoides) tuberculata (Müller, 1774)

Type locality: Coromandel coast of India.

Native from Africa eastward to the East Indies; introduced in the United States through the aquarium trade. First and only record in California: 1972, in a drainage ditch tributary to the Salton Sea, Riverside County.

Habitat: Drainage ditch.

Status: Exotic, and a potential colonizer of spring outflows, ditches, and canals where winter temperatures are mild. It might prove a threat to native species localized in warm springs.

Thiara (Tarebia) granifera mauiensis (Lea, 1856)

Type locality: Maui, Hawaii.

Native to the larger islands of Hawaii; introduced through the aquarium trade in the southern United States. First recorded in California in 1969, in a drainage ditch tributary to Salton Sea, Riverside County, and subsequently found in another such ditch (Oglesby 1977) also tributary to Salton Sea.

Habitat: Drainage ditches.

Status: Exotic; introduced into the continental United States through the aquarium trade about 1935 (Abbott 1952). A potential colonizer of spring outflows, ditches, and canals where winter temperatures remain above 75° F. (Abbott 1952). It might prove a threat to native species localized in warm springs.

Superfamily Viviparacea

FAMILY VIVIPARIDAE

Subfamily Bellamyinae

Most species of Viviparidae were classified in *Viviparus* for a long time on conchological grounds. Rohrbach (1937) found trenchant morphological characters that distinguished the mainly tropical Bellamyinae. Generic limits and nomenclature are not firmly established within the subfamily, as noted by Pace (1973).

Bellamyia japonica (Martens, 1860)

Type locality: Japan (no specific locality).

Native in Japan; sporadic in several of the United States. Earliest record in California: 1891, specimens purchased in a market in San Francisco. The earliest record in the wild is from an irrigation ditch near Hanford, Kings County (Hannibal 1911). The only other population known in the state is in Mountain Lake in San Francisco.

Habitat: Ditches and ponds.

Status: Exotic; not spreading rapidly and posing no threat to native fauna.

Cipangopaludina chinensis malleata (Reeve, 1863)

Type locality: Japan (no specific locality).

Native in Japan; now found in many of the United States. In California in the Sacramento-San Joaquin Valley, and from the San Francisco Bay region to southern California. Earliest record in California: 1891. "The species was brought from Yokohama and originally planted between Alameda and Centerville to supply the markets about San Francisco bay" (Hannibal, 1911).

Habitat: Irrigation ditches, sloughs, natural and artificial ponds.

Status: Exotic, but posing no threat to native fauna.

Superfamily Littorinacea

FAMILY LITTORINIDAE

Littorina (Algamorda) subrotundata (Carpenter, 1865)

Type locality: Neah Bay, Clallam County, Washington.

Neah Bay, Washington, to Humboldt Bay, California; in California known only from Humboldt Bay.

Habitat: *Salicornia* salt marshes below mean high water.

Status: Narrowly localized. Only five populations are known, and only one in California.

Threats: Elimination of habitat by land fill or construction; pollution by municipal wastes, oil spill, or sawmill or pulp mill operations.

Synonym: *Paludinella newcombiana* Hemphill, 1877; type locality Humboldt Bay, Humboldt County.

Superfamily Rissoacea

FAMILY ASSIMINEIDAE

Assiminea californica (Tryon, 1865)

Type locality: Martinez and Oakland, California.

Southern British Columbia (Puget Sound) to the Gulf of California, principally in bays. Probably in every bay along the coast of California.

Habitat: Upper part of intertidal zone, especially in *Salicornia* marshes beneath dead wood and drift; less often on protected rocky shores beneath rocks or among cobbles where humidity remains high between tides.

Synonyms: ?*Jeffreysia translucens* Carpenter, 1866; type locality San Diego. *Assiminea californica* O. Boettger, 1887; type locality San Francisco Bay.

Assiminea infima S. S. Berry, 1947

Type locality: Bad Water, Death Valley National Monument, California.

Found only in the two saline pools at Bad Water.

Habitat: Saline seepage into the salt-saturated pools, as well as protected situations just out of water on salt crust or vegetation.

Status: Narrowly localized; only two populations known, both at Bad Water.

Threats: Tourist foot traffic at margin of pools; ground water development that might reduce inflow into the pools and increase salinity of the habitat.

FAMILY HYDROBIIDAE

Subfamily Hydrobiinae

Fontelicella californiensis Gregg and Taylor, 1965

Type locality: Campo Creek, San Diego County, California.

West side of southern Sierra Nevada and Tehachapi Mountains through San Gabriel and Laguna Mountains to northermost Baja California.

Habitat: Springs and small spring-fed streams, commonly in soft mud among dense watercress or sedges.

Fontelicella stearnsiana (Pilsbry, 1899)

Type locality: Near Oakland, Alameda County, California.

Central California, from Sonoma County to Monterey County along the coast, and inland in the foothills of the Sierra Nevada. Precise limits of range are uncertain.

Habitat: Springs and small spring-fed streams, commonly in soft mud among dense watercress or sedges.

Pyrgulopsis archimedis S. S. Berry, 1947

Type locality: Upper Klamath Lake near Algoma, Klamath County, Oregon.

Upper Klamath Lake, Oregon; formerly in Tule Lake, Modoc County, Califor-

nia, where presumed extinct; possibly Lower Klamath Lake, Siskiyou County, but no definite records.

Habitat: Large shallow lakes.

Status: Narrowly localized; presumed extinct in California.

Threats: Pollution and agricultural development.

Savaginius yatesianus (J. G. Cooper, 1894)

Type locality: Mission San Jose, Santa Clara County, California; fossil.

Only one collection is known that indicates the species lived in modern times: Iron District, 8 miles east of Antioch, Contra Costa County, collected by Miss Ward and pupils prior to 1870; reported by Carlton (1870) as "*Fluminicola nuclea*".

Habitat: Sloughs of San Joaquin River.

Status: Probably extinct, from effects of placer gold mining and reclamation of Delta for agriculture.

Subfamily Lithoglyphinae

The American species of *Lithoglyphus* were separated for some time in a separate genus *Fluminicola*. With increased knowledge of morphology of both the European species and those of America the supposed differences appear inconsequential.

Lithoglyphus seminalis (Hinds, 1842)

Type locality: Sacramento River below mouth of American River, California.

Sacramento River from near its mouth upstream into Pit River, including large spring-fed tributaries. Possibly extinct over most of former range in Sacramento River.

Habitat: Large creeks and rivers.

Synonym: *Lithoglyphus cumingi* Frauenfeld, 1863; type locality "California" (no specific locality).

Lithoglyphus turbiniiformis (Tryon, 1865)

Type locality: West side of Steens Mountains, Harney County, Oregon.

Central and southern Oregon and northeastern California.

Habitat: Springs and spring-fed creeks.

Synonym: *Fluminicola modoci* Hannibal, 1912; type locality Fletcher spring, south end of Goose Lake, Modoc County.

FAMILY LITTORIDINIDAE

Tryonia imitator (Pilsbry, 1899)

Type locality: Santa Cruz, California.

Salmon Creek, Sonoma County, to Imperial Beach, San Diego County.

Habitat: Brackish lagoons and estuaries.

Status: Restricted to areas where fresh water and sea water mix to create brackish water, too saline for freshwater species and too fresh for all but a very few more characteristically marine forms, such as *Batillaria* and *Cerithidea*. It lives in soft mud or fine sand, in uppermost layers of the substratum. Most populations are now extinct, perhaps less than eight surviving.

Threats: Pollution; dredging of channels or marinas; restriction of sea-water exchange.

Tryonia protea (Gould, 1855)

Type locality: Colorado Desert, California.

Western Utah to southeastern California, adjacent Baja California, and southwestern Arizona. Only two populations are known in California: Hot Creek, Mono County; and Dos Palmas Spring, Riverside County.

Habitat: Outflows of thermal springs.

Synonyms: *Melania exigua* Conrad, 1855; type locality Colorado Desert, Imperial County. *Pyrgulopsis blakeana* D. W. Taylor, 1950; type locality Fish Springs, Imperial County. *P. cahuillarum* D. W. Taylor, 1950; Colorado Desert near "Fish Traps," Riverside County.

FAMILY POMATIOPSIDAE

Pomatiopsis binneyi Tryon, 1863

Type locality: "Bolinás" imprecise, probably from nearby Mt. Tamalpais, Marin County, California.

Marin County, California, from Mt. Tamalpais northwest along Bolinas Ridge to Walker Creek.

Habitat: Perennial seepages and rivulets, where protected from seasonal flushing in the rainy season.

Status: Narrowly localized in coastal Marin County.

Pomatiopsis californica Pilsbry, 1899

Type locality: San Francisco, California.

Southwestern Oregon to northern San Mateo County, California, in the narrow coastal fog belt.

Habitat: Semiaquatic. The snails are characteristically found among wet leaf litter and vegetation beside flowing or standing water in shaded situations where humidity remains high.

Synonym: *Pomatiopsis chacei* Pilsbry, 1937; type locality "a swampy place 6 miles up the highway from Klamath," Del Norte County.

Subclass Pulmonata

Order Limnophila

Superfamily Lymnaeacea

FAMILY LYMNAEIDAE

Some authors classify nearly all Lymnaeidae in *Lymnaea*, while others recognize numerous genera. The present system is intermediate.

Subfamily Lymnaeinae

Lymnaea (s. s.) *stagnalis appressa* Say, 1821

Type locality: Lake Superior.

Widespread over most of northern North America, as far south as southern Utah and Colorado. In California in the northeastern part of the state only.

Habitat: Lakes, ponds, and slow streams.

Lymnaea (*Hinkleyia*) *caperata* Say, 1829

Type locality: Near New Harmony, Posey County, Indiana.

Widespread over most of northern North America, as far south as southeastern California and southern Colorado. In California in the northeast, and in eastern Inyo County.

Habitat: Ditches, marshes, seepages, and small streams, characteristically in situations subject to seasonal drying.

Lymnaea (Hinkleyia) montanensis (F. C. Baker, 1913)

Type locality: Hayes Creek near Ward, Ravalli County, Montana.

Northwestern United States, south and southeastward as far as northern California, southern Utah, and northwestern Colorado; sporadic. In California only three occurrences are known: one in Shasta County, two in Warner Mountains, Modoc County.

Habitat: Seepage areas, wet meadows, and small streams, characteristically in situations subject to seasonal drying. Compared to *L. caperata* it is more often found in flowing and clear waters.

Lymnaea (Stagnicola) palustris—group

The several probable species of this group in western North America cannot be identified consistently by shell features. In California there may be one or more. The following nominal species are based on specimens from the state: *Lymnaea proxima* Lea, 1856; type locality San Antonio Creek, Marin County. *L. traski* Tryon, 1863; type locality Mountain Lake, San Francisco County. *L. traski* Lea, 1864, preoccupied, = *Limnophysa tryoni* "Lea" Tryon, 1865 and *Lymnaea tryoniana* Lea, 1867; type locality San Antonio Creek, Marin County. *L. gabbi* Tryon, 1865; type locality Clear Lake, Lake County. *L. rowelli* Tryon, 1865; type locality San Francisco. *L. californica* Sowerby, 1872; type locality California (no specific locality). *L. interstriata* Sowerby, 1872; type locality California (no specific locality). *L. leai* F. C. Baker, 1907; type locality near San Francisco. *Stagnicola palustris magister* F. C. Baker, 1934; type locality Tule Lake, Modoc County.

In California the species-complex is general in the northernmost part of the state; southward along the coast and at higher elevations; the southernmost occurrences in the San Bernardino Mountains.

Habitat: Lakes, ponds, marshes, ditches, slow streams.

Bakerilymnaea bulimoides (Lea, 1841)

Type locality: Oregon; no specific locality, but probably from near mouth of Willamette River, Columbia County.

Coastal southern Alaska to southern California, principally along the Pacific Coast; eastward as far as western Idaho. In California general in the northernmost part of the state; southward along the coast to Santa Barbara County, and in the interior at higher elevations to Kern County.

Habitat: Seepage areas and small streams; characteristically in seasonal flowing water.

Synonyms: *Lymnaea adelinae* Tryon, 1863; type locality San Francisco. *L. bryanti* F. C. Baker, 1905; type locality Alameda County (no specific locality). *L. cubensis sanctijosephi* Hannibal, in Keep, 1910; type locality Calabazas Creek between Alviso and Lawrence, Santa Clara County.

Bakerilymnaea cubensis (Pfeiffer, 1839)

Type locality: Cuba (no specific locality).

Southern United States from Pacific to Atlantic; Mexico and West Indies. Common at lower elevations in southern California from San Luis Obispo County southward; recorded rarely and perhaps not established permanently to the north, in Pajaro and San Joaquin valleys.

Habitat: Ditches and small streams, characteristically just out of water or just submerged on bare mud.

Synonym: *Galba bulimoides cassi* F. C. Baker, 1911; type locality Rose Canyon, near Pacific Beach, San Diego County.

Bakerilymnaea techella (Haldeman, 1867)

Type locality: Texas (no specific locality).

Western United States from the Great Plains westward; adjacent Plains in Canada; northern Mexico. In California from the central Coast Ranges to the northeastern part of the state.

Habitat: Seasonal ponds and small lakes, even those with water only a few months of the year. It is more tolerant of desiccation than any other freshwater mollusk in the state and may be the only species present in a given locality.

Synonym: *Lymnaea bulimoides sonomaensis* "Hemphill" Pilsbry and Ferriss, 1906; type locality Sonoma County (no specific locality).

Group of *Fossaria modicella*

Shell characters are poorly marked in this group, hence the number of species, their names and distribution are not firmly established. Further revisions are likely to add rather than subtract from the two listed here.

Fossaria cooperi (Hannibal, 1912)

Type locality: Wrights, Santa Clara County.

Central California in the Coast Ranges and foothills of Sierra Nevada; southward at higher elevations as far as Kern County.

Habitat: Springs and perennial creeks; usually in shallow running water, rather than in quiet water or on mud just out of water as *F. modicella* occurs.

Fossaria modicella (Say, 1825)

Type locality: Owego, Tioga County, New York.

Widespread over most of North America; general in California.

Habitat: Just out of water, or in shallow water, on mud at the edges of ditches and small streams. In life the shell is characteristically mud-coated.

Group of *Fossaria parva*

Fossaria parva (Lea, 1841)

Type locality: Cincinnati, Ohio.

Widespread over most of North America; general in California.

Habitat: Just out of water on wet mud in seepage areas, marshes, or along small streams.

Pseudosuccinea columella (Say, 1817)

Type locality: Not specified, but probably near Philadelphia, Pennsylvania.

Native over most of the eastern United States, now common over much of central and southern California. Earliest record: 1921, irrigation ditch between Felix and Milton, Calaveras County.

Habitat: Small creeks to larger rivers, irrigation ditches, garden pools, natural ponds, and lakes. A common occurrence is in the film of water on lily pads, or on floating wood or vegetation.

Status: Exotic, but posing no threat to native fauna.

Subfamily Radicinae

Radix auricularia (Linnaeus, 1758)

Type locality: Europe (no specific locality).

Europe and northern Asia to Alaska; in the conterminous United States wide-

spread; introduced, presumably from Europe. In California at first restricted to artificial bodies of water in metropolitan areas, but now found in rivers and lakes even in remote areas. It is likely to become general in the state within a few decades. Earliest record in California: about 1920, in artificial ponds in Los Angeles (Gregg, 1923).

Habitat: Lakes, ponds, reservoirs, rivers, creeks, and ditches, generally in situations with abundant submergent aquatic vegetation.

Status: Exotic, but posing no threat to native fauna.

FAMILY LANCIDAE

Lanx alta (Tryon, 1865)

Type locality: Klamath River (no specific locality).

Drainages of Umpqua and Klamath rivers, Oregon, to South Fork of Trinity River (tributary to Klamath River), California; Smith River, California.

Habitat: Larger rivers and major tributaries, on boulders or rock in current.

Lanx klamathensis Hannibal, 1912

Type locality: South end of Upper Klamath Lake, Klamath Falls, Oregon.

Klamath Lake, Oregon, and slow tributary streams; in California known only in Sheepy Creek, Siskiyou County, tributary to Lower Klamath Lake.

Habitat: Lake and slow, spring-fed, larger tributary streams.

Lanx patelloides (Lea, 1856)

Type locality: Sacramento River (no specific locality).

Pit River below the falls; Sacramento River from Pit River downstream to Mill Creek, Tehama County; and lower parts of larger streams tributary to both rivers.

Habitat: Larger rivers and major tributaries, on firm substratum in slow to moderate current.

Synonyms: *Ancylus newberryi* Lea, 1858; type locality "Klamath Lake" by error, probably Rising River, Shasta County. *Lanx hannai* Walker, 1925; type locality McCloud River, about 2 miles upstream from Baird, Shasta County.

Superfamily Planorbacea

FAMILY PLANORBIDAE

Subfamily Planorbinae

Gyraulus (s. s.) *circumstriatus* (Tryon, 1866)

Type locality: Artificial pond at Weatogue, Hartford County, Connecticut.

Central North America, from Pacific to Atlantic Ocean. Widespread but sporadic in northern and central California; an isolated southern occurrence in the San Bernardino Mountains.

Habitat: Ponds and cienegas subject to seasonal fluctuation of water level.

Gyraulus (s. s.) *parvus* (Say, 1816)

Type locality: Delaware River, near Philadelphia, Pennsylvania.

Widespread over most of North America; general in California, but along the northern and central coast mostly replaced by *Menetus*.

Habitat: Lakes, ponds, reservoirs, rivers, creeks, and ditches; perennial or subject to seasonal fluctuation but not drying entirely. Characteristically it is found among dense submergent aquatic vegetation.

Gyraulus (*Armiger*) *crista* (Linnaeus, 1758)

Type locality: Germany (no specific locality).

Circumboreal; widespread over northern North America, but sporadic. In California known only from the Santa Cruz Mountains, San Mateo and Santa Clara counties.

Habitat: Seasonal ponds.

Subfamily *Biomphalariinae*

Biomphalaria obstructa (Morelet, 1849)

Type locality: Isla del Carmen, Campeche, Mexico.

Southernmost United States through Mexico. In California originally native in distributaries of the Colorado River in what is now Imperial Valley. Occurrences in drainage ditches tributary to Salton Sea, Riverside County, might be due to natural spread from native populations, or to introductions through aquarium trade.

Habitat: Drainage ditches, ponds.

Synonym: *Planorbis gracilentus* Gould, 1855; type locality Colorado Desert.

Subfamily *Helisomatinae*

As classified herein, the larger species are grouped into genera according to direction of coil. *Planorbella* includes orthostrophic species, i.e., the shell is sinistral, coiled in the same sense as the animal. *Helisoma* includes heterostrophic species, in which the shell is dextral and coiled in sense opposite to the animal. In both genera height of spire is variable. In the classification used by F. C. Baker (1945) the dextral, high-spined shell of *Carinifex* is emphasized by distinguishing it as a genus, whereas all other species are grouped in *Helisoma*.

Helisoma (s. s.) *anceps* (Menke, 1830)

Type locality: Virginia (no specific locality).

Widespread over much of North America; general in the United States except for the southwest, and sporadic in the Pacific Northwest. Found in Dog Lake, Lake County, Oregon, tributary to Goose Lake, California-Oregon, and thus expected in northeastern California.

Habitat: Perennial creeks, rivers, and lakes.

Helisoma (*Carinifex*) *minus* (J. G. Cooper, 1870)

Type locality: Clear Lake, Lake County, California.

Restricted to Clear Lake and nearby Blue Lakes, Lake County.

Habitat: Little known; perhaps principally in soft substratum.

Status: Narrowly localized in two lakes.

Helisoma (*Carinifex*) *newberryi* (Lea, 1858)

Type locality: Hat Creek, Shasta County, California; the more precise location Rising River suggested as "a lectotype locality" by Hanna and Gester (1963).

Lakes and larger, slow streams in and around the northern Great Basin. In California known from six local drainages, in which the species survives in probably only four. Lower Klamath Lake, Siskiyou County; possibly extinct in the Lake, but surviving in the spring-fed tributary Sheepy Creek. Tule Lake, Modoc and Siskiyou counties, where probably extinct. Pit River, including the large spring-pools and their outflows of Fall River and Hat Creek; known downstream to above Squaw Creek, but probably extinct in the lower segment of its range. Eagle Lake, Lassen County. Lake Tahoe and adjacent slow segment of its outflow, Truckee River. Formerly in Fish Springs, Owens Valley, Inyo County; exterminated by construction of a fish hatchery.

Habitat: Larger lakes and slow rivers, including larger spring sources and spring-fed creeks. The snails characteristically burrow in soft mud and may be invisible even when abundant.

Synonyms: *Carinifex ponsonbyi* E. A. Smith, 1876; type locality "California," more precisely Lower Klamath Lake. *C. occidentalis* Hanna, 1924; type locality Eagle Lake. *C. newberryi subrotunda* Pilsbry, 1932; type locality head of Fall River. *C. newberryi malleata* Pilsbry, 1934; type locality "Pitt River and Canoe Creek"; probably from Pitt River above Squaw Creek.

Planorbella (Pierosoma) subcrenata (Carpenter, 1857)

Type locality: Oregon (no specific locality).

Northern and eastern limits of range uncertain. Widespread in Pacific Northwest and northern Rocky Mountains; southward at higher elevations to northern California and southern Colorado; isolated populations in the San Bernardino Mountains, southern California.

Habitat: Lakes, ponds, marshes, and slow streams.

Synonyms: *Planorbis subcrenatus disjunctus* Cooper, in Raymond and Cooper, 1890; type locality Soda Springs, Tuolumne County. *Helisoma occidentale depressum* F. C. Baker, 1934; type locality Lower Klamath Lake.

Planorbella (Pierosoma) tenuis (Dunker, 1850)

Type locality: Vicinity of Mexico City.

Southwestern Oregon to the southern Plateau of Mexico; eastward as far as New Mexico and trans-Pecos Texas. Widespread in California, but replaced at higher elevations by *P. subcrenata*.

Habitat: Lakes, ponds, artificial garden ponds and reservoirs, marshes and slow streams; even in seasonal water bodies.

Synonyms: *Planorbis ammon* Gould, 1855; type locality Colorado Desert. *Helisoma tenue californiense* F. C. Baker, 1934; type locality Guadalupe Creek, San Jose, Santa Clara County. *Helisoma hemphilli* F. C. Baker and Henderson, in F. C. Baker, 1934; type locality Mountain Lake, San Francisco County.

?*Planorbella (Pierosoma) traski* (Lea, 1856)

Type locality: Kern Lake, Tulare County, California.

Lakes in southern San Joaquin Valley, all now eliminated or highly modified through agricultural development.

Habitat: Large, shallow, marshy lakes.

Status: Taxonomic rank uncertain; possibly only an extreme ecophenotype of *P. tenuis*. As the populations are all presumed extinct, the validity of the species may never be established.

Planorbella (Seminolina) duryi (Wetherby, 1879)

Type locality: "Somewhere along the eastern border of Volusia County," Florida, as interpreted by Pilsbry (1934).

Native to Florida; becoming widespread through the aquarium trade, known in the albino form as the "red ramshorn". Common in southern California, especially in artificial ponds and outflow of warm springs; northward in the immediate vicinity of the coast as far as Humboldt County. Earliest record in California: 1931, Loma Linda, San Bernardino County.

Habitat: Outflow of warm springs; drainage ditches and irrigation ditches; garden ponds; natural lagoons and lakes. The northern limit of range is presumably controlled by winter minimum temperatures.

Status: Exotic, but posing no threat to native fauna.

Vorticifex effusus (Lea, 1856)

Type locality: Sacramento River, California (no specific locality).

Southern Washington to northern and east-central California; eastward to the Snake River, southern Idaho. In California in the Klamath and upper Sacramento drainages, and interior drainage in the northeastern part of the state; Lake Tahoe. Local in the Owens Valley, Inyo County, where now possibly extinct.

Habitat: Larger lakes, rivers, spring sources, and spring-fed streams; restricted to perennial well-oxygenated water.

Synonyms: *Parapholyx mailliardi* Hanna, 1924; type locality Eagle Lake, Lassen County. *Pompholyx solida optima* Pilsbry, 1934; type locality "Lake Bigler," an old name for Lake Tahoe.

Subfamily Neoplanorbinae

Micromenetus dilatatus (Gould, 1841)

Type locality: Nantucket and Hingham, Massachusetts.

Widespread in the eastern United States, southwestward to southern Texas; sporadic on the Plateau of Mexico. Northern and central California, sporadic in the Coast Ranges, Sacramento Valley, and foothills of Sierra Nevada.

Habitat: Ponds, slow streams, and springs, characteristically on dead wood.

Subfamily Planorbulinae

Menetus callioglyptus (Vanatta, 1895)

Type locality: "Freeport," no longer in existence, formerly west of Kelso, Cowlitz County, Washington.

Southern coastal Alaska southward to central California; eastward to northern Idaho. In California mainly in the north, but southward along the coast to Lake Merced, San Francisco County.

Habitat: lakes, rivers, and creeks.

Menetus centervillensis (Tryon, 1871)

Type locality: Centerville, Alameda County, California.

Oregon to southern California. In California common in the north, especially along the coast; southward to the central Sierra Nevada; in the Coast Ranges becoming sporadic to the south. In southern California formerly in Ballona Creek and Los Angeles River, Los Angeles County, presumably extinct; and in the San Bernardino Mountains.

Habitat: Ponds, small streams, springs, and seepage areas, in perennial oxygenated water.

Synonym: *Menetus labiatus* F.C. Baker, 1945; type locality Terminal Island, Los Angeles County.

Menetus opercularis (Gould, 1847)

Type locality: "Rio Sacramento" by error, actually Mountain Lake, San Francisco County, California.

Restricted to Mountain Lake; extinct.

Promenetus exacuus (Say, 1821)

Type locality: Lake Champlain, New York—Vermont.

Widespread in northern North America; southward to western Nevada, New Mexico, and Kansas. In California known from one occurrence in Modoc County.

Habitat: Ponds, marshes, and slow streams.

Promenetus umbilicatellus (Cockerell, 1887)

Type locality: Brandon and Birtle, Manitoba, Canada.

Widespread in northern North America; southward to central Nevada, Arizona, and northern New Mexico. Northeastern California only.

Habitat: Seasonal ponds, ditches, small streams, and marshes.

FAMILY ANCYLIDAE

Ferrissia californica (Rowell, 1863)

Type locality: Feather River, Marysville, Yuba County, California.

Widespread over the United States and northern Mexico. Found over most of California, but replaced along the northwestern coast and at higher elevations by *F. rivularis*.

Habitat: Streams, lakes, ponds, and garden ponds; on lily pads, cattails, dead leaves, or trash on which there is a thin film of plant growth.

Synonym: *Ancylus fragilis* Tryon, 1863; type locality Laguna Honda, San Francisco.

Ferrissia rivularis (Say, 1817)

Type locality: Presumably in the vicinity of Philadelphia, Pennsylvania.

Northern United States and southern Canada. General in northern California; southward in the Coast Ranges to Marin County, and in the Sierra Nevada to Mariposa and Mono counties.

Habitat: Rivers, creeks, lakes, and ponds; on lily pads, cattails, stones, or dead wood in well oxygenated if not flowing water.

Synonym: *Ancylus caurinus subalpinus* J. G. Cooper, in Raymond and Cooper, 1890; type locality Yosemite Valley, Mariposa County, and Bloody Canyon, Mono County.

Superfamily Physacea

FAMILY PHYSIDAE

The two common species of *Physa* are typically distinct in shell but not consistently so, hence the precise range and allocation of some synonyms are uncertain. Nevertheless the specific names are likely to be stable. *Physa gyrina* in California agrees well with the diagnostic features of the species as described by Clappitt (1970) from Iowa. *Physa virgata* is widespread and morphologically consistent over the southwest, with no likely older names. Subgeneric names of these two species are less certain to prove stable, as classification within the genus is not well understood.

Physa (Alampetista) virgata Gould, 1855

Type locality: Gila River, Arizona, and near San Diego, San Diego County, California.

Southwestern Oregon to southern Mexico, widespread in the southwestern United States but eastern limits of range uncertain. General in the southern third of California, but becoming sporadic in the central Coast Ranges and Sacramento Valley. At higher elevations and along the northwestern coast replaced by *P. gyrina*.

Habitat: Springs, creeks, and rivers, in perennial water; less often in ponds, lakes, and reservoirs.

Synonyms: *P. humerosa* Gould, 1855; type locality Colorado Desert. *P. striata* Lea, 1864, preoccupied, = *P. dorbigniana* Lea, 1866; type locality "Salt Lagoon, near Monterey". *P. traski* Lea, 1864; type locality Los Angeles River, Los Angeles County. *P. distinguenda* Tryon, 1865; type locality Stockton, San Joaquin County. *P. occidentalis* Tryon, 1865, in part; no specific type locality. *P. sparsestriata* Tryon, 1865; type locality San Joaquin Valley, no specific locality. *P. marci* F. C. Baker, 1924; type locality "Little Valientia Spring" (probably Little Caliente Spring), Santa Barbara County.

Physa (Costatella) costata Newcomb, 1861

Type locality: Clear Lake, Lake County, California.

Restricted to Clear Lake and nearby Blue Lakes, Lake County.

Habitat: Rocky areas near shore of the lakes.

Status: Narrowly localized in two water bodies.

Physa (Physella) gyrina Say, 1821

Type locality: Boyer River near Council Bluffs, Iowa.

Widespread over much of northern North America; general in northern California, ranging as far south as the central Coast Ranges (Monterey County) and central Sierra Nevada.

Habitat: Springs, creeks, rivers, lakes and reservoirs.

Synonyms: *P. virginea* Gould, 1847; type locality "Rio Sacramento" by error, actually Mountain Lake, San Francisco County. *P. triticea* Lea, 1856; type locality Shasta County, no specific locality. *P. gabbi* Tryon, 1863; type locality Mountain Lake, San Francisco County. *P. blandi* Lea, 1864; type locality California, no specific locality. *P. cooperi* Tryon, 1865; type locality spring in Crane Lake Valley (Crane Lake is now Cowhead Lake), Modoc County. *P. diaphana* Tryon, 1865, preoccupied, = *P. binneyana* Ancey, 1886; type locality Oakland, Alameda County. *P. occidentalis* Tryon, 1865, in part; several localities in Washington, Oregon, and California were cited, none specified as type locality. *P. politissima* Tryon, 1865; type locality Sacramento. *P. carltoni* Lea, 1865; type locality near Antioch, Contra Costa County.

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THE ROLE OF TEMPERATURE AND PHOTOPERIOD IN THE ONTOGENETIC MIGRATION OF PREJUVENILE *SEBASTES DIPLOPROA* (PISCES: SCORPAENIDAE) ¹

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Prejuvenile *Sebastes diploproa* migrate from the seasonally warm surface waters of the northeast Pacific Ocean to depths of 200 to 500 m, encountering a major change in thermal environment. To better understand the factors important in initiation and timing of the migration, temperature tolerance and thyroid follicle cell height were monitored on a seasonal basis and in fish acclimated to nine difference photoperiod-temperature regimes. In field-acclimatized specimens thyroid follicle cell height was negatively correlated and temperature tolerance was positively correlated with collection temperature; no changes were noted during the migratory season. In laboratory-acclimated fish temperature tolerance and follicle cell height maintained the same relationship with acclimation temperature. Whereas temperature tolerance showed no response to photoperiod, follicles in the shortest photoperiod of acclimation (8L:16D) were characterized by hypertrophy and hyperplasia. A temperature-dependent size threshold may exist for the state of thyroid hypertrophy which appears to be related to the size threshold for migration. It is suggested that timing of the migration is controlled by rate of change of photoperiod subject to a temperature-dependent endogenous program.

INTRODUCTION

Habitat segregation among ontogenetic stages of fishes is a common phenomenon. Early life history stages of highly fecund marine species, for example, are generally planktonic for varying lengths of time; drift during the pelagic phase may result in distributional differences among ontogenetic stages. Several mechanisms exist for the recruitment of the juvenile stages to the adult habitat. Norris (1963) suggested that temperature selection was an important factor in the movement of prejuvenile *Girella nigricans* from pelagic to nearshore habitats. Prejuvenile *Sebastes diploproa* from 9-50 mm SL are common under drifting kelp in the southern California bight (Mitchell and Hunter 1970; Boehlert 1977) and co-occur with prejuvenile *G. nigricans*. Benthic juvenile and adult *S. diploproa*, however, inhabit depths of 200 to 500 m in the northeast Pacific Ocean in contrast with the nearshore environment of juvenile and adult *G. nigricans*. Prejuvenile *S. diploproa* are present at the surface year-round and emigrate from surface waters at an age of approximately 1 year; they apparently have a transitional midwater stage at depths near 250 m prior to recruitment to the benthic adult habitat (Boehlert 1977). This migration occurs over a relatively short season during which prejuveniles encounter a major change in physical and biotic characteristics of their environment.

As part of an investigation of factors important in the timing of the migration, the present study analyzes seasonal changes in upper lethal temperature and thyroid follicle cell height to develop criteria for the state of "migratory readiness" in surface prejuvenile *S. diploproa*. To assess the effect of temperature and

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photoperiod upon observed changes prejuveniles were acclimated to photoperiod-temperature regimes in the laboratory. Several specimens were also held beyond the size and age at which migration normally occurs to ascertain the presence or absence of an endogenous program related to migration.

MATERIALS and METHODS

Experimental Animals

Pelagic prejuveniles were collected by dipnet under drifting algae 8–18 km offshore from San Diego, California; benthic juveniles and adults used for thyroid histology were collected in otter trawls at depths from 200–400 m (Boehlert 1977).

Holding facilities and acclimation schedules have been described (Boehlert 1978). Briefly, pelagic prejuveniles were maintained in running seawater; photoperiod and temperature were changed at rates of 15 min per day and 0.5°C per day, respectively, until desired photoperiod-temperature regimes were reached. Fish were acclimated to the final regime for a minimum of 4 weeks prior to experimental use. Three photoperiods (8 Light:16 Dark, 12L:12D, and 16L:8D) and three acclimation temperatures (10°, 15°, and 20°C) combined to nine acclimation treatments. The fish for the 8L:16D acclimation were collected 30 December 1975 at 13.8°C and acclimated during January and early February; those for the 12L:12D acclimation were collected 17 March 1976 at 15.5°C and acclimated during the month of April; those for the 16L:8D acclimation were collected 14 May 1976 and 21 May 1976 at 17.7° and 17.6°C, respectively, and acclimated during the month of June. Captive fish were fed a mixture of commercial trout chow, frozen brine shrimp, and ground squid.

Critical Thermal Maxima

For determination of lethal temperatures, single fish were placed in gallon jars of filtered seawater with aeration to prevent temperature stratification and depletion of dissolved oxygen. These jars were placed in a temperature-controlled water bath agitated by a mechanical stirrer to insure uniform temperature. Five to seven fish were used in each determination of lethal temperature. Experiments began at the temperature of collection or acclimation. Determinations made on the field-acclimatized fish were conducted within a week on specimens maintained at the photoperiod and temperature of capture.

Temperature was raised 4.2°C per hour. Fish were considered dead when no respiratory movements were observed 30 s after mechanical stimulation with a glass probe. At this point, the temperature was recorded to the nearest 0.1°C.

Thyroid Histology

The thyroid region was dissected from freshly collected or laboratory-acclimated fish, placed in Bouin's solution for 48 h, dehydrated, and infiltrated with paraffin. Tissues were serially sectioned at 6 μ m between the first and fourth basibranchials. To prevent measurement of the same follicle, only the first 2 of each 15 sections were mounted; subsequent measurements were made on the better of the two sections. Sections were stained in Harris' hematoxylin and eosin-phloxine B.

Depending on the size of the specimen and the number of follicles present in the sample, 12 to 50 unbroken thyroid follicles were chosen at random.

Follicle cell height was measured at an angle normal to the colloid-cell interface with an ocular micrometer at 1200 magnifications. Four cells were measured in each follicle; these were generally the two cells at the ends of the long axis of the follicle and the two at the ends of the short axis. The mean of the total number of measurements represented the value for a given fish. Thyroid follicle cell height was determined for three to nine fish for each collection or acclimation treatment.

RESULTS

Critical Thermal Maxima (CTMax)

CTMax was determined monthly from February 1976 to January 1977 for field-acclimatized prejuveniles and after complete acclimation for the nine photoperiod-temperature treatments (Table 1). Variability in CTMax proved to be very low within a group of fish with similar thermal histories. No difference was apparent among the mean values for fish acclimated to the same temperatures but to different photoperiods. CTMax was proportional to temperature of collection or of acclimation (Figure 1). Within the tested groups, no consistent effect of size was apparent.

TABLE 1: Critical Thermal Maxima (CTMax) for Field-acclimatized and Laboratory-acclimated Prejuvenile *Sebastes diploproa*. Temperatures Are Those of Collection for Acclimatized Fish and Acclimation Temperature for Acclimated Fish. N = Number of Fish Used in the Determination.

Collection date	Temperature (°C)	SL (mm) range	N	CTMax (°C)	Standard deviation
<i>Field-acclimatized</i>					
26 February 1976.....	14.7	33-44	6	27.5	0.23
17 March 1976.....	15.5	32-46	5	28.1	0.05
19 April 1976.....	14.5	37-43	6	28.2	0.27
14 May 1976.....	17.7	44-50	6	29.4	0.17
16 June 1976.....	19.2	33-42	6	29.9	0.28
27 July 1976.....	20.8	25-32	6	30.0	0.16
12 August 1976.....	19.5	38-42	6	30.3	0.11
7 September 1976.....	20.8	35-45	6	30.1	0.05
15 October 1976.....	21.2	26-37	6	30.1	0.21
23 November 1976.....	18.4	23-37	6	29.4	0.24
10 December 1976.....	17.4	29-37	6	28.9	0.26
11 January 1977.....	16.3	32-40	6	29.1	0.26
<i>Laboratory-acclimated</i>					
8L:16D.....	10.0	43-50	7	26.1	0.25
8L:16D.....	15.0	47-56	6	28.5	0.25
8L:16D.....	20.0	40-48	7	30.0	0.10
12L:12D.....	10.0	41-53	6	25.9	0.19
12L:12D.....	15.0	37-47	6	27.8	0.20
12L:12D.....	20.0	37-44	6	29.8	0.10
16L:8D.....	10.0	49-57	6	26.5	0.16
16L:8D.....	15.0	42-60	6	28.5	0.33
16L:8D.....	20.0	52-56	6	30.1	0.18

Thyroid Histology

Thyroid follicle cell height was determined for 66 field-acclimatized prejuveniles collected on a monthly basis during 1975; dates and temperatures of

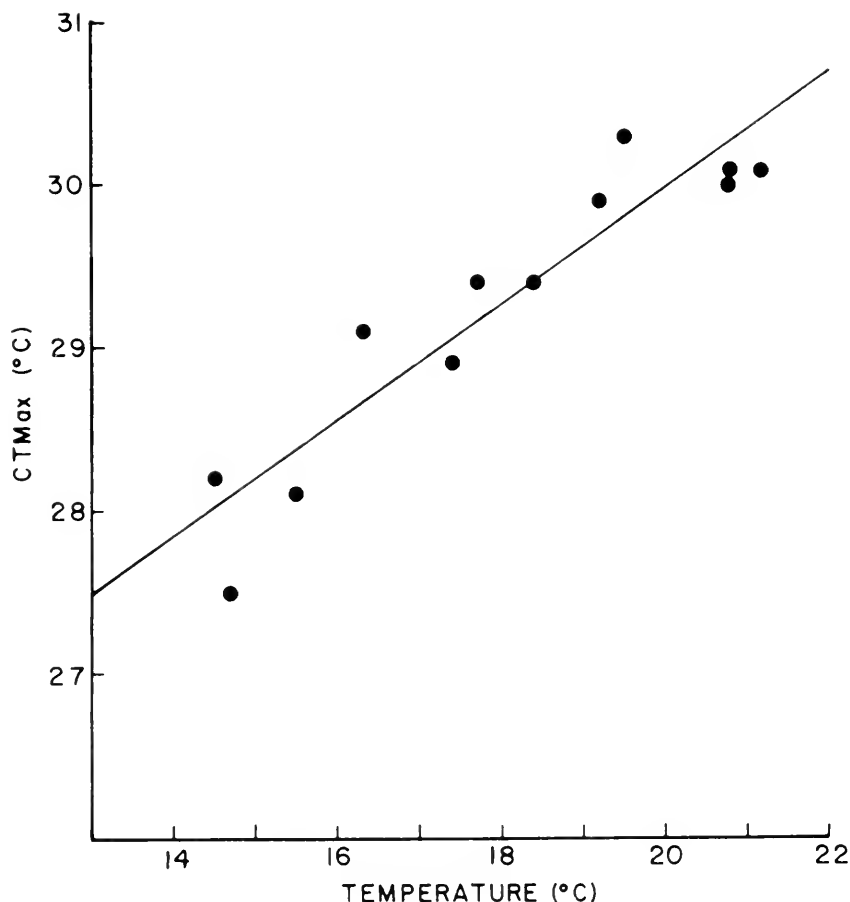


FIGURE 1: Relationship of critical thermal maximum (CTMax) to temperature of collection for field-acclimatized prejuvenile *S. diploproa*. The relationship is described by the equation $Y = 0.36X + 22.8$ ($r^2 = 0.87$).

collection, the number of specimens, size range, and mean follicle cell height were recorded. No trend of follicle cell height with body size was apparent over the size range studied, nor was an increase apparent during the season of migration (Table 2). Follicle cell height was, however, inversely proportional to temperature. Two benthic collections were made to determine whether this relationship held over the temperature range encountered by adults. Mean follicle cell height for 15 benthic juveniles and adults plotted against temperature of collection with the data from the prejuveniles is negatively correlated with temperature (Figure 2; $r = -0.78$).

Mean follicle cell heights measured for the laboratory-acclimated fish were also negatively correlated with temperature (Table 2 and Figure 3). For the same temperatures, no significant difference existed between mean follicle cell heights of fish acclimated to 12L:12D and 16L:8D; mean values of follicle cell height for

8L:16D specimens, however, were much higher with greater variability (Figure 3). The source of the increased variability in these samples came primarily from one fish at each acclimation temperature. At 10°C the smallest specimen was 30.0 mm SL with a mean follicle cell height of 6.2 μm . This value lies quite close to the line determined for the field-acclimatized fish (Figure 2). The other four fish acclimated to 10°C (36.3 to 50.6 mm SL), however, had mean follicle cell heights ranging from 11.1 to 14.8 μm . At 15°C one specimen (33.9 mm SL) had a mean follicle cell height of 4.6 μm , whereas the other specimens (52.2 to 56.6 mm SL) had follicle cell heights from 9.8 to 11.6 μm . At 20°C the variability was contributed by the largest fish (54.8 mm SL, follicle cell height 11.5 μm); the mean value for the other fish acclimated to 20°C (41.0 to 49.6 mm SL) was $5.9 \pm 0.4 \mu\text{m}$. Thyroid follicle cells from the four largest specimens in 10°C and 15°C acclimations and for the single largest specimen in the 20°C acclimation were characteristically hypertrophied and hyperplastic (Figures 4A–C). Those of the smallest fish acclimated 10° and 15°C, and of the four smallest fish acclimated to 20°C, however, were similar in appearance to field acclimatized specimens (Figures 4D–F).

TABLE 2: Information on Follicle Cell Height of the Thyroid Gland for Field-acclimatized and Laboratory-acclimated *Sebastes diploproa*.

Collection date	T(°C) ¹	N	SL (range) (mm)	FCH (μm) ²
20 January 1975.....	14.3	6	22–48	5.7 (0.3)
24 February 1975.....	13.3	3	34–46	6.4 (0.3)
2 April 1975.....	13.5	5	35–49	5.8 (0.5)
29 April 1975.....	14.2	7	38–59	4.9 (0.2)
10 June 1975.....	16.9	7	37–51	4.9 (0.6)
7 July 1975.....	19.4	7	15–43	5.1 (0.5)
11 August 1975.....	20.6	6	20–50	3.4 (0.5)
25 August 1975.....	17.5	6	13–44	5.7 (1.2)
25 September 1975.....	20.8	5	33–44	4.4 (1.3)
27 October 1975.....	16.7	6	25–47	6.0 (0.5)
24 November 1975.....	15.2	4	42–49	4.3 (0.4)
30 December 1975.....	13.8	4	33–45	5.3 (0.2)
<i>Benthic</i>				
22 May 1975.....	7.5	9	49–216	8.8 (1.3)
8 November 1975.....	9.0	6	42–58	6.0 (1.2)
<i>Acclimated</i>				
8L:16D.....	10.0	5	30–51	11.3 (3.3)
8L:16D.....	15.0	5	34–57	9.5 (2.9)
8L:16D.....	20.0	5	41–55	7.0 (2.6)
12L:12D.....	10.0	5	41–56	5.1 (0.9)
12L:12D.....	15.0	5	42–55	4.5 (0.4)
12L:12D.....	20.0	4	43–47	3.8 (0.2)
16L:8D.....	10.0	5	41–58	6.1 (0.6)
16L:8D.....	15.0	5	46–61	4.7 (0.9)
16L:8D.....	20.0	4	40–53	3.5 (0.3)

¹T = temperature of collection or acclimation.

²FCH = mean thyroid follicle cell height. The number in parentheses indicates the standard deviation of follicle cell height measurement.

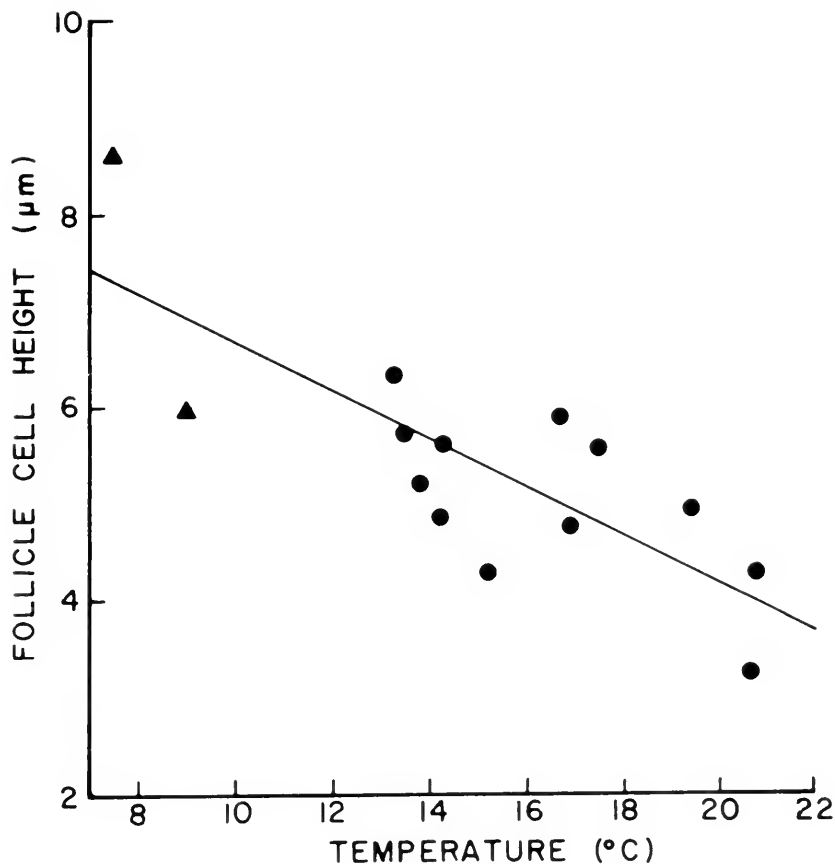


FIGURE 2: The relationship between mean thyroid follicle cell height and temperature of collection for *S. diploproa*. Circles indicate monthly mean values for surface prejuveniles; triangles, benthic juveniles and adults.

DISCUSSION

During the migration from epipelagic prejuvenile to mesopelagic juvenile (Boehlert 1977) to benthic juvenile and adult, *Sebastes diploproa* experiences major changes in temperature, ambient light, hydrostatic pressure, and dissolved oxygen (Reid, Roden, and Wyllie 1958). Changes in respiratory physiology occur prior to the migration and are apparently triggered by environmental factors (Boehlert 1978). Environmental factors important in timing of migrations may include temperature, photoperiod, and rate of change of photoperiod (Wagner 1974). Temperature in aquatic systems, however, is not a conservative property and is therefore an unreliable seasonal cue (Wagner 1974); certain species, in fact, use photoperiod to modify metabolic compensation as exhibited in metabolic rate (Roberts 1961; Burns 1975; Boehlert 1978) or heat tolerance (Hoar and Robertson 1959; Terpin, Spotila, and Coons 1976; Hettler and Colby 1979). In the present study the only variable affecting critical thermal maximum

was temperature of acclimation or acclimatization (Figure 1). Photoperiod-modified heat tolerance in freshwater species is undoubtedly of adaptive value since thermal stress may cause high mortalities and increased vulnerability to predation if temperature alone were the sole controlling factor in acclimation (Hoar and Robertson 1959; Coutant 1973). Thermal shock is less likely in the surface marine habitat of prejuvenile *S. diploproa*, and temperatures within this species' geographic range do not exceed 23°C (Reid et al. 1958). Based upon the proposed migration scheme for this species (Boehlert 1977) temperature changes of 12°C between surface and benthic habitats exist. For critical thermal maximum there appears to be no correlate of the photoperiod-related metabolic changes observed in May through September (Boehlert 1978).

Certain adaptations to environmental parameters may reach a maximum during early ontogenetic development (Kinne 1962); this may also be true of temperature selection and tolerance in fishes (Ferguson 1958; Fry 1937). Benthic juvenile and adult *S. diploproa* live in relatively low, constant temperatures, and are probably stenothermal, whereas the larvae and pelagic prejuveniles withstand the variable thermal regime of surface waters. Wilson, Somero, and Prosser (1974) found that *S. miniatus*, which as an adult lives in shallower water than *S. diploproa*, was unable to acclimate fully to temperatures of 20°C and that several specimens died at temperatures of 22°C. It is likely that similar results would be obtained with adult *S. diploproa*; thus the change in thermal habitats involved in the migration to deep water is probably irreversible.

Changes in thyroid follicle cell height have been demonstrated in several studies dealing with migratory fishes (Woodhead 1959 *a, b*; Woodhead and Woodhead 1964). Environmental parameters important in thyroid cycles include photoperiod (Gross, Fromm, and Roelofs 1963), temperature (Swift 1960; Eales 1964), and rate of change of photoperiod (Eales 1965). In the present study, thyroid follicle cell height was negatively correlated with temperature of collection (Figure 1) as has been noted in other studies (Swift 1960; Eales 1964). There was, however, no evidence of a thyroid cycle or an increase in follicle cell height during the migratory season (Table 2). Similarly, Moser (1966) found no cycle of thyroid activity associated with the reproductive season in *S. paucispinis*. Woodhead (1959*a*) observed thyroid cycles associated both with reproductive seasons and migration in the cod *Gadus callarius* and also observed such a cycle in immature fish (Woodhead 1959*b*). The migratory season for prejuvenile *S. diploproa* occurs in the warmest months of the year (Boehlert 1977) and the state of migratory readiness is metabolically characterized by a change in thermal sensitivity (Boehlert 1978). Eales (1964) suggested that high temperature may increase thyroid activity irrespective of the TSH pathway with no apparent change in follicle cell height. Increased thyroxine may increase respiratory rate (Müller 1953); increased metabolic rates at low temperatures were observed in *S. diploproa* during the migratory season (Boehlert 1978). Thyroid activity expressed as concentration of plasma thyroid hormones may therefore be increased in the migratory season.

As in the field-acclimatized fish, follicle cell height in laboratory-acclimated fish was negatively correlated with temperature (Figure 3). The appearance of the thyroid follicles of the animals acclimated to 12L:12D and 16L:8D were similar to those in the field-acclimatized fish; fish acclimated to 8L:16D, howev-

er, showed an increase in both mean follicle cell height and in variability within each treatment (Table 2) with follicles characterized by hypertrophy and hyperplasia (Figure 4). This suggests that a threshold photoperiod exists between 8 and 12 h which may stimulate an increase in follicle cell height. Hoar and Robertson (1959) and Gross et al. (1963) suggested thyroid activity is increased in shorter photoperiods. Eales (1965), however, found increased follicle cell height associated with lengthening photoperiod. To attain the acclimation photoperiods, a decrease was necessary for the 8L:16D, no change for the 12L:12D, and an increase for the 16L:8D. Moreover, in the 8L:16D acclimation the animals were collected after the winter solstice, when rate of change of photoperiod had changed from negative to positive; to attain 8L:16D, the rate was returned to negative. It is interesting to note that the summer solstice, when rate of change of photoperiod changes from positive to negative, occurs early in the migratory season. Rate of change of photoperiod may thus be involved in initiating changes necessary for migration and should be more fully investigated.

The increased variability of mean follicle cell height in the 8L:16D acclimated fish was size and temperature dependent. Variability was increased in the 10° and 15°C acclimations by the low value of the smallest fish in each case, whereas the variability in the 20°C acclimation was contributed by the high value of the largest fish. Hypertrophy and hyperplasia (Figure 4) were apparent only in the four largest specimens in the 10° and 15° acclimations, and in the largest specimen in the 20°C acclimation. If a size threshold for increased follicle cell height exists, it appears to depend upon the temperature and occurred between 30.0 and 36.3 mm SL in 10° C acclimated fish, between 33.9 and 52.2 mm SL for the 15° C acclimated fish, and between 49.6 and 54.8 mm SL for the 20° C acclimated fish.

Based on distributional evidence, Boehlert (1977) suggested a size threshold for migration between 40 and 50 mm SL. If the thyroid is involved in the migration, the size of 40–50 mm is close to the threshold size for hypertrophy in animals acclimated to 8L:16D between 15° and 20°C. This is indeed the temperature range during which the majority of migration takes place (Boehlert 1977, 1978). The extended migratory period, from May to September, may therefore be a temperature-related endocrinological function. This hypothesis would predict a smaller size threshold for migration in colder years when the change in temperature from surface to bottom (and therefore thermal stress in the migration) would be minimized. This is similar to smoltification and downstream migration in salmonids, which are characterized by both temperature dependence and a size threshold (Foerster 1937; Elson 1957; Hoar 1976); moreover, changes in the temperature cycle change the duration of the migratory period in steelhead (Wagner 1974) but in a direction opposite that proposed for *S. diploproa*.

Photoperiod length, temperature, and endogenous rhythms alone do not appear to be critical factors in determining timing of this migration since laboratory acclimated animals held beyond the size and age at which migration normally occurs do not exhibit the metabolic state of "migratory readiness" (Boehlert 1978). The presence of a size threshold for migration observed by Boehlert (1977) and the temperature-dependent size threshold for thyroid hypertrophy

observed in the present study suggest some involvement of endogenous patterns. I suggest that the timing of this migration is a function of rate of change of photoperiod subject to the control of a temperature-related, endogenous size threshold.

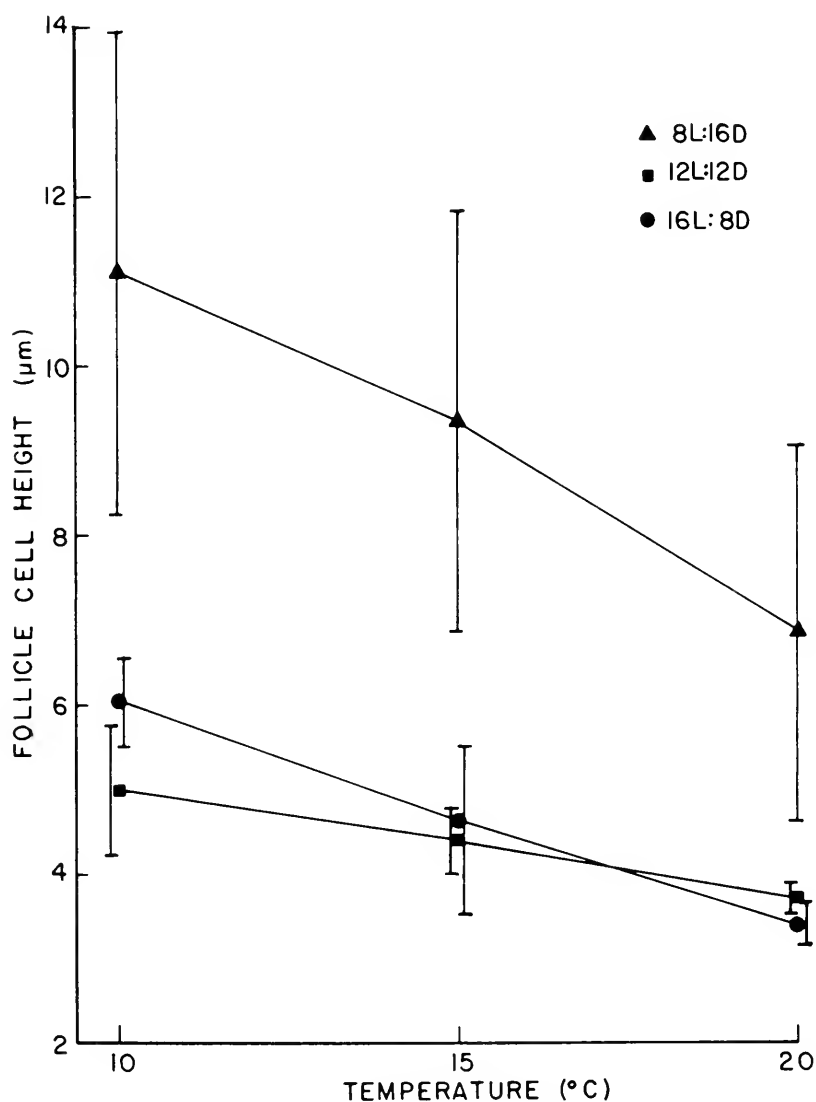


FIGURE 3: The relationship between mean thyroid follicle cell height in acclimated *S. diploproa* and temperature of acclimation for three photoperiods. Vertical lines indicate ± 2 standard errors of the mean. Note the increased variability in the 8L : 16D acclimated groups at all three temperatures.

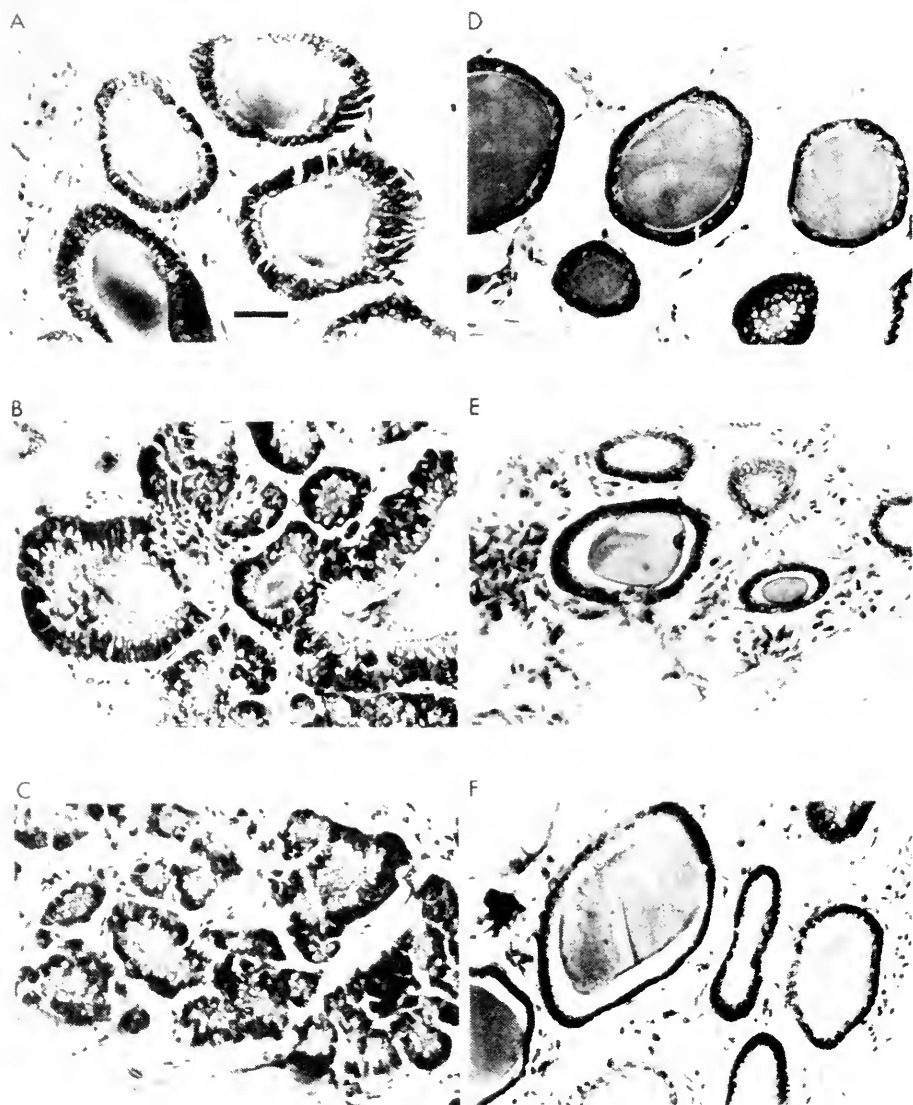


FIGURE 4: Thyroid follicles of prejuvenile *Sebastes diploproa*. A–C: hypertrophied follicle cells from 8L : 16D fish acclimated to 10°, 15°, and 20°C, respectively. Note the increase in follicle cell height and the loss of colloid within the follicles. D–F: “normal” thyroid follicles. D: field-acclimatized specimen (46 mm SL) collected 6/10/75 at 16.9°C. E: 8L : 16D, 10°C acclimated fish (30 mm SL). F: 8L : 16D, 15°C acclimated fish (34 mm SL). The bar in plate A indicates 10 μ m. C: colloid. f: follicle cell.

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COPPER, ZINC, AND CADMIUM CONCENTRATIONS OF RESIDENT TROUT RELATED TO ACID—MINE WASTES¹

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Resident trout from four locations in the upper Sacramento River basin, California were surveyed for copper, zinc, and cadmium concentrations in their flesh (muscle) and liver tissues to determine the impact of acid-mine wastes on tissue metal contaminations. Three of the sampling locations receive acid-mine drainage containing copper, zinc, and cadmium; the fourth location was believed to be devoid of these influences. Metal analyses of water samples collected near the sampling locations confirmed the presence or absence of acid-mine wastes.

No relationship was obvious between the flesh metal concentrations and the size or age of trout, nor between the flesh metal concentrations and the concentrations of copper, zinc, or cadmium in the water. Mean flesh concentrations (fresh weight) from the four locations varied between <0.20 and <0.31 ppm Cu, 2.50 and 4.61 ppm Zn, and <0.020 and <0.021 ppm Cd. These levels are similar to published "background" levels in the continental United States. However, liver metal concentrations increased with increased copper, zinc, and cadmium concentrations in the water, and copper and cadmium liver concentrations increased with fish length, weight, and age at several of the locations. Mean liver concentrations (fresh weight) from the locations of lowest and highest water metal concentrations were 76 and 287 ppm Cu, 35 and 57 ppm Zn, and <0.3 and 4.0 ppm Cd, respectively, suggesting that liver metal concentrations rather than flesh metal concentrations reflect available metal concentrations present in the environment. Additionally, the higher copper and cadmium concentrations in liver were above published background levels which indicates that the fish populations at these locations are receiving detrimental exposures to these metals.

INTRODUCTION

The discharge of acid-mine wastes into waters inhabited by trout is widespread in California. Significant examples of these problem areas are the Penn Mine discharge into Lake Camanche in Calaveras County (R. Dunham, Dept. Fish and Game, unpubl. data; Finlayson and Rectenwald 1978), the Walker Mine discharge into Little Grizzly Creek in Calaveras County, and several mines in the

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east and west Shasta Mining District which discharge into Shasta Lake and the Sacramento River (Fuller et al. 1978). Of these, the mines in the west Shasta Mining District, Balakala-Keystone (Little Squaw Creek), Mammoth (Little Backbone Creek), and Iron Mountain (Spring Creek) directly influence fishery resources (Hansen and Weidlein 1974; Finlayson and Wilson 1979). Together the mines in the west Shasta District contribute 86% of the dissolved copper and 81% of the dissolved zinc to the Shasta Lake-upper Sacramento River basin (Fuller et al. 1978). The major contributor of cadmium (78% of the dissolved cadmium) is the Spring Creek drainage (Fuller et al. 1978).

Copper, zinc, and cadmium concentrations control the toxicity of the Spring Creek acid-mine waste to fish. Recent studies have defined the short (96 h) and long (80 to 90 d) term toxicity of copper and zinc to several life history stages of salmonids and have estimated "safe" (no effect) levels for these metals in the upper Sacramento River basin (Finlayson and Ashuckian 1979; Finlayson and Verrue 1980). The toxicological interactions of copper, zinc, and cadmium to juvenile salmonids also have recently been studied to assist future water quality management decisions (Finlayson, unpubl. data 1980). A water quality management program to partially control metal concentrations in the Sacramento River resulting from the introduction of the Spring Creek acid-mine waste has been in progress since 1963 following the construction of Spring Creek Reservoir (Lewis 1963; Prokopovich 1965; Wilson 1978). While this program has curtailed the number of fish kills under controlled release conditions from the Spring Creek Debris Dam, the more subtle, sublethal effects on wild fishes resulting from the long-term, chronic exposure to the metals are not presently known.

One chronic effect could be the bioaccumulation of these metals in the tissues of the fish, thus causing potential health problems for the fish and possibly for the anglers who consume them. Benoit et al. (1976) and Kumada et al. (1973) have examined the effects on trout from long-term exposures to cadmium, and Benoit (1975) has examined the effects on fish from long-term exposure to copper. Phillips and Russo (1978) have summarized these and other metal bioaccumulation studies on fishes and aquatic invertebrates. For humans, the uptake of copper and zinc from ingested food is regulated metabolically but consumption of cadmium contaminated food items could cause potential health problems (Flick, Kragbill, and Dimitroff 1971; Fassett 1975). Although the majority of reported cadmium poisonings to humans has resulted from industrial exposures, a cadmium caused disease ("itai-itai") has resulted from cadmium pollution of a river in Japan by a mine (Kobayashi 1969; 1970).

To determine the influences acid-mine wastes from Little Squaw, Little Backbone, and Spring creeks discharges have on copper, zinc, and cadmium concentrations in fish muscle and liver tissues, 38 fish from four locations (Figure 1) in the upper Sacramento River basin were captured and analyzed. Three of the locations receive documented inputs of acid-mine wastes while the fourth location does not; fish from this latter location served as a study control. If metal concentrations in fish taken from the acid-mine waste influenced locations were above "background", a reevaluation of the water quality management programs associated with the mine discharges would be required.

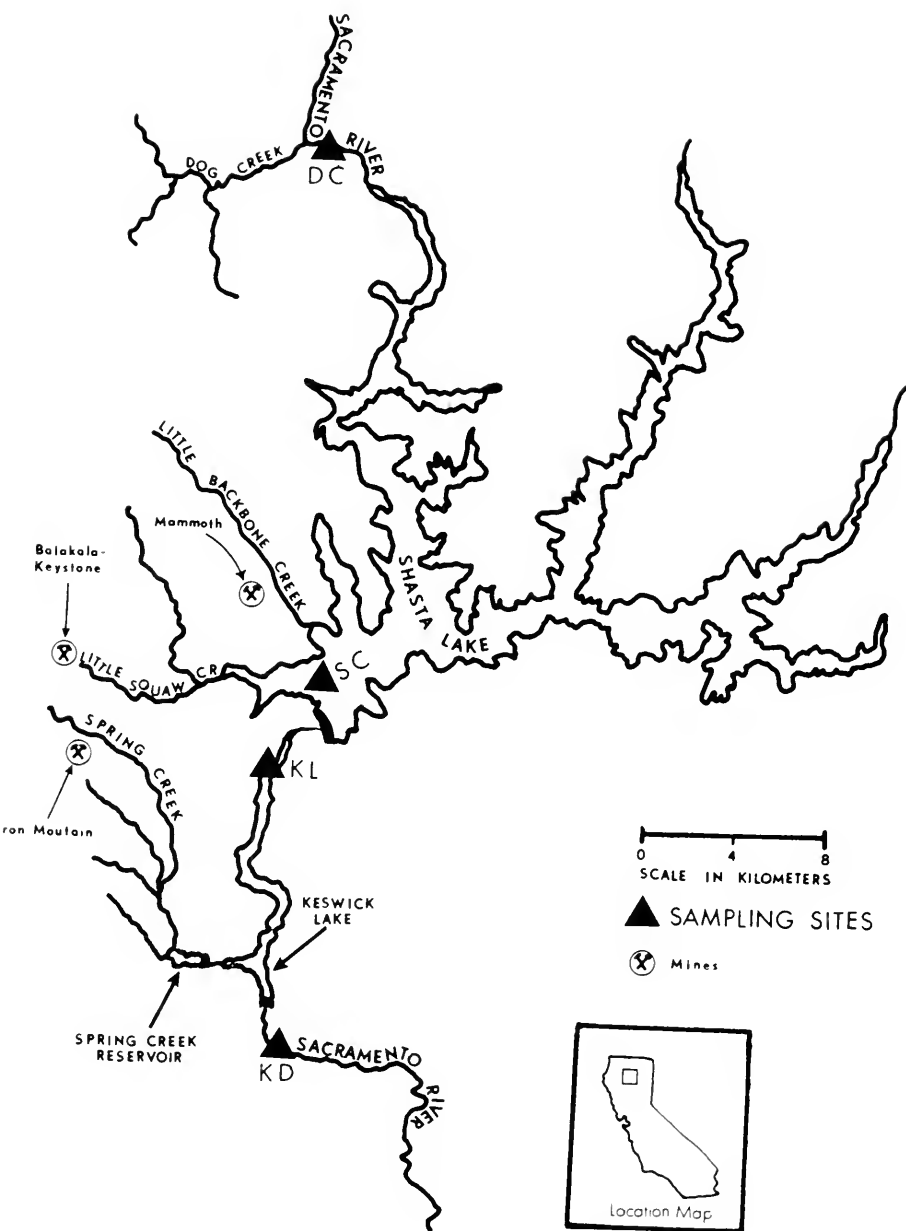


FIGURE 1. Shasta Lake drainage, showing location of mines and sampling sites for both fish and water samples.

MATERIALS AND METHODS

Rainbow, *Salmo gairdneri*, and brown trout, *Salmo trutta*, were collected by electrofishing between 18 December 1979 and 10 January 1980 from the following locations (Figure 1):

- 1) Sacramento River above Shasta Lake near the confluence with Dog Creek (DC);
- 2) Little Squaw Creek Arm of Shasta Lake (SC);
- 3) Keswick Lake below Shasta Dam and above Spring Creek Arm (KL); and
- 4) Sacramento River below Keswick Dam (KD).

The fish were put into plastic bags and iced immediately after collection. The fish were frozen and transported to the Department's Water Pollution Control Laboratory (WPCL) and remained frozen until analyzed for copper, zinc, and cadmium.

Water samples were collected for trace-metal and standard mineral analyses at the fish sampling locations (except at SC) on 18 March 1980. Dissolved and total metal samples were collected using the materials and methods outlined by Finlayson and Verrue (1980), and all samples were analyzed by Standard Methods (American Public Health Association 1975). The trace-metal water concentrations were determined by graphite furnace atomic absorption spectrophotometry, except zinc, which was determined by air-acetylene flame atomic absorption spectrophotometry.

Prior to analyses, the fish were defrosted, measured, weighed, and a scale sample taken for age determination. Each fish was dissected with chemically clean carbon steel and plastic utensils; the tools were kept metal free by first washing them in hot soap and water followed by rinsing in dilute nitric acid (0.5 N HNO_3) and then rinsing in de-ionized water. The flesh sample for analyses (0.5 g fresh weight) was taken from above the lateral line at a point perpendicular to the middle of the dorsal fin. Each fish was analyzed separately, with about 20% of the fish analyzed in replicate as a quality control measure. All replicate flesh samples were within $\pm 10\%$ in copper, zinc, and cadmium concentrations. The mean was reported when replicate samples were analyzed. At the time the flesh sample was taken, the liver of each fish was excised and refrozen for later analysis. The entire liver of each fish was later analyzed by dissecting it into several pieces (0.5 g fresh weight) and separately analyzing each piece. The mean of the liver pieces for each fish was reported.

The excised tissues were digested in metal-free Nalgene® 30-ml linear polyethylene (LPE) wide-mouth bottles. The LPE bottles were cleaned after each use by adding 20 ml of dilute sodium hydroxide (0.5 N NaOH) and tumbling in a water bath at 65°C for 30 min. The LPE bottles were then rinsed three times with de-ionized water, followed by two rinses with 1.0 N HNO_3 , and subsequently rinsed three more times with de-ionized water. Following the rinses, the LPE bottles were filled with 2.0 N HNO_3 and allowed to stand for at least 24 h. Finally, the 24-h soak solutions were analyzed for metal content; if any of the three metals were detected, the bottle was recleaned.

The fish tissues were digested with 2.0 ml of concentrated (16 N) HNO_3 while

tumbling in a water bath at 65°C for 2 h. Then, the bottles were filled with 18 ml of the metal-free water (20 ml total volume) and reheated in a tumbling water bath at 65°C for an additional 30 min. All analytical values were corrected with procedural blanks.

All copper and zinc concentrations and cadmium liver concentrations were determined by air-acetylene flame atomic absorption spectrophotometry while flesh cadmium concentrations were determined by graphite furnace atomic absorption spectrophotometry. The lower detection limit of copper was 0.20 ppm, for zinc it was 0.10 ppm, and for cadmium it was 0.020 ppm. Analytical precision for the analyses (2σ) was determined from the modified Shewhart equation: $\sigma = \sqrt{(\bar{x} - x)^2 / N - 1}$ where the absolute value of $x = [A_1 - A_2] / [A_1 + A_2]$, and A_1 and A_2 are paired observations. Analytical precision for copper concentrations was $\pm 11\%$, for zinc concentrations it was $\pm 5.0\%$, and for cadmium concentrations it was $\pm 14\%$. Correlation coefficients were developed by multivariate regression analysis (Sokal and Rohlf 1969) to examine the relationships between fish age, weight, and length and copper, zinc, and cadmium concentrations in flesh and liver tissue.

RESULTS AND DISCUSSION

The water quality in the upper Sacramento River basin was basically soft (37 to 39 mg/l CaCO_3), low in alkalinity (37 to 45 mg/l CaCO_3), and near neutral in pH (7.3 to 7.8) (Table 1). In the Sacramento River there was a progressive increase in sulfate concentrations from the low near Dog Creek (DC) to the high downstream below Keswick Dam (KD); the sulfate concentration below Shasta Dam (KL) was within the two extremes. The increases in sulfate concentrations at the two lower locations are an indication of the oxidized, metal-containing sulfide ores entering the Sacramento River system from the copper mines located in the Little Squaw Creek and Spring Creek drainages (Nordstrom 1977). The progressive increase in dissolved concentrations of aluminum, cadmium, copper, iron, and zinc from DC to KD also confirms this mine pollution of the upper Sacramento River basin. Based on the analyses of these water grab samples, dissolved copper, zinc, and cadmium concentrations in the upper Sacramento River basin increased more than tenfold from DC to KD downstream. The metal concentrations in the basin vary depending on time of year and controlled flows from Shasta and Whiskeytown lakes (Fuller et al. 1978; Finlayson and Wilson 1979). Finlayson (unpubl. data 1980) found dissolved metal concentrations at KD as high as 51 $\mu\text{g/l}$ Cu, 214 $\mu\text{g/l}$ Zn, and 2.3 $\mu\text{g/l}$ Cd. Limited monitoring data at KD (Central Valley Regional Water Quality Control Board, unpubl. data 1977 to 1980), indicates that cadmium levels are continually above the U.S. Environmental Protection Agency recommended criterion of 0.4 $\mu\text{g/l}$ for protection of salmonid fishes in soft water (U.S. Environmental Protection Agency 1976). Water samples were not collected from the Little Squaw Creek Arm of Shasta Lake (SC) during our study. However, previous sampling of Little Squaw Creek has documented concentrations as high as 2.0 mg/l Cu, 3.8 mg/l Zn, and 11 $\mu\text{g/l}$ Cd, and previous sampling of Little Backbone Creek has documented concentrations as high as 3.9 mg/l Cu, 9.5 mg/l Zn, and 60 $\mu\text{g/l}$ Cd (Fuller et al. 1978).

Unlike the water samples, there was not a progressive downstream increase in the concentrations of copper, zinc, and cadmium in the flesh of trout (Table 2). This suggests that flesh concentrations of these metals do not reflect the availability of metals in the environment. The mean fish flesh concentrations of copper, zinc, and cadmium were similar at DC and KD. However, the copper and cadmium concentrations in flesh were often below detection limits (0.20 ppm Cu and 0.020 ppm Cd); consequently, we do not know if the flesh concentrations of these metals reflect environmental conditions. However, several fish from both DC and SC had copper concentrations in flesh which were above the detection limit, and several fish from KD had cadmium concentrations in flesh which were detectable. Mean flesh concentrations (fresh weight) from the locations of lowest (DC) and highest (KD) water metal concentrations varied between <0.22 and <0.20 ppm Cu, 4.61 and 4.24 ppm Zn, and <0.020 and <0.021 ppm Cd, respectively. These findings support the conclusion of Phillips and Russo (1978) that there is no significant accumulation of these metals in fish muscle tissue.

TABLE 1. Water Quality Characteristics and Dissolved Trace Metal Concentrations With Total Metal Concentrations (in parentheses) of Sampling Locations (see Figure 1) in the Upper Sacramento River Basin.

<i>Water quality characteristics (mg/l)</i>	<i>Sacramento River near Dog Creek (DC)</i>	<i>Sacramento River below Shasta Dam (KL)</i>	<i>Sacramento River below Keswick Dam (KD)</i>
Alkalinity	37	45	39
Ca	0.48	0.90	0.87
Cl	1.6	1.6	1.0
Hardness	37	39	39
K	0.6	1.1	0.9
Mg	5.6	4.2	4.2
Na	3.6	6.0	4.7
pH	7.3	7.6	7.8
Specific cond. ^a	87	110	105
SO ₄	2.0	5.4	7.1
TDS	63	79	78
<i>Trace metals (µg/l)</i>	<i>Sacramento River near Dog Creek (DC)</i>	<i>Sacramento River below Shasta Dam (KL)</i>	<i>Sacramento River below Keswick Dam (KD)</i>
Al	<10 (<10)	<10 (40)	50 (50)
Cd	0.1 (0.2)	0.3 (0.4)	1.0 (1.9)
Co	<10 (<10)	<10 (<10)	<10 (<10)
Cr	1.0 (2.0)	0.5 (1.0)	0.9 (1.6)
Cu	2 (6)	25 (39)	26 (65)
Fe	<10 (110)	<10 (750)	510 (1,050)
Ni	4.8 (9.1)	1.0 (1.7)	2.5 (3.9)
Pb	<0.5 (0.5)	<0.5 (0.5)	<0.5 (0.9)
Zn	<2 (4)	4 (38)	59 (104)

^a As umhos/cm

The upper Sacramento River basin fish flesh concentrations probably represent published (background) concentrations normally found in the environ-

ment. Goettl, Sinley, and Davies (1972) determined background concentrations (dry weight) of copper and zinc in rainbow trout. We converted their numbers to the equivalent of approximately 0.50 ppm Cu and 6.0 ppm Zn (fresh weight) by multiplying with a conversion factor of 0.3 (Kumada et al. 1973). Lovett et al. (1972) found the majority of freshwater fish (including trout) from New York state waters contained <0.020 ppm Cd (fresh weight). The metal concentrations in fish from the four locations in the upper Sacramento River are similar to these background concentrations. However, additional sampling at KD is needed for confirmation. This is because approximately 40% of the trout from this location contained detectable levels of cadmium in their flesh, and therefore, these fish may be accumulating this metal in their muscle tissue.

Copper, zinc, and cadmium concentrations in the trout livers progressively increased downstream with available trace-metal concentrations in the water. Mean liver concentrations (fresh weight) from the locations of lowest (DC) and the highest (KD) water metal concentrations varied between 76 and 287 ppm Cu, 35 and 57 ppm Zn, and <0.3 and 4.0 ppm Cd, respectively. Increased metal concentrations in the environment were reflected by increases of metal concentrations in fish livers. This supports the conclusion of Phillips and Russo (1978) that the liver of fish accumulate metals from the environment and the degree of accumulation is directly related to the environmental availability of the metals.

From DC downstream to KD, metal concentration increases in liver were greatest with cadmium (over 1200% increase), followed by copper (277% increase), and least with zinc (62% increase). However, increases in dissolved metal concentrations of the water samples were greatest with zinc (2800% increase), followed by copper (1200% increase), and least with cadmium (900% increase). This indicates that, if the water analyses were representative of the metal concentrations that fish were continually exposed to, the trout liver has the greatest ability for accumulating cadmium and the least ability for accumulating zinc. Marafante (1976) found that all cadmium present in the livers of goldfish, *Carassius auratus*, was associated with a specific cadmium-binding protein (possibly metallothionein), however, only 40% of the zinc in the liver was associated with this protein. Moreover, the presence of copper was shown to enhance cadmium but not zinc accumulation in the marine mummichog, *Fundulus heteroclitus* (Eisler and Gardner 1973).

The process of metal accumulation in fish livers is complex and not solely dependent on the availability of metals in the environment but should also be related to the duration of exposure. Fish age, weight, and length were positively correlated with the copper and cadmium liver concentrations at several of the locations (Table 3). However, the concentrations of zinc in the liver did not correlate with the duration of exposure; this further supports the hypothesis that the ability of the liver to accumulate zinc is not as great as it is for cadmium and copper.

The copper, zinc, and cadmium concentrations of trout liver from DC may approximate background concentrations. We converted the dry weight basis data of Goettl et al. (1972) and Mount and Stephan (1967) to a fresh weight basis by multiplying by a conversion factor of 0.3 (Kumada et al. 1973). Goettl et al. (1972) found background liver concentrations in rainbow trout from

uncontaminated areas in Colorado to be approximately 80 ppm Cu and 30 ppm Zn (fresh weight), and Mount and Stephan (1967) concluded that liver concentrations ≤ 0.30 ppm Cd (fresh weight) were representative of trout from waters uncontaminated by cadmium. The data base from California waters shows background metal concentrations (fresh weight) of trout livers to be approximately 100 ppm Cu, 39 ppm Zn, and 0.38 ppm Cd (McCleneghan and Rectenwald 1979; McCleneghan et al. 1980). The copper, zinc, and cadmium concentrations in livers of fish from DC are similar to these background concentrations. However, the copper concentrations in livers of fish from the other three locations were 3 to 4 times higher than background. Additionally, the cadmium concentrations in livers of fish collected at SC and KL were 2 to 3 times higher and KD samples exceeded the published background concentrations by more than tenfold.

The significance of fish liver copper and cadmium levels which exceed background concentrations has been investigated. Benoit (1975) found a good correlation between the onset of copper accumulation in livers above background levels and the development of chronic symptoms (reduced survival of fry) in bluegills, *Lepomis macrochirus*. Thus, the elevated copper concentrations found in livers of trout from SC, KL, and KD indicate that these fish populations are probably receiving detrimental exposures to copper. More specific conclusions can be drawn from the elevated cadmium concentrations present in trout liver from KD. Benoit et al. (1976) found liver residues to reach equilibrium after constant, chronically toxic exposure to cadmium; they suggested that analyses of wild trout populations might be useful in determining whether the fish had been subjected to detrimental cadmium levels. They also determined that cadmium concentrations between 2 and 3 ppm Cd (our conversion to fresh weight) in the livers of brook trout, *Salvelinus fontinalis*, were representative of trout exposed to detrimental concentrations of cadmium and which resulted in decreased larval growth and survival. Similar information has been developed for cadmium concentrations in rainbow trout (Kumada et al. 1973). This information suggests that in addition to the possible detrimental levels of copper, the fish from KD are also being exposed to detrimental concentrations of cadmium. This indicates that a reevaluation of the water quality management program controlling the discharge of the Spring Creek acid-mine waste is needed. Additionally, long-term laboratory studies are needed to further identify and confirm the detrimental effects on the trout populations in the upper Sacramento River.

In conclusion, we have shown that flesh concentrations of copper, zinc, and cadmium in resident trout from the upper Sacramento River basin are similar to background concentrations in fish from the continental United States. Metal concentrations in water and trout liver did, however, progressively increase downstream from DC as influences from the acid-mine wastes increased. Additionally, there is good evidence that the trout populations of both Shasta Lake and the Sacramento River below Shasta Dam are receiving detrimental exposures to copper and cadmium, and new programs controlling the discharges of the acid-mine wastes influencing these areas may be needed.

TABLE 2. Species Data, and Copper, Zinc, and Cadmium Concentrations (\pm SD in parentheses) of Flesh and Liver Tissues (ppm as fresh weight) from Fish Collected in Sacramento River at Dry Creek (DC), Little Squaw Creek Arm of Lake Shasta (SC), Keswick Lake (KL), and Sacramento River below Keswick Dam (KD).

Location	Species data				Fish flesh ^b			Fish liver ^b		
	Species ^a	L (mm)	Wt (g)	Age (yr)	Cu	Zn	Cd	Cu	Zn	Cd
DC	RT	281	334	2	<0.22	4.61	<0.020	76	35	<0.3
	(10)	(82)	(420)	(1)	(0.05)	(1.44)	(0.000)	(87)	(14)	(0.2)
SC	BRN	396	980	4	<0.31	2.84	<0.020	270	47	0.7
	(9)	(107)	(803)	(1)	(0.18)	(0.81)	(0.000)	(157)	(16)	(0.4)
KL	RT	248	259	1	<0.20	3.56	<0.020	150	42	0.7
	(6)	(75)	(234)	(1)	(0.00)	(1.18)	(0.000)	(99)	(15)	(0.8)
KL	BRN	410	971	—	<0.20	2.50	<0.020	254	72	0.5
	(2)	(127)	(758)	—	(0.00)	(0.28)	(0.000)	(100)	(37)	(0.1)
KD	RT	283	301	3	<0.20	4.24	<0.021	287	57	4.0
	(10)	(49)	(111)	(1)	(0.00)	(0.89)	(0.003)	(120)	(19)	(1.1)

^a Numbers of individuals analyzed in parentheses.

^b Means represent mathematical evaluations of the data and do not necessarily represent the actual lower detection limits of the metals.

TABLE 3. Significant ($P \leq 0.05$) Correlation Coefficients Among Fish Length, Weight, and Age, and Flesh Zinc, Liver Copper, Liver Zinc, and Liver Cadmium Concentrations of Trout Collected in Sacramento River Below Keswick Dam (KD), Keswick Lake (KL), Little Squaw Creek Arm of Shasta Lake (SC), and Upper Sacramento River at Dog Creek (DC).

Partial Correlation Matrix

Fish Variable	Flesh Zn	Liver Cu	Liver Zn	Liver Cd
Length	a ^a b ^b c ^c d ^d	0.71		0.90
Weight				0.81
Age		0.73		0.97
Flesh Zn	1.00	0.68		0.76
		1.00		0.84
			1.00	0.75
				0.67
				0.77
Liver Cd				1.00

^a coefficient from location KD

^b coefficient from location KL

^c coefficient from location SC

^d coefficient from location DC

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LABORATORY STUDIES OF INTRASPECIFIC BEHAVIORAL INTERACTIONS AND FACTORS INFLUENCING TIDEPOL SELECTION OF THE WOOLY SCULPIN, *CLINOCOTTUS ANALIS*¹

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Behavioral interactions of the wooly sculpin, *Clinocottus analis*, and their preference for tidepool characteristics (depth, amount of cover, and height of cover above bottom) were tested in an experimental pool containing artificial "potholes." Fish tended to select deeper potholes and greatest amounts of cover, but statistically significant preferences were not shown consistently. Strong behavioral interaction was noted, evidenced by a propensity for aggregation. Interactions were more evident in larger fish (> 45 mm) than in smaller ones. Fish exhibited following behavior and a kinesis-type response to the presence of other individuals, with both behavioral patterns leading to the formation of aggregations. This behavior would appear to ensure the survival of fish straying from their home territory into novel surroundings where suitability of tidepools for survival during low tides would be unknown.

INTRODUCTION

Many species of fish that inhabit the intertidal zone survive during low tides by seeking refuge in tidepools. Numerous studies have shown that for some species a significant percentage of individuals may be found in the same pool at several successive low tides or after periods of many weeks (e.g., Aronson 1951; Gibson 1967; Richkus 1978). Findings of a field study of intertidepool movements of the wooly sculpin, *Clinocottus analis* (Richkus 1978), suggested that the quantity and quality of cover available in a particular pool had a strong influence on the probability of fish recurring and also on the numbers of fish present. However, cover could not be quantitatively defined in the field, and thus its influence could not be statistically evaluated. Data also suggested that undetermined pool characteristics influenced the mean size of fish likely to occur in some pools. Although other studies have examined interspecific differences in preference of intertidal fish for types of microhabitat (Nakamura 1976), no similar studies have been done for a single tidepool species. Studies with other fish species have shown that active behavioral responses are involved in their distribution among habitats in nature, and that these responses are amenable to testing in the laboratory (Reynolds and Thomson 1974; Casterlin and Reynolds 1978).

To investigate the influence of certain pool characteristics on pool selection behavior, a laboratory study was designed to examine sculpin preference for three factors: pool depth, amount of cover, and height of cover above bottom. Casual observation in the field had suggested that pool depth might be related to size of fish present. Amount of cover and height from bottom were quantifiable in the laboratory and were considered to reflect the "quantity and quality"

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of cover deemed important in field study findings. Results of initial experiments suggested that behavioral interaction among individual fish was occurring and was strongly influencing experimental results. To determine the nature of this interaction, observations of fish behavior during pool selection experimental runs were made. Additional studies of behavioral interactions were carried out to fully describe these interactions. Although limited in scope, the studies revealed significant behavioral interactions, which would be of adaptive advantage in the intertidal environment. The findings of all laboratory studies are interpreted in the context of the field data previously reported (Richkus 1978).

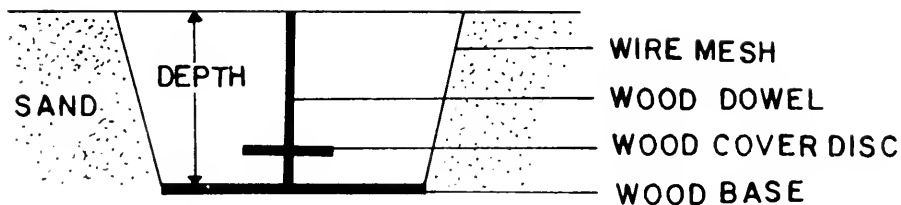
MATERIALS AND METHODS

Studies were carried out in an outdoor polyethylene pool 2.4 m in diameter and 50.8 cm deep. The pool was filled to a depth of 30.5 cm with sand. The three tidepool characteristics experimentally quantified (amount of cover, cover height from bottom, and pool depth) were combined in a latin square arrangement (Cochran and Cox 1957). Nine flat-bottomed "potholes," with bottom diameters of 30.5 cm and top diameters of 45.7 cm, three each of 10, 20, and 30 cm depth, were sunk in the sand so that their tops were flush with its surface (Figure 1). Each pothole consisted of a wire mesh form attached to a plywood base, covered with fiberglass cloth and resined, with a wooden dowel in the center extending to the level of the top. Sand was placed on the resin while wet to create a rough, more natural surface. Amount of cover was represented by plywood discs, 7.6-, 16.8-, and 25.4-cm in diameter, with holes drilled in their centers. These discs were slid on the dowels and fastened at heights of 4, 7, and 10 cm above the bottom of the potholes. Assignment of factors to potholes and potholes to pool position (Figure 1) was done using a table of random numbers.

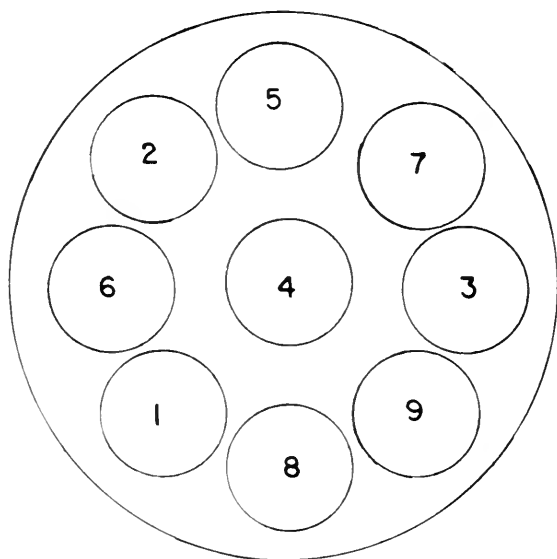
Fish were placed in the pool while it was full. After a 24-hour period, a drain was opened and the water level lowered, over a period of 2 to 2.5 hours, to just below the surface of the sand. The number of fish in each pothole was recorded, food was distributed on the surface of the sand, and, after a period of 1 to 3 hours, water was run into the pool. Because of irregularities in the sand surface, some small puddles of water remained after draining, and fish were occasionally found in them at the end of an experimental run. Replicate trial runs during a single experiment were made on consecutive days. At the end of a run, fish were evenly redistributed among potholes before refilling the pool.

Experiment 1, consisting of five trials, was conducted from 30 May to 4 June 1968, using 25 fish of mixed sizes (37 to 130 mm) which had been kept in laboratory aquaria from 3 to 15 weeks prior to the test. Experiment 2, consisting of three trials, was run from 5 to 8 June with 40 recently caught fish 60 to 80 mm in length. Experiment 3, consisting of three trials, was run from 17 to 20 July using 10 fish 55 to 90 mm in length and 10 fish 30 to 45 mm long, all recently captured.

The statistical distributions of data recorded during these experiments were strongly non-normal. Thus, parametric analysis of variance, normally applied to data collected using a latin square experimental design, could not be used to test for the significance of fish preferences. Analyses were done using a modified version of the Friedman non-parametric analysis of variance (Bradley 1968). Because of the three factor latin square design, interactions between factors could not be investigated.



A.



B.

	C_1	C_2	C_3	
H_1	$D_1(1)$	$D_2(2)$	$D_3(3)$	$H_1 = 4 \text{ cm}$ $C_1 = 7.6 \text{ cm diam.}$ $D_1 = 10 \text{ cm}$
H_2	$D_2(4)$	$D_3(5)$	$D_1(6)$	$H_2 = 7 \text{ cm}$ $C_2 = 16.8 \text{ cm diam.}$ $D_2 = 20 \text{ cm}$
H_3	$D_3(7)$	$D_1(8)$	$D_2(9)$	$H_3 = 10 \text{ cm}$ $C_3 = 25.4 \text{ cm diam.}$ $D_3 = 30 \text{ cm}$

C.

FIGURE 1. A. Vertical cross-section of an experimental "pothole"; B. top view of experimental pool with numbered "potholes" in place. C. latin-square arrangement of factors among potholes; C = cover D = pothole depth H = cover height; subscript represents the class of the factor; number in parentheses is the pothole number.

Observations of behavioral interactions among fish were made during the pool selection experiments as well as during separate experimental periods. Fish were observed from behind a screen for 15 to 20 min periods, and notes on fish behavior were recorded. Three sets of observations were made during Experiment 3, at times when the pool was full. Six sets of observations were made during Experiment 2, three prior to draining and three when the pool was being drained. Additional observations of behavioral interactions between individuals were made in the experimental pool when pairs of fish were placed in the pool and observed from behind a screen. After a single fish had been in the pool for 30 min, a second fish was introduced and observations were continued for an additional 30 min. The observational data consisted of a sequential record of fish location and the time spent at each location. Five sets of observations were made during a 2-week period in July, all during daylight hours, and all using newly captured fish.

RESULTS

Fish showed a strong tendency to aggregate during each trial of Experiment 1 (Table 1). No preference for specific cover height or amount was shown (Friedman ANOVA; $H_{[N=5]} = 1.6; 3.6; p > 0.05, 0.05$). A significant difference among pool depth choices was found ($H_{[N=5]} = 3.9; p < 0.05$), with the shallowest pool depth being avoided. Fish remaining in puddles on the sand surface tended to be the smaller individuals.

TABLE 1. Numbers of *Clinocottus analis* Present in Each Pothole in Each Trial of Experiment 1 and the Totals for Each Class of the Three Factors.

Pothole number	Trial					Totals		
	1	2	3	4	5			
1.....	0	0	0	0	0			
2.....	13	0	0	5	0	C ₁ -21	H ₁ -53	D ₁ - 3
3.....	5	0	8	7	15	C ₂ -20	H ₂ - 9	D ₂ -47
4.....	0	0	0	6	0	C ₃ -64	H ₃ -43	D ₃ -55
5.....	0	1	0	2	0			
6.....	0	0	0	0	0			
7.....	0	1	16	0	0			
8.....	0	3	0	0	0			
9.....	0	18	0	1	4			
on sand.....	7	2	1	4	6			
Number of potholes occupied.....	2	4	2	5	2			

In Experiment 2, run with newly caught fish, the tendency for aggregation was stronger than in Experiment 1 (Table 2). No fish remained on the sand surface in any trial. A significant effect of amount of cover was found ($H_{[N=3]} = 6.0; p < 0.05$). No statistically significant influence of cover height or pool depth was found ($H_{[N=3]} = 4.7; 4.7; p > .19$), despite an apparent strong trend in preference for the deeper pools and lowest cover heights. The small number of trials run caused the statistical test to be relatively insensitive.

Results of Experiment 3 revealed no statistically significant preference for any category of the three test factors by both size classes of fish, together or separately (Table 3) ($H_{[N=3]}$ values $< 4.0; p > 0.20$). Results here are confounded by

the fact that water in the deeper potholes was visibly discolored and did not appear to be flushed on some occasions when the pool was refilled. For some periods of time water in these pools may have been low in dissolved oxygen. More small fish remained on the sand surface than did large fish (4 vs 1 over three trials).

TABLE 2. Numbers of *Clinocottus analis* Present in Each Pothole in Each Trial of Experiment 2 and the Totals for Each Class of the Three Factors.

Pothole number	Trial				Totals	
	1	2	3			
1.....	0	0	0	C ₁ -3	H ₁ -86	D ₁ -6
2.....	3	5	2	C ₂ -22	H ₂ -13	D ₂ -28
3.....	17	27	32	C ₃ -95	H ₃ -21	D ₃ -86
5.....	1	0	0			
5.....	0	5	3			
6.....	0	1	3			
7.....	0	2	0			
8.....	2	0	0			
9.....	17	0	0			
Number of potholes occupied.....	5	5	4			

TABLE 3. Numbers of *Clinocottus analis* Present in Each Pothole in Each Trial of Experiment 3 and the Totals for Each Class of the Three Factors.

Pothole number	Trial ¹				Trial ²			
	1	2	3		1	2	3	
1.....	0	0	0	C ₁ -10	1	0	0	C ₁ -13
2.....	0	1	5	C ₂ -12	0	1	0	C ₂ -4
3.....	0	0	0	C ₃ -7; D ₁ -3	3	2	2	C ₃ -9; D ₁ -3
4.....	0	4	5	D ₂ -13	1	3	4	D ₂ -16
5.....	0	2	0	H ₁ -6; D ₃ -13	1	1	0	H ₁ -9; D ₃ -7
6.....	5	1	0	H ₂ -17	2	0	0	H ₂ -12
7.....	1	0	0	H ₃ -6	1	0	3	H ₃ -5
8.....	2	2	0		0	1	0	
9.....	1	0	0		0	0	0	
on sand.....	1	0	0		1	2	1	
Number of potholes occupied.....	4	5	2		6	5	3	
Number of potholes occupied, both sizes combined.....	8	6	4					

¹ Results for fish > 45mm

² Results for fish < 45mm

Over three behavioral observation periods during Experiment 3, an average of seven small fish were out of potholes at all times, whereas an average of 0.5 large fish were not in potholes. Larger-sized fish showed a tendency to direct

their movements toward individuals of their own size, but this behavior was difficult to quantify, because a number of fish were constantly moving at the same time. Small fish did not appear to exhibit any response (either attraction or escape) to larger fish. A kinesis-type response to proximity of other fish was evident. Fish not in the presence of others tended to be active during most of the observation periods, moving in and out of potholes. Upon encountering a pothole or pool area occupied by several fish, the amount of movement declined markedly.

Fish activity increased dramatically in response to draining of the pool during Experiment 2. For the three 20-min periods before draining, an average of 3.5 moves by fish in and out of potholes was observed. For the three 20-min periods immediately after initiation of draining, total numbers of moves were 35, 26, and 21. Many of these moves were by groups of fish and involved movement into and out of the same pothole. Thus, distribution did not change to any major degree. Increased movement of both size classes of fish during draining in Experiment 3 was also noted. But the smaller fish, which tended to remain out of potholes most of the time, appeared to actively avoid entering pools until the last moment. Often the small fish would remain on the sand surface until water depth was barely sufficient for swimming, and then enter the nearest pothole.

Behavioral data collected during observations of pairs of fish in the experimental pool revealed distinct interactions between individuals (Table 4). In general, the first fish introduced to the pool tended to be continuously active, entering potholes in no particular pattern and remaining in them for short periods of time. When a second fish was placed in the pool and it moved into view of the first, in four of the five cases the first swam directly to it. For most of the remainder of the observation period, the two fish tended to be in the same locations at the same time. There was also a decrease in movement, as indicated by a decline in the number of changes in locations occurring. For example, in Table 4, Fish I changed locations 18 times in 30 minutes when alone, whereas Fishes I and II, when together, changed locations 8 and 10 times, respectively, during a similar time period. The data presented in Table 4 are typical of the results from three of the five sets of observations. In the fourth experiment, the second fish introduced swam into a pothole, followed immediately by the first fish, and both remained there for the rest of the observation period. In the fifth experiment, the first fish was in a pothole when the second was introduced and it remained there for the rest of the period, never coming into view of the second fish. Thus, although fish behavior in the experimental pool was variable, in the 4 cases out of 5 when fish had an opportunity to interact, attraction or following behavior was exhibited.

DISCUSSION

Tests of fish preference for pool characteristics proved less than conclusive, although some trends were evident. Preference for deeper pools (or avoidance of shallowest pools) was evident in Experiments 1 and 2 (Tables 1 and 2). In Experiment 2, representing the only trial runs unbiased by prior history of the fish or by possible degraded water quality in the experimental potholes, findings suggested a preference for greater amounts of cover and lowest cover heights. Such responses are consistent with the field data, which had suggested that

TABLE 4. Record of Movements of a Single *Clinocottus analis* (I) and That Fish Together With a Second (II) in the Experimental Pool During a 1-Hour Period on 18 July 1968. Pothole Numbers Correspond to Numbers in Figure 1; 0 Represents Fish Presence on the Sand Surface, Out of Potholes; Brief Periods of Transit are Not Included.

FISH I (ALONE)															
Location.....	0	3	0	1	0	7	0	6	0	3	2	0	9	0	8
Duration of Stay (minutes)	1.0	6.5	0.1	0.2	0.1	5.0	0.1	0.5	0.1	1.5	1.0	0.1	1.5	0.1	3.0
FISH I AND II (TOGETHER)															
Location															
I.....	2	0	0	2	0	0	0	2	9	6	6	6	5	0	0
II	2	2	0	2	0	9	0	2	9	9	6	5	5	0	0
Duration of Stay (minutes)	1.5	1.5	5.0	1.5	5.0	1.2	3.0	1.5	0.2	0.1	0.1	1.0	0.1	7.0	7.0

cover was important in determining fish presence in a given pool. Thus, the tests tend to confirm the importance of the test factors in pool selection. However, these laboratory experiments did not prove to be the rigorous test of preference desired.

Although these experiments were inconclusive in demonstrating preference for certain pool characteristics, they did reveal what may be ecologically important behavioral interactions among individuals. A propensity for aggregation of individuals was evident in most trial runs (Tables 1, 2, and 3). This tendency was most erratic during Experiment 1, in which the fish used had been out of their natural environment for numbers of weeks. During Experiments 2 and 3, aggregation increased over the course of the experiment, based on progressively fewer potholes being occupied with each successive trial (Tables 2 and 3). Aggregations of *Clinocottus analis* are often observed in the field (Richkus 1978), as is the case in studies of other tidepool cottids (Nakamura 1976). In evaluating field data, I had earlier interpreted these aggregations merely as responses of individual fish to certain preferred microhabitats within pools. Observational data reported here suggest that in fact behavioral mechanisms actively operate to create these aggregations. The kinesis-type response to presence of other individuals that generated these aggregations in preference experiments was particularly evident during initial runs of given experiments, when fish were in what constituted unfamiliar surroundings. Findings of a field study (Richkus 1978) point to the adaptive significance of such behavior.

In that study, all tidepools in a selected area of the intertidal zone were searched biweekly and all fish present were marked. Over a 16-week period, approximately 50% of the fish present on each sampling date had never before been present in that area. Williams (1957), in discussing the adaptive advantage of tidepool fish returning to the same tidepool at each low tide, noted that such behavior insured that a fish would not inadvertently occupy a pool that may drain over the course of a low tide period or be otherwise unsuitable for survival. This concept does not, of course, take into account fish that stray into unfamiliar regions, in which case the "home" pool is no longer available. The field data noted above indicate that such fish are very common, particularly among the younger age groups (Richkus 1978). For such fish, the following or attraction behavior observed (Table 4) and the kinesis-type response to presence of other fish would both serve to direct fish to and have them remain in safe pools when they enter strange territory, where resident or experienced fish would dominate the population during any given tidal cycle. Such behavior also complements another behavioral characteristic noted: a high level of activity exhibited by fish when present by themselves or when first placed in the tank. This response can be categorized as "anxiety" behavior (Welty 1934). The increased locomotor activity that results from such a response generates increased exploration of unfamiliar environs, thus increasing the probability of encountering other fish.

This theory also suggests an evolutionary basis for the absence of inter- or intraspecific aggressive interactions among tidepool cottids. Aggressive behavior is not evident in such species even when they are present in very high density, as has been noted by Nakamura (1976) and Richkus (1978). This occurs despite the fact that such densities could be expected to be indicative of competition for food or cover. Yet, such aggregations ensure survival during low tides, and guaranteed survival of a potentially lethal environmental change that occurs

twice daily would be more advantageous than outcompeting other individuals for resources whose influence on survival would be much more indirect and long-term in nature.

Behavior of small fish (< 35 mm) did not generally fit the pattern shown by larger individuals. Behavioral interactions were much less pronounced, and the fish tended not to seek out potholes. Very small *C. analis* also exhibit behavior different from larger adults in the field. During field studies at times when recruitment is known to occur, small individuals were found in all pockets of water left as the tide receded, including small pools on sandy beaches that would drain in a matter of an hour (Richkus 1968). In a sense, this lack of selectivity and the absence of behavioral interactions that could enhance survival suggest that the function of these small fish is to serve as colonizers of unoccupied habitat. Mortality would, of course, be high but settlement of previously unexploited habitat might be more advantageous to the population on an evolutionary scale.

The increased movement of fish initiated by draining of the experimental pool is remarkably similar to the behavior of *Oligocottus maculosus*, another intertidal sculpin, reported by Nakamura (1976). The arrangement of the experimental pool here very nearly precludes the possibility that fish could have been responding to currents created by draining. The only other stimulus present would be hydrostatic pressure changing at a rate of $0.13 \text{ g/cm}^2/\text{min}$. Sensitivity of this species to pressure change is unknown.

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NOTES

**HYBRIDIZATION BETWEEN HITCH, *LAVINIA EXILICAUDA*,
AND SACRAMENTO BLACKFISH, *ORTHODON
MICROLEPIDOTUS*, IN SAN LUIS RESERVOIR,
CALIFORNIA**

INTRODUCTION

Hybridization between species of Cyprinidae is a common occurrence in North America, but large numbers of any hybrid combination are rarely found (Schwartz 1972). Few hybrids have been found among the 10 species of native cyprinids found in the Sacramento-San Joaquin drainage of central California. All known cases of hybridization involve the hitch, *Lavinia exilicauda*, which has been reported to hybridize with thicktail chub, *Gila crassicauda* (Miller 1963); California roach, *Lavinia symmetricus*¹ (Avisé, Smith, and Ayala 1975); and Sacramento blackfish, *Orthodon microlepidotus* (Hopkirk 1973). While hitch-roach hybrids may be locally abundant, the other hybrids are known only from a few individuals. The hitch-blackfish hybrid combination has been previously represented by a single juvenile individual from Coyote Creek, Alameda County (Hopkirk 1973). This note reports the presence of adult hitch-blackfish hybrids in the catches of commercial blackfish fishermen from San Luis Reservoir, Merced County. The hybrids are common and distinct enough that they were noticed by the fishermen and consequently called to our attention.

METHODS

Six hybrids, nine blackfish, and nine hitch were obtained from the commercial fishermen in February 1977. Morphometric and meristic data (Table 1) were collected according to the methods of Hubbs and Lagler (1958). Gill raker counts are lower than those reported by Hopkirk (1973) because rudimentary elements at the extreme top and bottom of each gill arch were not counted. For the morphometric characters, standardized ratios based on standard length were not used because the fish were about the same age (III+ and IV+). Differences among the three groups most likely reflected real differences in morphology. For each morphometric and meristic character in which the parental species differed, a hybrid index (Hubbs, Hubbs, and Johnson 1943) was calculated as follows:

$$H.I. = 100 (H-L/B-L),$$

where H is the mean value of the character for the hybrids, L is the mean value for the hitch, and B is the mean value for the blackfish. For most characters, the value of the index is between 0 and 100, where values of less than 50 indicate more similarity to hitch than to blackfish and values greater than 50 indicate more similarity to blackfish than to hitch. When values for the hybrid are less than that of either parent, the hybrid index will be a negative number (e.g. -204).

Although more rigorous methods for hybrid analysis are available (Neff and Smith 1978), they were not used here because their main advantage is that they do not require the *a priori* identification of the hybrids and the parental species for the analysis. In this case, the nature of the hybrids was obvious (Figure 1).

¹ The generic name for the California roach is usually given as *Hesperoleucus*. However, evidence presented by Avisé et al. (1975) and Moyle (1980) indicates that hitch and roach are congeneric.

Table 1. Means, standard deviations, and hybrid indices for morphometric and meristic characters from hitch, Sacramento blackfish, and hybrids between them. Values for the hybrid index are not given if the character values for the two parent species are similar.

	<i>Blackfish</i> <i>N</i> = 9)		<i>Hitch</i> <i>(N</i> = 9)		<i>Hybrids</i> <i>(N</i> = 6)		<i>Index</i>
	\bar{x}	<i>S.D.</i>	\bar{x}	<i>S.D.</i>	\bar{x}	<i>S.D.</i>	
Morphometric Characters (mm)							
Standard length	334	37	264	23	283	21	28
Body depth	78	10	74	9	67	4	-204
Head length	84	12	54	5	65	4	37
Predorsal length	176	21	143	12	150	10	20
Prepelvic length	177	19	132	15	151	11	42
Caudal peduncle depth	27	3	23	2	22	1	13
Caudal length	26	11	47	4	60	5	13
Dorsal fin length	68	8	57	2	63	6	49
Pectoral fin length	55	6	41	3	49	5	15
Pelvic fin length	52	5	40	3	49	5	68
Anal fin length	50	4	58	5	53	6	59
Snout length	28	4	16	2	21	1	37
Orbit length	12	1	10	1	11	1	23
Upper jaw length	21	3	14	2	17	2	30
Meristic Characters (Numbers)							
Dorsal rays	10.5	0.5	10.4	0.5	10.2	0.4	-
Anal rays	8.4	0.5	12.9	0.3	10.5	1.1	53
Pelvic rays	10.4	0.5	9.7	0.7	10.5	0.8	-
Pectoral rays	16.5	1.3	15.1	0.3	16.8	0.7	-
Gill rakers	28.1	1.5	25.9	1.2	22.3	1.6	-161
Lateral line scales	109.1	4.4	62.3	1.0	78.2	4.8	35
Scales above lateral line	25.8	1.7	11.8	0.8	16.5	0.8	34
Scales below lateral line	14.1	1.2	7.4	0.5	10.5	1.4	27

RESULTS AND DISCUSSION

The hybrids are clearly intermediate between hitch and blackfish (Table 1). The characters of the hybrids were similar to those of the hybrid described by Hopkirk (1973). The pharyngeal teeth, examined in four of the hybrids, had the slightly hooked appearance of the teeth of hitch, rather than the straight blade-like character of blackfish teeth. The hybrids were, on the average, less deep-bodied than either parent species, although this character was highly variable. More remarkable is the lower number of gill rakers in the hybrids, because both blackfish and hitch use their closely-spaced gill rakers to assist in feeding on small organisms and particles (Moyle 1976). Four of the six hybrids appeared to be males, although the gonads were small; one had unidentifiable gonads, and one appeared to have small, malformed ovaries. This was in marked contrast to the hitch and blackfish taken at the same time, in which the gonads of both sexes were well developed. Presumably, the hybrids were incapable of reproduction and were all F_1 crosses between the parent species.

Just how the hybrids originated is not known, but because both species will spawn in large numbers in shallow, gravel bottomed areas (Moyle 1976), it is likely that the hybrids resulted from the accidental mixing of gametes of the two parent species. According to Hubbs (1955), such accidental mixing of gametes is apparently the method by which most cyprinid hybrids originate.

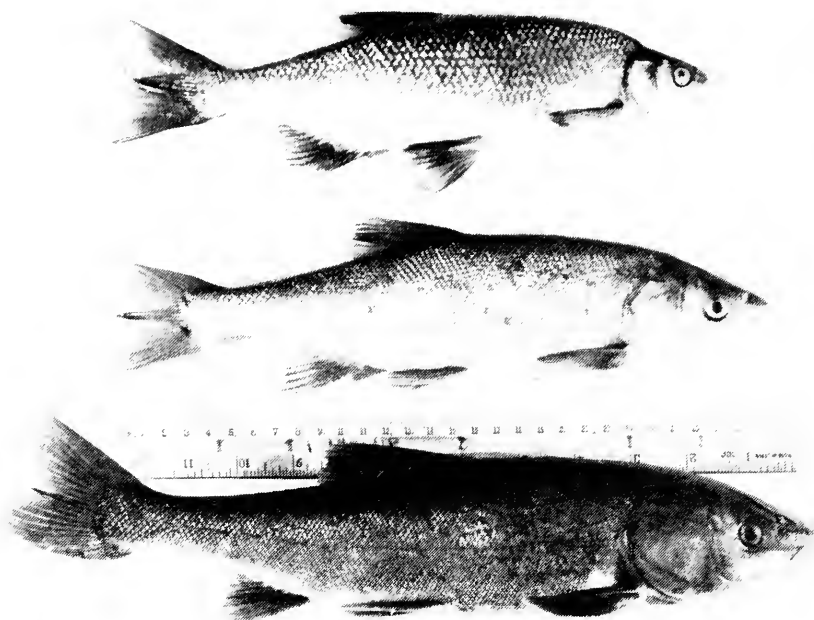


FIGURE 1. Hitch (top), Sacramento blackfish (bottom) and their hybrid (middle), from San Luis Reservoir, California. Photograph by T. L. Taylor.

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BOOK REVIEWS

Fish Physiology, Volume VIII, Bioenergetics and Growth

Edited by W.S. Hoar, D.J. Randall, and J.R. Brett; Academic Press Inc., New York, NY; 1979; 786 pp.; \$68.00.

This volume is one of the best in an already excellent series. The papers, collected under the title *Bioenergetics and Growth*, are clearly relevant to the needs and interests of the scientific fish culturist and the physiological ecologist. However, the broad scope of the volume's contents makes it a valuable reference for fish biologists in general, including those working at the population and ecosystem levels. I have examined the book from the latter viewpoints.

Some of the chapters are highly relevant to population and ecosystem biology. Brett's chapter on environmental factors and growth is a case in point. Also, Allendorf and Utter's chapter on population genetics is an excellent introduction to the rapidly expanding field of isozyme analysis, and should be required reading for newcomers to the field.

Even the chapters which would seem to be far removed from population considerations often contain information bearing on population analysis. For example, Fange and Grove's chapter on digestion contains a lengthy review of gastric evacuation times. This parameter is vital to interpretation of stomach contents if one wishes to quantify daily rations or to construct an ecosystem energy budget.

There were some minor weaknesses and omissions. Hyatt's review of feeding strategy seems overly devoted to freshwater predatory fishes, and would benefit from expanded discussion of schooling, filter feeding, and grazing or browsing, with more marine examples. The chapter on early development unfortunately is confined to cellular physiology. The extensive literature on physiological ecology and growth of fish larvae is inadequately covered in the various chapters, and could have been the subject of a chapter of its own.

The final chapter by Ricker on growth rates and models is an excellent review, and is presented in the handbook style characteristic of much of his work. Ricker concludes that there is no simple general growth model which is based on physiologically meaningful concepts. This seems an ironic ending for a volume which has dedicated hundreds of pages to detailed discussion of fish physiology and metabolism. However, from the modeler's viewpoint, this conclusion may have a positive effect, in that it liberates the modeler from attempting futile physiological justifications, and opens the door for flexible empirical approaches.

After reading the volume, I was struck by the limits of our knowledge of fish nutrition and growth. Most of what is known has been gained from hatchery and aquaculture experience, and most of that has been restricted to salmonids. How much and how far this information can be extended to other species and other habitats is unclear. More comparative studies are needed, and perhaps can contribute to development of an empirical generalized growth model.

This is an expensive book, but the quantity and quality of its contents is worth the money.—*Alec D. MacCall*

Fieldbook of Pacific Northwest Sea Creatures

By Don H. McLachlan and Jak Ayres; Naturegraph Publishers, Inc.; 1979; illustrated; \$10.00.

Fieldbook of Pacific Northwest Sea Creatures is the latest attempt to provide an adequate color field guide for Pacific Coast marine life. Unfortunately, it falls far short of the very ambitious goal set by the authors in the Introduction—"Included are most of the animals a tidepool gazer or a diver is ever likely to see."

First of all, for the geographic area of coverage of Alaska to northern California, they have left out a very large number of invertebrates and fishes that are commonly encountered by the diver and tidepooler. It appears that the guide would be most useful in the Puget Sound area.

Secondly, the authors' attempt to provide a guide to both intertidal and subtidal animals is an almost impossible task, considering the hundreds of species of fish and invertebrates that inhabit the region.

To compound the problems with this guide, there are at least five species that are misidentified: on page 80, the sea star listed as *Evasterias troscheli* is actually *Orthasterias koehleri*; the nudibranch on page 105 listed as *Archidoris montereyensis* is *Anisodoris nobilis*; the nudibranchs listed as *Cadlina luteomarginata* and *Dendronotus rufus* on page 106 are instead *Acanthodoris nanaimoensis* and *D. iris*, respectively; and the fish on page 183 listed as *Leptocottus armatus* is *Enophrys bison*.

The book also suffers from poor color reproduction of what appear to be, in most cases, high quality original photographs.

To sum up, by limiting the geographic area of coverage, limiting the coverage to either intertidal or subtidal animals, correcting the identifications, and redoing the color separations, the authors and publisher could, in their next edition, provide another valuable field guide for Pacific coast divers and tidepoolers.—*Daniel W. Gotshall*

Intertidal Invertebrates of California

By Robert H. Morris, Donald P. Abbott, and Eugene C. Hoderlie; Stanford University Press, Stanford, CA; 1980; 695 pp.

Intertidal Invertebrates of California is an excellent and informative book dealing with animal life, from foraminiferans to insects and arthropods, found along California's shoreline. The book does not attempt to be encyclopedic, but treats the hundreds of more conspicuous and/or easily identified animals in the intertidal zones.

A chapter is devoted to each major taxonomic group and in most cases is authored or coauthored by recognized experts in that particular field. Brief yet comprehensive discussions of the taxonomy, evolution, general biology, and natural history introduce each major group. The reader seeking more detailed knowledge is given many pertinent references. Each interestingly written species account contains information on range, identifying characteristics, biology, ecological relationships, and any human use. In addition to a taxonomic breakdown including synonyms and a common name, if any, references and a line drawing of each species are presented.

Identification of each species is aided by a separate section of 900 good color photographs (paintings of some flatworms) of live animals. The variable colors or patterns of some animals are also pictured and should be helpful to the novice shoreline explorer. A brief section on photographic techniques will be an aid to those taking a camera to the shore.

I found nearly every page of this book to contain useful and interesting information. In addition, the authors have been successful in encouraging the reader, regardless of biological expertise, to seek further knowledge and appreciation of intertidal marine life.

I believe that this book will be a valuable source of information for those currently studying or working in marine biology, as well as a fine introduction to those with a growing curiosity about life in the sea.—*David Parker*

Fisheries of the North Pacific

By Robert J. Browning; Alaska N.W. Publishing Co. Anchorage, Alaska; 1980; 432 pp.; \$24.95.

This is a well written book which will give the reader a good overall understanding of the commercial fishing activities of the Northeastern Pacific Ocean.

It is written so that the layman as well as the person involved in the industry or the scientific community can fully comprehend the overall picture.

The author first describes the area and field of his undertaking and then moves on to the various species of fishes and invertebrates. Through the following extensive chapters the following topics are covered: vessels, gear, handling and preservation, salting and smoking, and canning. Each one is thoroughly discussed from the history and early activities up to the most modern undertakings.

The quality of the illustrations is excellent throughout and there are many excellent color plates. There is also an excellent glossary which covers the complete text.

This book, or guide as the author depicts it, should be a welcome addition to the library of anyone who has any interest in commercial fishing activity and is reasonably priced.—*Hugh L. Thomas*

Wolves, Bears, and Bighorns

By John S. Crawford; Alaska Northwest Publ. Co., Anchorage AK; 1980.

Wolves, Bears and Bighorns is composed of selected articles which have all appeared in national magazines. Their theme shows the appreciation of the wilderness country and the wildlife that live there.

The book is not technical and is written so a person lacking outdoor experience or training can understand and thoroughly enjoy it, and it covers many more animals than the title suggests. The writing is very descriptive and gives the reader an opportunity to share the thoughts and ideals of the author. Some of his experiences with the grizzlies (and the elements) are harrowing, to say the least. I hope that no one reading the book will get the impression that with patience and understanding anyone can photograph dangerous wild animals.

The photography is extraordinary, the author's expertise in this realm is outstanding and, coupled with his knowledge and understanding of his subjects, the results are beautiful.

I would recommend this book to anyone who enjoys excellent photography and good reading.—*Hugh L. Thomas*

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