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CALIFORNIA FISH AND GAME

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ERRATUM

Smith, Gary E., 1978. An evaluation of disk-dangler tag shedding by striped bass (Morone saxatilis) in the Sacramento-San Joaquin Estuary. California Fish and Game, 64(2):93–97.

Page 94: The equation printed as: $\log [{}_{A+B}N_i / ({}_{A+B}N_i + {}_{B-A}N_i)]$

should read: $\log [{}_{A+B}N_i / ({}_{A+B}N_i + {}_{B-A}N_i)] = \log (1 - {}_{A}K) + i \log (1 - {}_{A}S)$

Page 95: The last sentence of Figure 1's caption (Numbers in parentheses indicate number of fish from which tags were obtained.) should be deleted.

CHANGE OF EDITORSHIP

With this issue Kenneth A. Hashagen, Jr. of Inland Fisheries Branch assumes the duties of Editor-in-Chief of *California Fish and Game.*

Mr. Hashagen's assumption of the editorship follows the Department's policy of rotating the editorship between staff members representing Marine Resources, Inland Fisheries, and Wildlife Management.

For 7 years Mr. Hashagen, Senior Fishery Biologist, has served as Inland Fisheries Editor of the Quarterly. Through this service he has gained a knowledge of editorial policies and procedures of the Journal.

Under his guidance, the Journal will continue its policy of presenting to the public the results of scientific investigations as they relate to management programs and the conservation of California fish and wildlife resources.

Mr. Hashagen will be ably assisted in his duties by five associate editors: Darlene A. Osborne, Inland Fisheries; Ronald M. Jurek, Wildlife Management; J. R. Raymond Ally, Marine Resources; Donald E. Stevens, Anadromous Fisheries; and David A. Hoopaugh, Salmon and Steelhead.

To Mr. Collins, Editor-in-Chief the past 4 years, we wish to express our appreciation for a job well done. *E. C. Fullerton, Director, California Department of Fish and Game.*

Calif. Fish and Game 64(3): 139–174. 1978

TAXONOMY AND DISTRIBUTION OF THE BULL TROUT, *SALVELINUS CONFLUENTUS* (SUCKLEY), FROM THE AMERICAN NORTHWEST [1]

by
Ted M. Cavender
Museum of Zoology
The Ohio State University

Morphological and distributional evidence is presented favoring the specific distinction of the bull trout, *Salvelinus confluentus* (Suckley), a currently unrecognized form of *Salvelinus* native to western North America. This species has been confused with the Dolly Varden, *Salvelinus malma* (Walbaum). Separation of the two is based primarily on characters of the head and cranial skeleton. Diagnosis and description are given for the bull trout along with a history of its early taxonomy. Past and present distribution of the bull trout ranges between lat 41° and 60° N. North of the 49th parallel it is found in most of the major drainages originating on both sides of the Continental Divide. The bull trout is or at one time was sympatric with the Dolly Varden in at least three major river systems, as well as the waters of Puget Sound.

INTRODUCTION

The salmonid genus *Salvelinus* has long been recognized as a difficult taxonomic group. Without exaggeration, Vladykov (1954) referred to the taxonomy of *Salvelinus* (along with other salmonid genera) as "extremely involved and time-consuming." This is particularly true for species which are native to areas bordering the North Pacific Ocean. McPhail (1961) referred to these populations of *Salvelinus* as part of the *Salvelinus alpinus* (Linnaeus) (arctic char) complex because of their similarity, the unsatisfactory state of their taxonomy, and the incompleteness of representative material.

The possible existence of more than one species of *Salvelinus* in the American northwest has been a controversial subject since the days of the Pacific Railroad surveys in the 1850's. Morton (1970) was the last to deal with the subject. He concluded that only one species, *Salvelinus malma* (Walbaum) was recognizable, while none of the proposed subspecies was valid. However, in this paper I will present morphometric, meristic, osteological, and distributional evidence to show that there are two widely distributed forms of *Salvelinus* native to the western United States and Canada; the Dolly Varden, *S. malma,* and the bull trout, *S. confluentus*.

Although primarily an inland species, collection records show that the bull trout is not strictly an interior, nonanadromous form, but combines coastal and inland, as well as northern and southern aspects to its distribution. Because of the taxonomic difficulties with this species, the bull trout has lacked uniform scientific recognition even though it is a well-known sport fish. The scientific literature, especially compendia of regional fish faunas, has for so long lumped information about their ecology, morphology, and life history, that *S. malma* and *S. confluentus* have been largely confused. If there are morphological characters and aspects of their biology that consistently separate *S. malma* and *S. confluentus* over their distributional ranges, why then has there been a taxonomic prob-

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[1] Accepted for publication September 1977.

lem? The answer is due primarily to the lack of adequate comparative material available to any one investigator.

The findings in this paper are part of a more extensive systematic treatment of the genus *Salvelinus* I began at the University of Michigan in 1968 and have continued at Ohio State University. Conclusions on the specific distinction of the bull trout reached here are essentially those presented in a preliminary report at the 1969 Annual Meeting of the American Society of Ichthyologists and Herpetologists in New York City (Cavender 1969).

MATERIALS AND METHODS

Specimens of *Salvelinus* studied were principally those in the collections of the University of Michigan Museum of Zoology (UMMZ); the National Museum of Natural Sciences, Canada (NMC); and the United States National Museum of Natural History (USNM). Locations given on the distribution map represent collections housed in these institutions (Figure 1). Other material was examined from the California Academy of Sciences (CAS).

Morphometric data were taken only from specimens from which standard length could be recorded. The specimens of *S. malma* compared morphometrically with *S. confluentus* were taken from the Pacific drainages of the United States, including Alaska, and Canada. Most represent a type which McPhail (1961) has termed the southern form of the Dolly Varden. The National Museum of Natural Sciences, Canada, possesses excellent material both of *S. confluentus* and *S. malma*. A large part of this material came from the University of British Columbia, Vancouver (UBC). A number of old and valuable specimens of *Salvelinus* are at the United States National Museum, including holotypes of *Salmo spectabilis* and *Salmo confluentus;* Livingston Stone's collection from the McCloud River, California, in the 1870's; and specimens taken in the early 1880's from Puget Sound and coastal waters of British Columbia. In 1974 I collected bull trout from the Flathead River drainage in Montana, which are now housed at the Ohio State University Museum of Zoology (OSUM).

Osteological data were obtained from both dry-skeletal and cleared-and-stained material housed at the Ohio State University and the University of Michigan.

The number of gill rakers was determined by removing the first gill arch on the right side and counting under a dissecting microscope the individual rakers, including all rudimentary ones. Branchiostegal rays were counted after locating the smallest, most anterior ray by dissection. Mandibular pores were counted by exposing the openings of the mandibular sensory canal with a fine jet of compressed air. The count includes all pores, but not the opening from which the canal exists at the rear of the lower jaw. Pyloric caeca were cleaned of connecting tissue and fat deposits prior to counting. Vertebrae were counted from radiographs, which have been deposited at the University of Michigan Museum of Zoology. Counts were repeated until the same number was obtained twice.

To study gill raker morphology, the anterior right gill arch was removed, stained in alizarin red-s, and cleared in glycerin. The most posterior gill raker on the lower limb was then illustrated with the aid of a Wild-M5 Stereoscope with integral camera lucida attachment.

Osteological abbreviations are as follows: AO (antorbital); ART (articular-

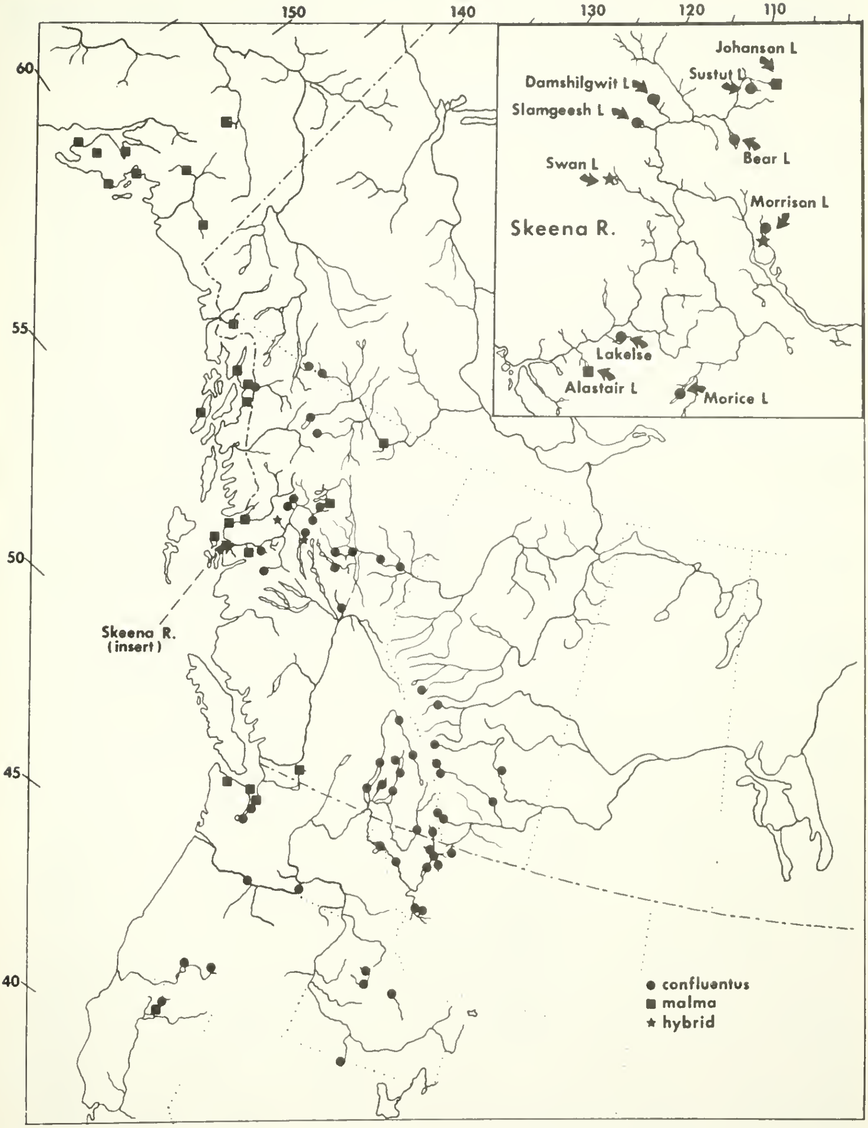

FIGURE 1. Distribution of *Salvelinus confluentus* and *Salvelinus malma* over same latitudinal range in North America; plotted from localities of specimens examined.

angular); ATL (atlas vertebra); BOC (basioccipital); BR (branchiostegal ray); BS (basiphenoid); DE (dentary); ECPT (ectopterygoid); ENPT (endopterygoid); EOC (exoccipital); EPO (epiotic); FR (frontal); HYO (hyomandibular); INT (intercalar); IO (infraorbital); IOP (interopercle); LE (lateral ethmoid); MPT (metapterygoid); MX (maxilla); NA (nasal); ORS (orbitosphenoid); OP (opercle); P (parasphenoid); PA (parietal); PMX (premaxilla); POP (preopercle); PRO (prootic); PTF (posttemporal fossa); PTO (pterotic);

QU (quadrate); SE (supraethmoid); SO (supraorbital); SOC (supraoccipital); SOP (subopercle); SPO (sphenotic); SPOP (suprapreopercle); SY (symplectic); V (vomer).

Specimens Examined

Salvelinus confluentus (Suckley)

Sacramento R. Basin, McCloud R. drainage, Calif.: CAS 25691, (1), 110 mm,[2] Shasta Co.; CAS 38787, (1) 136 mm, near Nosoni Cr., Shasta Co.; CAS 19889, (1), 147 mm, near Bollibokka Mt., Shasta Co.; CAS 38788, (1), 173 mm, Mt. Shasta State Hatchery near Mt. Shasta, Shasta Co.; USNM 26196, (1), skeleton, USNM 10547, (1), 175 mm; USNM 27820, (3), 211–284 mm, USNM 15549, (2), 101–163 mm; USNM, (1), 339 mm; USNM 22452, (1), 301 mm.

Klamath R. Basin, Ore.: UMMZ 188849, (5—two cleared and stained), 140–168 mm, Long Cr., Lake Co.; UMMZ 188851, (1 skeleton), 169 mm, Long Cr., Lake Co.; USNM 16793, (1 skin and skeleton), Linn Creek, Ft. Klamath.

Columbia R. Basin, Snake R. Drainage: USNM 125309, (2), 142–154 mm, Meadow Cr. near Sawtooth, Ida.; UMMZ 117879, (1), 216 mm, Stanley Lake, a tributary to the Salmon R., Custer Co., Ida.; UMMZ 162298, (1), 166 mm, Dave Cr., Elko Co., Nev., a tributary to the Jarbidge R.; Univ. Utah No. 1, (1), 103 mm. Dave Cr., Elko Co., Nev.; CAS 38789, (6—one cleared and stained[3]), 90–155 mm, West Fork Jarbidge R., Elko Co., Nev.; UMMZ 127607, (1), 134 mm, Little Lost R. on Custer Co.-Butte Co. line, Ida.

Columbia R. Basin, mainstream and minor tributaries: USNM 7078, (1), type of *Salmo spectabilis,* Columbia R. at The Dalles, Ore.; USNM 25273-25276, (4), 279–313 mm, Walla Walla, Wash.; NMC 66-61, (1), Columbia R. at Arrowhead, Brit. Col.; NMC 66-63, (22), Mars Cr., tributary to Columbia R. at Big Bend Highway, Brit. Col.; NMC 66-64, (5) Kinbasket Lake at Tsar Cr., tributary to Columbia R., Brit. Col.; NMC 66-70, (3—includes one head), Lower Arrow Lake off Deer Cr., tributary to Columbia R., Brit. Col.; NMC 59-169, (20), Luthead Lake, Banff National Park, Brit. Col.; UMMZ 164591, (1), 252 mm, Emerald Lake, Yoho National Park, Brit. Col.

Columbia R. Basin, Clark Fork Drainage: USNM 38028, (1), 310 mm, Clark Fork River; USNM 44002, (1), 158 mm, Rattlesnake Cr. at Missoula, Mont.; NMC 59-148, (11), Shepp Cr., tributary to Flathead R., Brit. Col.; NMC 66-72, (77), Pollock Cr., tributary to Flathead R., Brit. Col.; NMC 66-77, (17), Gumbo Flats Cr., tributary to Flathead R., Brit. Col.; UMMZ 161871, (3), 134–166 mm, Flathead Lake, Lake Co., Mont.; UMMZ 172458, (7—including three cranial skeletons), 212–423 mm, Flathead Lake, Lake Co., Mont.; UMMZ 161866, (1), 350 mm, Flathead Lake, Lake Co., Mont.; UMMZ 188857, (3—one cleared and stained), 130–145 mm, Morrell Cr. near Seeley Lake, tributary to Clearwater R.; UMMZ 188856, (4), 47–90 mm, Big Creek, tributary to North Fork Flathead R. on western boundary of Glacier National Park; OSUM 25212, (2—one cleared and stained), 208–235 mm, Hungry Horse Cr., tributary to Hungry Horse Reservoir on South Fork Flathead R., Mont.; OSUM 25213-5, (1 skeleton), Flathead R.

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[2] All fish lengths are standard length.

[3] The cleared and stained specimen from this lot has since been given a separate number: CAS 38790.

at Coram below the confluence of North and Middle Forks, Flathead Co., Mont.; UMMZ 102948, (1), 257 mm, Pend Oreille Lake, Banner Co., Ida.

Columbia R. Basin, Kootenay Drainage: NMC 66-52, (2), Slocan Lake, tributary to Kootenay R., Brit. Col.; NMC 66-57, (4) Duncan Lake near Howser, tributary to Kootenay R., Brit. Col.; NMC 66-59, (1), Kootenay Lake at the mouth of the Duncan R., Brit. Col.; NMC 66-68, (6), Kootenay R. at Canal Flats, Brit. Col.; NMC 66-74, (1), mouth of Wolf Creek at Skookumchuck, tributary to Kootenay R., Brit. Col.; NMC 66-78, (2), mouth of Gold Cr. near Newgate, tributary to Kootenay R., Brit. Col.; NMC (no number), (12), Lardeau R., tributary to Duncan R., Brit. Col.

Puget Sound, Washington: USNM 1135, (1), 733 mm, Pullayup R. at Steilacoom, type of *Salmo confluentus*; USNM 27264, (2), 295–568 mm, D. S. Jordan, 1880; USNM 42044, (1), 297 mm, Elliot Bay, O. B. Johnson, 21 May 1889.

Fraser R. Basin, Brit. Col.; NMC 55-130, (2), 184–185 mm, Salmon R. at Hart Highway, north of Prince George.

Skeena R. Basin, Brit. Col.: UMMZ 159357, (3), 223–358 mm, Lakelse Lake; UMMZ 159345, (2), 181–195 mm, Damshilgwit (Cabin) Lake; UMMZ 159333, (1), 230 mm, Morrison Lake; UMMZ 159337, (2), 188–203 mm, Morice Lake; UMMZ 159352, (1), 368 mm, Slamgeesh Lake; UMMZ 159351, (1), 341 mm, Sustut Lake, USNM 86207, (1), 265 mm, Bear Lake.

Taku R. Basin: NMC 68-896, (5), 150–246 mm, Flannigan Slough, Taku R. at International boundary between British Columbia and Alaska.

Upper Yukon R. Basin: NMC 68-1231, (7 of 15), 97–198 mm, Partridge Cr., tributary to the Swift R. near Yukon-British Columbia boundary.

MacKenzie R. Basin, Liard Drainage, Brit. Col.; NMC 62-234, (1), 313 mm, Tatsho Cr. near Dense Lake, tributary to Liard R.; NMC 62-235, (2), 340–344 mm, Letain Lake near King Mt.; NMC 68-1230, (4), 129–176 mm, outlet from Little Lake.

MacKenzie R. Basin, Peace R. Drainage: NMC 66-435, (1), 375 mm, Chuchi Lake on Nation R., tributary to Parsnip R. N.W.T.; NMC 66-436, (1 of 2), 113 mm, Germansen Lake on Omineca R., Brit. Col.; NMC 66-437, (1), 510 mm, Finlay R., about 4 miles upstream from Ft. Grahame, Brit. Col; NMC 66-438, (7), 172–333 mm, mouth of Finlay R. to Manson R., Brit. Col.; NMC 66-440, (1), 206 mm, Peace R., 25 miles downstream from Hudson-Hope, Brit. Col.; NMC 68-802, (1) 171 mm, Peace R., 11 miles west of Hudson-Hope, Brit. Col.

MacKenzie R. Basin, Athabaska Drainage, Alberta: UMMZ 80837, (1), 253 mm, Jacques Lake, tributary to Rocky R., Jasper National Park; UMMZ 159930, (5), 225–324 mm, Jacques Lake, Jasper National Park; NMC 59-48, (4—including 2 heads), Jacques Lake, Jasper National Park.

Saskatchewan R. Basin: USNM 64326, (1), 715 mm, headwaters of Brazeau R., tributary to North Saskatchewan R., Alberta; UMMZ 164943, (1), 164 mm, Banff National Park, Spray R., tributary to Bow R. of South Saskatchewan drainage, Alberta; UMMZ 164928, (1), 190 mm, Bow Lake, Banff National Park, Alberta; UMMZ 164930, (1), 215 mm, Bow R., Alberta; NMC 60-343, (1), Red Deer R. drainage at Morrin, 65 miles northeast of Calgary, Alberta; USNM 44444, (1), 231 mm, Oldman R., tributary to S. Saskatchewan R., Alberta; UMMZ 188900, (8), 190–267 mm, Cracker Lake, tributary to St. Mary's R. of S. Saskatchewan R. drainage, Glacier National Park, Mont.

Salvelinus malma (Walbaum)

Sacramento R. Basin, McCloud River, Calif.: USNM 20819, (2), 235–241 mm, sent by Livingston Stone, catalog entry made Nov. 24, 1877.

Soleduck R., Washington: UMMZ 93829, (14—three cleared and stained), 100–134 mm, above Soleduck Falls, Olympic Peninsula.

Puget Sound, Washington: USNM 34301-34305, (5), 252–274 mm, Port Townsend, James G. Swan, coll. in 1884 or earlier.

Skagit R. Drainage, British Columbia: UMMZ 179422, (2), 50–65 mm, Skagit R. near Hope.

Skeena R. Basin, British Columbia: UMMZ 159323, (1), 200 mm, Alastair Lake; UMMZ 159344, (2), 140–144 mm, Johanson Lake.

British Columbia: NMC 59-150, (2 of 6), 126–130 mm, East Fork Seltat Cr. at Haines Rd. and about 1 mile below Snowater Lake, tributary to Klehin R.; NMC 65-213, (1 head), Nass Harbour, Iceberg Bay near mouth of Nass R.; NMC 65-212, (3), 146–159 mm, Nass Harbour just north of Jacques Point, Iceberg Bay; NMC 65-225, (5), 189–242 mm, mouth of stream, cove on south shore steamer passage about ¾ mile west of Khutzeymaten Inlet; NMC 65-159, (2), 197–293 mm, cove on west side of Refuge Bay and at north end of Porcher I., south of Prince Rupert; USNM 31979, (1), 285 mm, Port Simpson, Capt. H. E. Nichols, June 1882; USNM 37610, (1), 98 mm, taken in fresh water at Port Simpson.

Taku R. Basin, Alaska: NMC 58-402, (2), Twin Glacier Lake, tributary Taku R.; NMC (UBC 58-388), (5—part of large series), Canyon I., Taku R.

Alaska, Aleutian Islands: UMMZ 106266, (13—two cleared and stained), 52–127 mm, small stream on Atka I.; UMMZ 106529, (3), 383–497 mm, Unalaska I.

Alaska: UMMZ 128983, (4), 257–310 mm, vicinity of King Cove, Belkofski Bay, Alaska Peninsula; UMMZ 106260, (1), 288 mm, freshwater stream tributary to Three Saints Bay, Kodiak I.; UMMZ 126507, (2), 286–289 mm, Karluk R., Kodiak I.; UMMZ 126476, (11—two cleared and stained), 71–151 mm, Upper Thumb R., tributary to Karluk L., Kodiak I.; UMMZ 159395, (2), 100–125 mm, North Fork of Upper Thumb R. above falls, Kodiak I.; UMMZ 159393, (1), 53 mm, Falls Cr., above falls, tributary to Karluk L., Kodiak I.; OSUM 25213, (5), 98–138 mm, mouth of tributary entering Karluk L., Kodiak I.; UMMZ 106267, (1), 174 mm, Lake at north end of Sitkalijak I.; UMMZ 182299, (1), 134 mm, Baranof I., stream on north shore of Port Lucy at west end of Island.

Copper River Drainage, Alaska: UMMZ 162600, (1), 173 mm, Chitina R.; NMC (BC 58-227), (5), 205–327 mm, South L. of Chenan Lakes to Copper R.

Yukon River Basin: UMMZ 144581 [4], (1), 85 mm, Grant Cr. about 30 miles west of Tanana; UMMZ 133553 [4], (2), 186–194 mm, Riley Cr., McKinley National Park; NMC (UBC 58-271), (4), 152–190 mm, Dry Cr. near Alaska Highway, Tanana R. drainage.

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[4] Specimens that represent the "northern form" of *Salvelinus malma* (McPhail 1961).

MacKenzie R. Basin, British Columbia: USNM 147661, (1), 102 mm, Hot Springs, 3 miles WNW of junction of Trout R. and Liard R. July 6–8, 1948, J. R. Alcorn.

U.S.S.R.: UMMZ 145814, (1), 123 mm, Pogarna R., Kamchatka.

Japan and Kuril Islands: NMC 60-154, (6), Shokotsu R., Soya Province, Hokkaido; UMMZ 186872, (6—one cleared and stained), 130–135 mm, Pon-mataochi R., Nemuro Province, Hokkaido; UMMZ 188710, (9—one cleared and stained), 79–168 mm, Ishikari R. at Sounkei, Ishikari Province, Hokkaido; UMMZ 188711, (9), 65–180 mm, Kuzira Bay, Paramusiro I., Northern Kuril Islands.

Korea: UMMZ 188698, (4), 70–187 mm, Upper Tuman R., Mozan; UMMZ 188712, (1) 429, Joshin Bay near Seishin.

NOMENCLATURE

Salvelinus confluentus (Suckley)

Salmo spectabilis—Girard, 1856: 218 (orig. descr.)
Salmo spectabilis—Girard, 1858: 307–308 (amended descr.)
Salmo confluentus—Suckley, 1858: 8–9 (orig. descr.)
Salmo spectabilis—Suckley, 1860: 342–343 (correct locality given)
Salmo confluentus—Suckley, 1860: 334–335 (amended descr.)
Salmo bairdii—Suckley, 1861: 309 (orig. descr.)
Salmo parkei—Suckley, 1861: 309–310 (orig. descr.)
Salmo campbelli—Suckley, 1861: 313 (subst. name and amended descr.)
Salvelinus spectabilis—Jordan, 1879: 79–81 (amended diag.)
Salvelinus malma—(in part) Jordan and Gilbert, 1882: 319–320 (synonymy given)

For years the bull trout and the Dolly Varden, here considered specifically distinct, have been combined under one name, the Dolly Varden, *Salvelinus malma* (Walbaum). The latter name is correctly applied to the form which is generally characterized as anadromous. As now understood, the range of *S. malma* spans the entire arc of the North Pacific from the Sea of Japan and Kuril Islands, across the Aleutian chain to Alaska and south along the North American Pacific coast to the northwestern U. S. (Figure 1). Because of its international usage, the common name Dolly Varden is better reserved for *S. malma* although it may originally have applied to *S. confluentus.* The latter ranges well inland in the United States and Canada and is generally nonanadromous. Where *S. confluentus* reaches an adult size of several kilograms or more, such as in the Kootenay River of British Columbia and the Flathead River drainage of Montana, fishermen refer to this species as the bull trout (Dymond 1932; Brown 1971); a name inspired by its large, broad head, its large mouth and prominent jaws, and its highly piscivorous diet.

The original name for the bull trout, *Salmo spectabilis* Girard, is a secondary homonym (Suckley 1861, Morton 1970), but there are four other scientific names available for the bull trout, all proposed by Suckley (1858, 1861): *Salmo confluentus, Salmo bairdii, Salmo parkei,* and *Salmo campbelli.* The first binomen, *Salvelinus confluentus* (Suckley), is selected for use because, 1) it has precedence over the other three in date of publication (Suckley 1858), 2) fewer nomenclatural problems, including spelling, are anticipated for the name *con-*

fluentus, 3) Suckley's type, a dried head and skin (USNM 1135), is still in existence, and 4) *S. bairdii* and *S. parkei* lack type specimens. Jordan and Evermann (1896) placed *Salmo confluentus* Suckley in synonymy with *Oncorhynchus tshawytscha* (Walbaum), probably because Suckley's (1858, 1860) descriptions read, in part, like that of a Pacific salmon. However, careful comparison of the head of the type specimen with Suckley's description has led me to conclude they are the same.

TAXONOMIC HISTORY

As indicated above, the bull trout [5] was first described as *Salmo spectabilis* (Girard 1856). Girard gave the locality of the holotype of *spectabilis* (USNM 7078) as St. Mary's Mission on the Clark Fork of the Columbia River, Montana, but George Suckley (1860) who had collected the specimen in 1854, redescribed *spectabilis* and corrected Girard's locality information, stating that the holotype came from Ft. Dalles on the lower Columbia River. This specimen is now a mutilated, half-rotted individual estimated at 200 mm SL.

In another paper, Suckley (1861) realized that the name *spectabilis* was preoccupied and substituted *Salmo campbelli* (after Archibald Campbell, Chief of the N.W. Boundary Commission). Morton (1970) has given a detailed account of this name change and the rules that pertain to it. In the same paper, Suckley also described *Salmo bairdii* and *Salmo parkei,* which are both conspecific with *spectabilis.* I searched the USNM collections but failed to find the types of *bairdii* and *parkei.* However, the holotype of Suckley's *"Salmo confluentus"* was found (Figure 2A). This specimen consists of a dried head and skin now preserved in alcohol. The head is that of a bull trout, but the description by Suckley (1858) states that the dorsal, adipose, and caudal fins were spotted profusely with dark brown and black (unlike *Salvelinus*). This could not be confirmed, for on examination of the type, no dark spots were found. Thus, I believe it possible that the description of *Salmo confluentus* was based on the remains or observations of two different individuals, one of which was a bull trout and the other a Pacific salmon.

The type-locality for *Salmo confluentus* was given as the Puyallup River near Ft. Steilacoom, Washington Territory. The type was procured September 27, 1856 by Suckley, apparently from Indians who had captured the fish—a large (approximately 700 mm) male in spawning condition. It possesses a kype that fits into a deep notch between the premaxillae. The notch is accentuated because of the dried condition of the specimen.

Thus, we see that Suckley not only collected the holotype of *S. spectabilis* and later redescribed it as *Salmo campbelli,* but within a few years described the same species three more times under different names (*confluentus, bairdii, parkei*), using specimens he himself had collected.

Jordan (1879), in his key to the species of *Salvelinus* found within the United States, included characters of the bull trout—"head large, stout, broad and flattened above"—in his diagnosis of *Salvelinus spectabilis* (Girard). He apparently based his key characters on specimens taken from the Clackamas River, Oregon, by Livingston Stone. He also examined Girard's type of *Salmo spectabi-*

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[5] Although "char" may be a more appropriate term for members of the genus *Salvelinus* (Morton 1955), "trout" is used herein as the common name for the bull trout in accordance with the American Fisheries Society's attempt to stabilize fish nomenclature (Bailey 1970).

lis, noting that the holotype was still preserved in the U.S. National Museum, while that of *parkei* was lost. He added that *parkei* was unquestionably the same as *S. spectabilis*. In the same paper, Jordan recognized the bull trout from the McCloud River as *S. bairdii* (Suckley), believing it differed from *S. spectabilis* by lacking basibranchial teeth. He did not list *S. malma* (Walbaum) in his key.

Jordan and Gilbert (1882) were responsible for placing the bull trout in synonymy with *Salvelinus malma* (Walbaum). Jordan and Evermann (1896) followed this precedent, which has been continued to the present. Jordan never

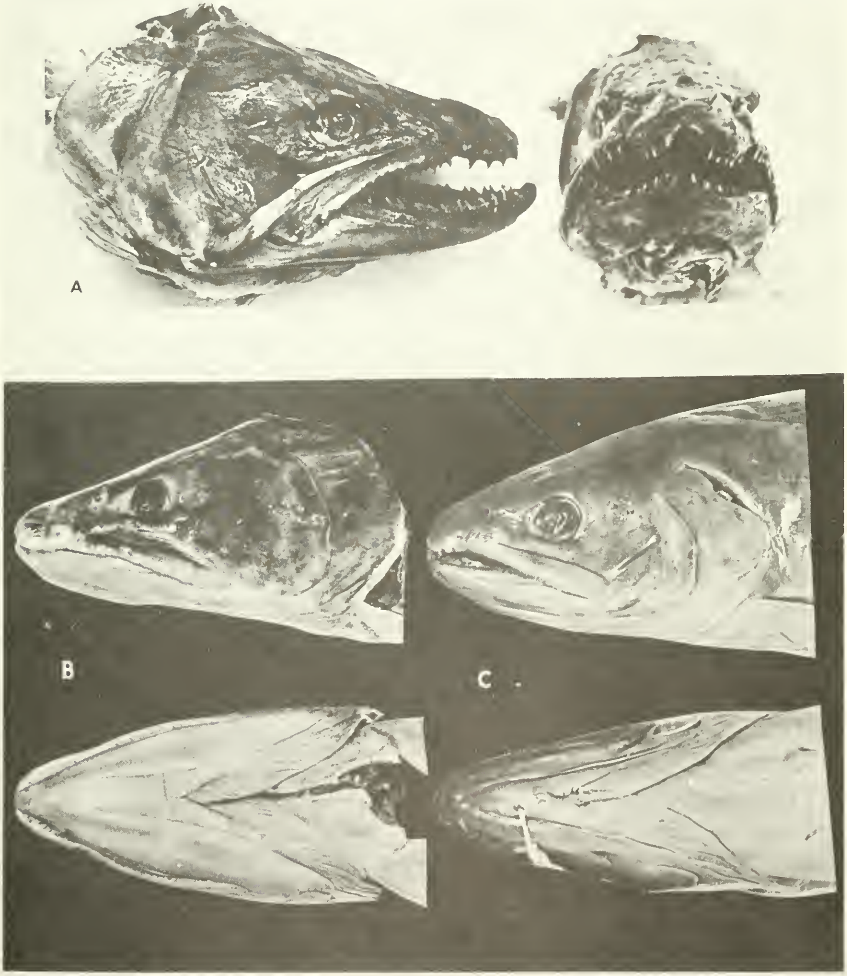

FIGURE 2. (A) Holotype of *Salmo confluentus* Suckley 1858, USNM 1135, head length 173 mm, Puyallup R. near Steilacoom, Washington; (B) lateral and ventral view of head of spawning male *Salvelinus confluentus*, NMC 66-70, estimated 550 mm standard length, Deer Cr., British Columbia; (C) lateral and ventral view of head of spawning male *Salvelinus malma*, UMMZ 126507, 295 mm, Karluk R., Kodiak I., Alaska. *Photograph by the author.*

correctly distinguished the bull trout from Dolly Varden where they occur together in Puget Sound. Under his use of the name, *"spectabilis"*, he lumped the bull trout with the Dolly Varden of coastal areas as far north as Alaska. In later papers (Jordan 1923, Jordan and McGregor 1925) the name *Salvelinus spectabilis* was used for a supposed "southern form" which ranged from northern California northward to Alaska and the name *Salvelinus malma* applied to a "northern form" known from Unalaska to Kamchatka.

The earlier descriptions of *"Salmo spectabilis"* mentioned a number of distinctive characteristics of the bull trout. Girard (1856, 1858) emphasized the curved maxilla in the type specimen and its elongate head which entered the standard length 3.5 times. Under his description of *Salmo confluentus*, Suckley (1858) was the first to mention the "projection of the chin anterior to the front teeth"; in fact, he confused this character with the hooked lower jaw of spawning male *Oncorhynchus*. He also added that the type of *confluentus* had 13 or 14 branchiostegals. Again, in listing characters for *Salmo bairdii,* Suckley (1861) described the "snout having a deep notch between the extremities of the premaxillaries receiving a conical fleshy protuberance projecting upwards from the chin." In the same paper under *Salmo parkei,* Suckley noted the large head "about four and a half times in the total length; its top flat; muzzel pointed" and "branchiostegals 13–14." Also in *parkei,* Suckley mentioned "a disposition toward the formation of a fleshy 'tit' projecting upwards at the point of lower jaws with a corresponding notch between the premaxillaries." Despite what Morton (1970) has published to the contrary, there is little doubt in my mind that in his description of *Salmo bairdii* and *Salmo parkei,* Suckley (1861) was writing about the bull trout and not the Dolly Varden.

To conclude this discussion of taxonomic history, it is emphasized that the name *confluentus* is to be substituted for *spectabilis* in accordance with the rules of zoological nomenclature (Article 53) and the holotype of this species becomes USNM 1135.

DIAGNOSIS

A large species of North American *Salvelinus* reaching a greater size (to 18.3 kg, about 40 lb, Hart 1973) than *S. malma*; distinguished from the latter by its long, broad head which is flat above and sharply tapered through the snout with the eye positioned near the dorsal margin; head measures 3.7 in standard length, averaging 3.6 in juveniles and 3.9 in large adults (*S. malma* measures about 4.3); jaws and teeth well-developed, with cleft of mouth terminal; maxilla constantly curved downward; branchiostegals typically 13 or 14 on the right side, 24–31 both sides combined; mandibular pores usually 7–9 on a side, 16 combined (*S. malma* typically has 6 on a side); gill rakers robust with strong teeth projecting from mesial edges toward the branchial cavity (whereas *S. malma* has relatively long, finely tapered flexible gill rakers that are much compressed dorsoventrally and lack teeth projecting from the mesial edge); gill rakers 14–19, pyloric caeca 21–36, and vertebrae 62–67; basibranchial teeth 0–11, averaging 4, and consistently arranged in a single longitudinal row; in all specimens examined, there is a pronounced gap on each side between the palatine and vomerine tooth rows; in anterior view, there is a notch at the lower terminus of the snout (between the premaxillae) that receives a fleshy protuberance on the symphysis of the mandibles, although best developed in the adult (both male and female). This character is also seen in larger juveniles and is not to be confused with the kype of spawning male salmonines, even though the same area is similarly modified in large, breeding males of *S. confluentus.*

DESCRIPTION

The characters of *S. confluentus* described below were found to be consistent in samples taken from localities throughout its known range. These samples comprise a total of 332 individuals from eight major river basins draining to the Pacific and Arctic oceans and Hudson Bay: Sacramento, Klamath, Columbia, Skeena, Taku, Yukon, MacKenzie, and the Saskatchewan.

Some of the characters which have been employed for many years in *Salvelinus* taxonomy, such as numbers of gill rakers and pyloric caeca, will not separate *S. malma* and *S. confluentus.* This is one reason why the bull trout has not been recognized as a distinct form. Most useful in separating *S. confluentus* from *S. malma* are the shape and size of the head. In addition, characteristics of the jaws, teeth, and gill rakers, number of mandibular pores, number of branchiostegal rays, arrangement of basibranchial teeth, neurocranium profile, and configuration of certain bones of the cranium, such as the supraethmoid, frontal, preopercle, and opercle, are very useful. Numbers of gill rakers, pyloric caeca, and vertebrae show considerable overlap between the two taxa.

Head Size and Shape

In dorsal view (Figure 3A) the head appears very broad and flat on top and is hard to the touch. The frontals slope only slightly in a lateral direction away from the midline. In *S. malma* (Figure 3B) the head is more compressed and the frontals usually peak at the midline. Unlike *S. confluentus,* the frontals of *S. malma* are usually covered with thick, fatty tissue underlying the skin. This is best observed in anadromous *S. malma.*

In lateral view (Figure 3A), the head of *S. confluentus* is low and sharply conical (also see Paetz and Nelson 1970). The terminal cleft of the mouth evenly divides the anterior profile of the head, while in *S. malma* the snout tends to be shorter and deeper and often overhangs the tip of the lower jaw, especially in juveniles (Figure 4B).

The eye of *confluentus* (Figures 2B, 3A) is more dorsal in position than in *S. malma* (Figures 2C, 3B). The vertical distance from the center of the eye to the top of the head falls well short of the distance from the center of the eye to the nares, while in *S. malma,* this distance reaches the nares or nearly so.

In anterior view, the greater breadth of the head is again noticeable in *S. confluentus* (Figure 3). A major characteristic seen in this aspect is the notch dividing the premaxillae, which receives a fleshy protuberance at the teminus of the lower jaw (Figure 3A). This character is best developed in adults of both sexes and reaches maximum development in spawning males (Figures 2A, 2B). Juveniles older than 2 years may also have this feature.

S. malma may have a well-developed kype in spawning males of anadromous populations, as shown by Morton (1965), but the kype is barely evident in spawning males of the nonanadromous *S. confluentus* (Morton 1965). On specimens I have examined, the kype was best developed on the largest spawning males (over 500 mm SL). Its existence is probably a function of size. The kype

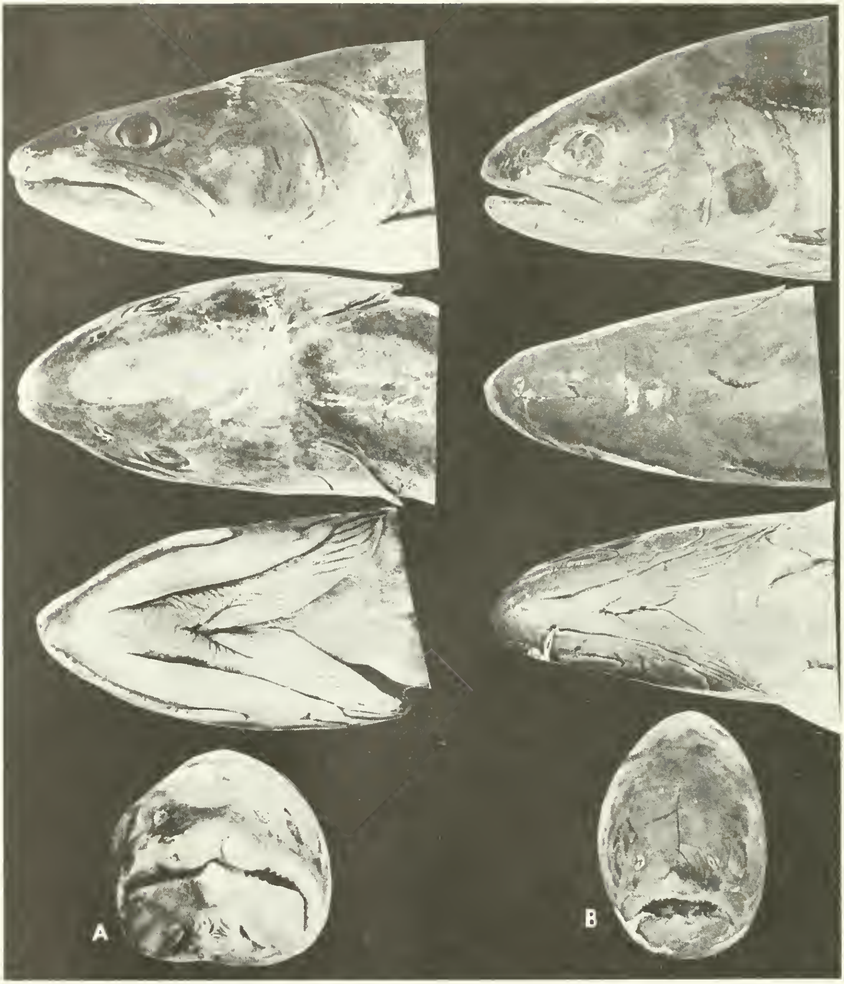

FIGURE 3. Head form (lateral, dorsal, ventral, and frontal views) in the adult female of (A) *Salvelinus confluentus,* NMC 66-437, 580 mm, Finlay R. trib., Brit. Col.; (B) *Salvelinus malma,* UMMZ 126507, 289 mm, Karluk R., Kodiak I., Alaska. *Photograph by the author.*

in *S. malma* is directed dorsally, whereas in *S. confluentus* it has a slightly more anterodorsal orientation.

The upper jaw of the bull trout in lateral view (Figure 3A) always exhibits a pronounced downward curve as seen in the concavity of the toothed margin and convexity of the dorsal margin, particularly where the supermaxilla is seated. Typically, the maxilla of *S. malma* is more slender, with the toothed shaft straight or only slightly curved downward.

Head length of *S. confluentus* (Table 1) typically enters the standard length less than 4.0 times, whereas in *S. malma* it enters the standard length about 4.25 times. The difference is greater when data from dwarf landlocked populations

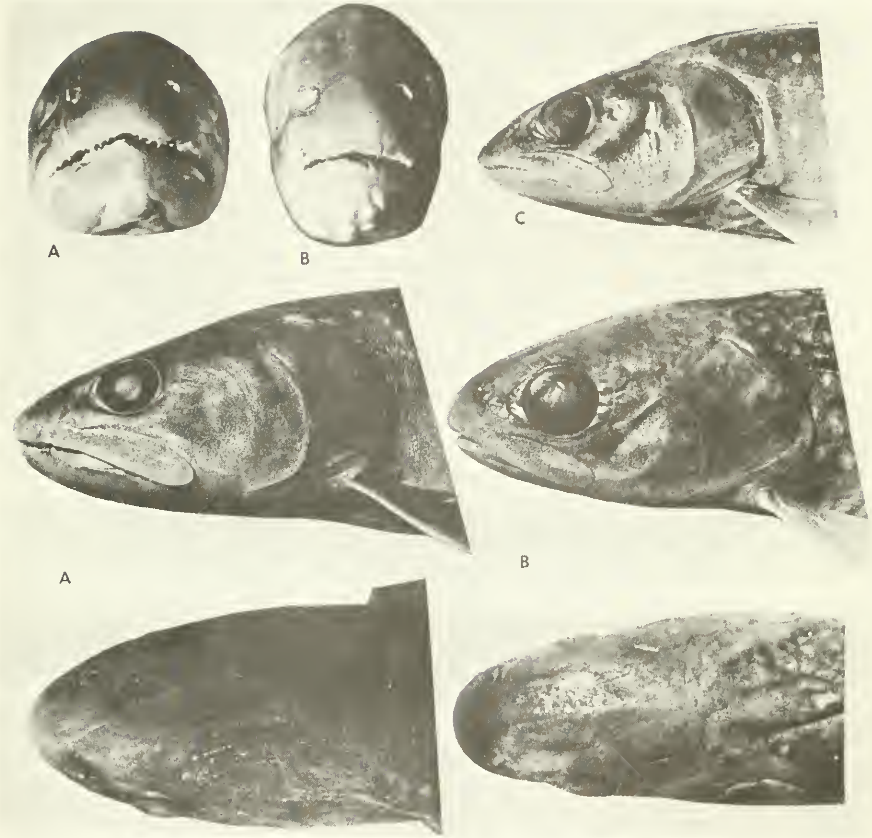

FIGURE 4. Head form in juveniles of (A) *Salvelinus confluentus,* OSUM 25212, 235 mm, female, trib. of S. Fork Flathead R., Montana, (frontal, lateral, dorsal views); (B) *Salvelinus malma,* OSUM 25213, 138 mm, female, trib. Karluk R., Kodiak I., Alaska, (frontal, lateral, dorsal views); (C) *Salvelinus confluentus* UMMZ 188857, 134 mm, male, trib. of Clearwater R., Montana (lateral view). *Photograph by Gus Spreitzer.*

of *S. malma* are excluded. However, the proportion of head length to standard length changes with the size of the fish in both *S. malma* and *S. confluentus* (Table 2). While individuals under 100 mm would be difficult to separate using this character, those over 250 mm show a high degree of separation. I found no difference in proportionate head size between adult male and female *S. confluentus,* although I suspect that males over 500 mm will have relatively longer heads. In *S. malma,* however, males over 200 mm tended to have larger heads than females of the same size.

Branchiostegal Rays

S. confluentus had the highest branchiostegal ray count of all *Salvelinus* I investigated. It averaged 14 rays on the left side and 13 on the right side in 120 specimens, with a range from 12 to 16 (Table 3). The range for both sides combined was 24 to 31 with a mean of 27 (Table 4). Among the species of

TABLE 1. Head Size as the Proportion of Standard Length to Head Length in *Salvelinus confluentus* and *Salvelinus malma.*

Drainage	*Sample size*	*Range*	*Mean*
	Salvelinus confluentus		
McCloud River, California	12	3.2–3.9	3.6
Klamath River Basin, Oregon	5	3.5–4.1	3.8
Columbia River Basin, Snake River drainage	11	3.6–4.7 [1]	3.8
Columbia River Basin (excluding Snake drainage) Puget Sound, Fraser River Basin	23	3.3–4.1	3.7
Skeena River Basin	10	3.5–4.0	3.7
Taku River Basin	5	3.7–4.1	3.9
Yukon River Basin	7	3.6–4.0	3.7
MacKenzie River Basin	25	3.5–4.1	3.7
Saskatchewan River Basin	13	3.5–4.0	3.7
TOTAL	111	3.2–4.1 (4.7) [1]	3.73
	Salvelinus malma		
McCloud River, California	2	4.5–4.7	4.6
Soleduck River, Washington	5	3.8–3.9	3.9
Puget Sound, Washington	4	4.2–4.6	4.4
Skeena River Basin	3	3.9–4.5	4.1
Coastal British Columbia	14	3.5–4.5	4.2
Taku River Basin	7	3.5–4.6	4.1
Gulf of Alaska, Kodiak Island, Coastal Streams and Islands	20	3.6–4.7	4.3
TOTAL	55	3.5–4.7	4.23

[1] One individual, Univ. Utah No. 1, with abnormally small head.

TABLE 2. Head Size as the Proportion of Standard Length to Head Length in *Salvelinus confluentus* and *Salvelinus malma,* in Relation to Body Size and Sex.

Standard length (mm)	*Sample size*	*Range*	*Mean*
	Salvelinus confluentus		
50–100	5	3.3–3.8	3.63
101–150	20	3.4–3.9	3.62
151–200	27	3.2–4.0	3.67
201–250	24	3.5–4.1	3.74
251–300	15	3.6–4.1	3.82
301–350	11	3.5–3.9	3.70
351–568	10	3.6–4.1	3.86
♀ (200–568)	20	3.5–4.0	3.73
♂ (200–423)	18	3.5–4.0	3.73
	Salvelinus malma		
50–100	10	3.3–4.1	3.63
101–150	10	3.8–4.3	4.00
151–200	10	3.6–4.5	4.16
201–250	9	3.9–4.7	4.36
251–300	14	4.0–4.7	4.38
301–445	8	3.8–4.7	4.40
♀ (200–380)	12	4.1–4.7	4.46
♂ (200–445)	10	3.8–4.4	4.10

Salvelinus, S. namaycush is closest to *S. confluentus* in number of branchiostegals. Vladykov (1954) reported *S. namaycush* to average 13 on the left side with a mean of 25.3 for both sides combined. This character is important in separating *S. confluentus* from *S. malma*. The average for 88 specimens of *S. malma* was 11.61 on the left side, 11.0 on the right side, with a range of 9 to 12 (Table 3).

TABLE 3. Frequency Distribution of Left and Right Branchiostegal Rays in *Salvelinus confluentus* and *Salvelinus malma*.

		Left									*Right*								
Drainage basin	*N*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*Mean*	*S.D.*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*Mean*	*S.D.*
							Salvelinus confluentus												
McCloud River, California	10				2	4	4		14.20	0.74				1	1	7	1	13.80	0.74
Klamath Basin, Oregon	7				3	4			13.57	0.49					5	2		13.29	0.45
Columbia Basin, Snake River	12				5	3	4		13.91	0.86				1	7	4		13.25	0.59
Columbia River, Fraser River, Puget Sound	30			1	3	16	9	1	14.23	0.80				1	12	14	3	13.63	0.70
Skeena Basin	10				3	6	1		13.80	0.60					6	4		13.40	0.48
Taku Basin	5				4	1			13.20	0.40					4	1		13.20	0.40
Yukon Basin	7					4	3		14.43	0.49						5	2	14.29	0.45
Mackenzie Basin	26				12	8	6		13.77	0.79				1	12	12	1	13.50	0.63
Saskatchewan Basin	13			2	6	3	2		13.38	0.92				5	4	4		12.92	0.82
TOTAL	120			3	38	49	29	1	13.89	0.82				9	51	53	7	13.48	0.71
							Salvelinus malma												
Soleduck River, Washington	11	1	3	7					11.54	0.65		2	9					10.82	0.38
Puget Sound, Skagit River	7	2	3	1	1				11.14	0.98		3	2	2				10.86	0.83
Skeena River Basin	3			2	1				12.33	0.47			3					11.00	0.00
Coastal British Columbia	15	1	3	9	2				11.80	0.74		1	8	6				11.33	0.59
Taku River	7		5	1	1				11.43	0.72		2	4	1				10.86	0.63
Gulf of Alaska, Coastal Drainages and Islands	32	1	10	17	4				11.75	0.70		7	18	7				11.00	0.66
Aleutians	13	3	4	5	1				11.31	0.91	1	5	5	2				10.62	0.83
TOTAL	88	8	28	42	10				11.61	0.80	1	20	49	18				10.95	0.68

TABLE 4. Frequency Distribution of Branchiostegal Rays (Right and Left Sides Combined) in *Salvelinus confluentus* and *Salvelinus malma*.

		Number of rays														
Drainage basin	*N*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*30*	*31*	*Mean*	*S.D.*
					Salvelinus confluentus											
McCloud River, California	10								2	1	2	5			28.00	1.18
Klamath Basin, Oregon	7								3	2	2				26.86	0.83
Columbia Basin, Snake River	12							1	4	3		4			27.17	1.40
Columbia Basin, Fraser River, Puget Sound	30							2	1	10	7	8	1	1	27.83	1.31
Skeena Basin	10								2	5	2	1			27.20	0.87
Taku Basin	5								3	2					26.40	0.48
Yukon Basin	7										3	3	1		28.71	0.69
MacKenzie Basin	26								10	6	4	5	1		27.27	1.25
Saskatchewan Basin	13						2	3	3	1	2	2			26.31	1.68
TOTAL	120						2	6	28	30	22	28	3	1	27.37	1.38
					Salvelinus malma											
Soleduck River, Washington	11			2	3	6									22.36	0.77
Puget Sound, Skagit River	7		2	1	1	2		1							22.00	1.69
Skeena River Basin	3					2	1								23.33	0.47
Coastal British Columbia	15			2		9	2	2							23.13	1.08
Taku River	7			2	3	1		1							22.28	1.27
Gulf of Alaska, Coastal Drainages and Islands	32		1	6	4	14	3	4							22.75	1.29
Aleutians	13	1	2	3	1	4	1	1							21.92	1.68
TOTAL	88	1	5	16	12	38	7	9							22.57	1.36

For both sides combined, *S. malma* had a range from 19 to 25 with a mean of 22.6. Counting branchiostegal rays on the right side separated 90% of the *S. confluentus* from *S. malma*. By combining both sides, the separation was not increased significantly.

Mandibular Pores

Of 118 *S. confluentus* examined, 63% had 16 or more mandibular pores on both sides with a range from 12 to 19 (Table 5). In *S. malma* there are 10 to 15 total with a mean of 12.1. Elsewhere among the species of *Salvelinus*, only *S. namaycush* has a higher mandibular pore count (Morton and Miller 1954).

Basibranchial Teeth

Basibranchial teeth of *S. confluentus* are characteristically arranged in a single longitudinal row. They usually number from 3 to 5; however, of 40 individuals, 6 (15%) had no basibranchial teeth. In *S. malma* basibranchial teeth are usually more numerous and arranged in one to three rows on the basibranchial plate. Three of 35 (9%) *S. malma* that I examined had no teeth, and Morton and Miller (1954) found that 4 of 20 (20%) specimens they examined had no basibranchial teeth.

Gill Raker Morphology

After examining large numbers of gill arches from *S. confluentus* and *S. malma*, I conclude that the form of the raker and the characteristics of its dentition are more important in separating *S. confluentus* from *S. malma* than actual gill raker counts, which have been employed so extensively in salmonid taxonomy. Gill raker morphology provided a high degree of separation (98%) of *S. confluentus* from *S. malma*. Features of the raker that are most distinctive are the shape and degree of dorsoventral compression, the relative size of the teeth, and their presence or absence along the mesial edge of the rakers (the edge that faces the branchial cavity).

The gill rakers of *S. confluentus* are robust and oval in cross section. They have strong teeth projecting well out from the mesial edge (Figure 5A) as well as having smaller teeth on the dorsal and ventral surfaces. The raker is ornamented with prominent ridges along its lateral margin. *S. malma*, in contrast, has rakers that are strongly compressed dorsoventrally so that the broad surfaces of the rakers are flat and weakly ridged (Figure 5B). Usually the rakers possess long tapered tips that are quite delicate. Although there are usually small teeth on these surfaces in *S. malma*, the mesial edge lacks the strong projecting teeth entirely.

Body Form

The trunk of *S. confluentus* tends to be slender and rounded with only slight lateral compression (Figure 6). In *S. malma* the trunk, like the head, is more laterally compressed. A proportional difference that helps to separate the two species is found by dividing the head length into the distance from the vent to the base of the tail. The head length nearly always equals or exceeds this distance in *S. confluentus*, whereas in *S. malma* it falls short.

Spotting Pattern

The size and distribution of spots are weak characters, although they have been used for identifying North American *Salvelinus*, especially by early taxono-

TABLE 5. Frequency Distribution of Mandibular Pores (Right and Left Sides Combined) in *Salvelinus confluentus* and *Salvelinus malma.*

		Number of pores												
Drainage basin	*N*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*Mean*	*S.D.*
	Salvelinus confluentus													
McCloud River, California	5					1	1	2	1				15.60	1.01
Klamath Basin, Oregon	7			1	1	4	1						13.71	0.88
Columbia Basin, Snake River	12				1	1	6	2	2				15.25	1.08
Columbia Basin, Fraser River, Puget Sound	33					4	4	12	4	6	3		16.39	1.45
Skeena Basin	11							6	3	2			16.64	0.77
Taku Basin	5					1		3	1				15.80	0.97
Yukon Basin	7					1	4	1	1				15.29	0.88
MacKenzie Basin	25				2	4	8	7	4				15.28	1.14
Saskatchewan Basin	13			2	1	5	2	2			1		14.46	1.78
TOTAL	118			3	5	21	26	35	16	8	4		15.57	1.49
	Salvelinus malma													
Soleduck River, Washington	11		1	7	3								12.18	0.57
Puget Sound, Skagit River	7		2	4		1							12.00	0.92
Skeena River Basin	3			3									12.00	0.00
Coastal British Columbia	15		1	11	2	1							12.20	0.65
Taku River	7			7									12.00	0.00
Gulf of Alaska, Coastal Drainages and Islands	32	1	5	18	5	2	1						12.16	0.97
Aleutians	12	1	2	6	3								11.91	0.86
TOTAL	87	2	11	56	13	4	1						12.10	0.80

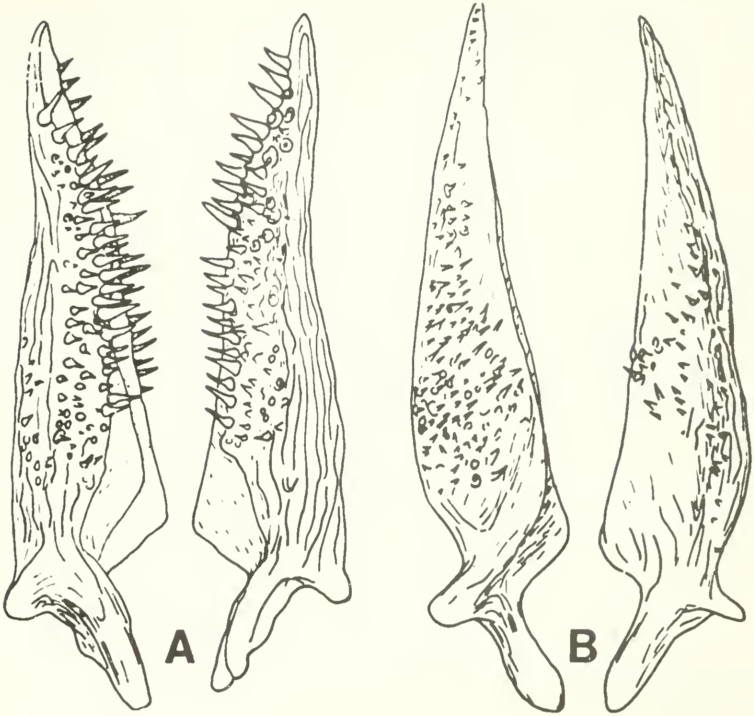

FIGURE 5. Most posterior gill raker of first arch, right side (ventral view, left; dorsal view, right) from (A) *Salvelinus confluentus*, UMMZ 17248, 285 mm, Flathead L., Montana; (B) *Salvelinus malma*, UMMZ 128983, 312 mm, King Cove, Alaska Peninsula. *Photograph by the author.*

FIGURE 6. Body form and pigmentation in *Salvelinus confluentus* (A) UMMZ 188857, 134 mm, juvenile, trib. Clearwater R., Montana; (B) OSUM 25212, 235 mm, juvenile, trib. S. Fork Flathead R., Montana. *Photograph by the author.*

mists. The light-colored spots of *S. confluentus* are normally smaller than the diameter of the pupil of the eye, yet large enough to be seen on a fish in clear water. Typically, they cover most of the back and are best developed around the dorsal fin. Suckley (1860) and Campbell (1882) noted these light-colored spots on the back of the bull trout.

Other Meristic Characters

The range of variation in numbers of vertebrae, gill rakers, and pyloric caeca were about the same in *S. confluentus* and *S. malma,* with almost a complete overlap between the two species. The mean numbers of pyloric caeca differed by less than two (Table 6). *S. confluentus* has a relatively high number of vertebrae (mean of 64.8) compared to other *Salvelinus* taxa from the Pacific basin (Table 7). Southern *S. malma* has a mean of 62.9. The increase in number occurs in the precaudal series (36 in *S. malma* vs. 39 in *S. confluentus*) and probably is correlated with the piscivorous habits of *S. confluentus.* Other fish eaters, such as species of *Esox,* have a long abdominal cavity to accommodate large prey.

The bull trout is characterized by a slightly lower number of gill rakers than other North American *Salvelinus.* The number was found to range between 14 and 20 in *S. confluentus* with a mean of 16.6. For *malma* the range was 14 to 23 with a mean of 18 (Table 8).

Osteology

The skeleton of *Salvelinus confluentus* offers an impressive set of characters that fully separate this species from *S. malma.* It was an examination of an osteocranium of a specimen from Flathead Lake that first led me to suspect that the bull trout was different from the Dolly Varden.

The external morphology of the head described previously is related to the features of the cranial skeleton. The distinctive features found are consistent in samples taken from the various drainages where the bull trout occurs. These characters have been carefully checked by dissecting preserved material, radiographing nearly 100 preserved specimens, clearing and staining, and by examining dried skeletal preparations. The latter have been used for purposes of illustration. A comparative osteological study of the head skeleton in certain *Salvelinus,* including *S. malma* from the western Pacific basin, has been published by Shaposhnikova (1971). This should be referred to in comparing *S. confluentus* with *S. malma.*

The articulated cranium shows: 1) a flattened skull roof; 2) an elliptical orbit with a longitudinal axis much longer than the vertical; 3) a large cavity behind the orbit which was occupied by the adductor muscle of the lower jaw, and 4) massive jaws with strong teeth (Figure 7A). The jaw teeth are best developed on the premaxilla, dentary, and anterior end of the maxillary alveolar shaft. The latter is curved with its dorsal margin covered posteriorly by a sigmoid-shaped supramaxilla.

The large area for attachment of the adductor mandibulae muscle is made possible by expansion of the lateral hyomandibular surface (Figure 8A). Because of this expansion, the hyomandibular is one of the most diagnostic of all the cranial elements. Among the *Salvelinus* investigated, the lake trout, *Salvelinus namaycush,* has a similar hyomandibular.

TABLE 6. Frequency Distribution of Pyloric Caeca in *Salvelinus confluentus* and *Salvelinus malma*.

Drainage basin	*N*	*Number of pyloric caeca* *19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*30*	*31*	*32*	*33*	*34*	*35*	*36*	*37*	*Mean*	*S.D.*
									Salvelinus confluentus													
McCloud River, California	6				1		1	2	1		1										25.00	1.82
Klamath Basin	1				1																22.00	0.00
Columbia Basin, Snake River	9				1	1	1	1		2	1						2				27.11	4.12
Columbia Basin, Fraser River, Puget Sound	20				1	1		1	2	2	2	2	7	1				1			28.30	2.88
Skeena Basin	7							1			1	1	1	1				2			30.43	3.37
Taku Basin	5					1		1	1	1	1										25.80	1.72
Yukon Basin	6							1	1		1	1	1				1				28.67	2.92
MacKenzie Basin	24			1		1		2	5	4	4	1	3	1	2						27.42	2.59
Saskatchewan Basin	12				1			3		1	2					2	2		1		29.17	4.41
TOTAL	90			1	5	4	2	12	10	10	13	5	12	3	2	2	5	3	1		27.82	3.44
									Salvelinus malma													
Soleduck River, Washington	11	3		3	1			3	1												22.09	2.57
Puget Sound, Skagit River	8			1	1					2	1	1	1	1							26.88	3.37
Skeena River Basin	1											1									29.00	0.00
Coastal British Columbia	12			1				3	3	1	1	1		2							26.67	2.68
Taku River	7						1		1	3	1						1				27.57	2.87
Gulf of Alaska, Coastal Drainages and Islands	28					1	2	4	4	2	5	2	3	1	2	1	1				27.82	2.91
Aleutians	11			1	2		2	1	2	1	1					1					25.27	3.22
TOTAL	78	3		6	4	1	5	11	11	9	9	5	4	4	2	2	2				26.04	4.56

TABLE 7. Frequency Distribution of Vertebrae in *Salvelinus confluentus* and *Salvelinus malma.*

Drainage basin	*N*	*Number of vertebrae*													*Mean*	*S.D.*
		58	*59*	*60*	*61*	*62*	*63*	*64*	*65*	*66*	*67*	*68*	*69*	*70*		
Salvelinus confluentus																
McCloud River, California	4					1	2	1							63.00	0.70
Klamath Basin, Oregon	8							2	4	2					65.00	0.50
Columbia Basin, Snake River	10							2	4	4					65.17	0.70
Columbia Basin, Fraser River, Puget Sound	17						1	5	9	2					64.70	0.56
Skeena Basin	11							3	5	2	1				65.09	0.83
Taku Basin	5								5						65.00	0.00
Yukon Basin	7								3	4					65.67	0.49
MacKenzie Basin	25						1	9	14	1					64.60	0.63
Saskatchewan Basin	12							4	7	1					64.18	0.84
TOTAL	99					1	4	26	51	16	1				64.82	0.82
Salvelinus malma																
Soleduck River, Washington	11				4	4	3								61.91	0.79
Puget Sound, Skagit River	2						1	1							63.50	0.50
Skeena River Basin	3				1	1	1								62.00	0.81
Coastal British Columbia	14				2	6	3	2	1						62.57	1.11
Taku River	4					1	1	2							63.25	0.82
Gulf of Alaska, Coastal Drainages and Islands	28					5	8	11	2	2					63.57	1.19
Aleutians	16			1	3	2	3	4	2	1					63.00	1.66
TOTAL	78			1	10	19	20	20	5	3					62.96	1.31

TABLE 8. Frequency Distribution of Gill Rakers in *Salvelinus confluentus* and *Salvelinus malma*. Number of gill rakers

Drainage basin	*N*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*Mean*	*S.D.*
Salvelinus confluentus																
McCloud River, California	12				4	6	2								16.83	0.68
Klamath Basin, Oregon	7				2	1	2	2							17.57	1.17
Columbia Basin, Snake River	12		1	1	3	5	2								16.50	1.11
Columbia Basin, Fraser River, Puget Sound	28		1	3	13	6	3	1	1						16.50	1.23
Skeena Basin	10		1	2	4	3									15.90	0.94
Taku Basin	5					1	3	1							18.00	0.63
Yukon Basin	7		1		3	2	1								16.28	1.16
MacKenzie Basin	26			2	10	8	4	1	1						16.81	1.14
Saskatchewan Basin	13		1	2	4	4	2								16.31	1.14
TOTAL	120		5	10	43	36	19	5	2						16.64	1.19
Salvelinus malma																
McCloud River, California	1						1								18.00	0.00
Soleduck River, Washington	11				1	5	4	1							17.45	0.78
Puget Sound, Skagit River	7				1	1	4	1							17.71	0.88
Skeena River Basin	3						2		1						18.87	0.94
Coastal British Columbia	15			1	1	3	5	3	1	1					18.00	1.46
Taku River	7				1		3	1	1	1					18.57	1.50
Gulf of Alaska, Coastal Drainages and Islands	30				1	4	7	10	3	4					18.90	1.57
Aleutians	13		2	3	3	1	1	2	1						16.46	1.91
TOTAL	87		2	4	8	14	27	18	7	6		1			18.08	1.58

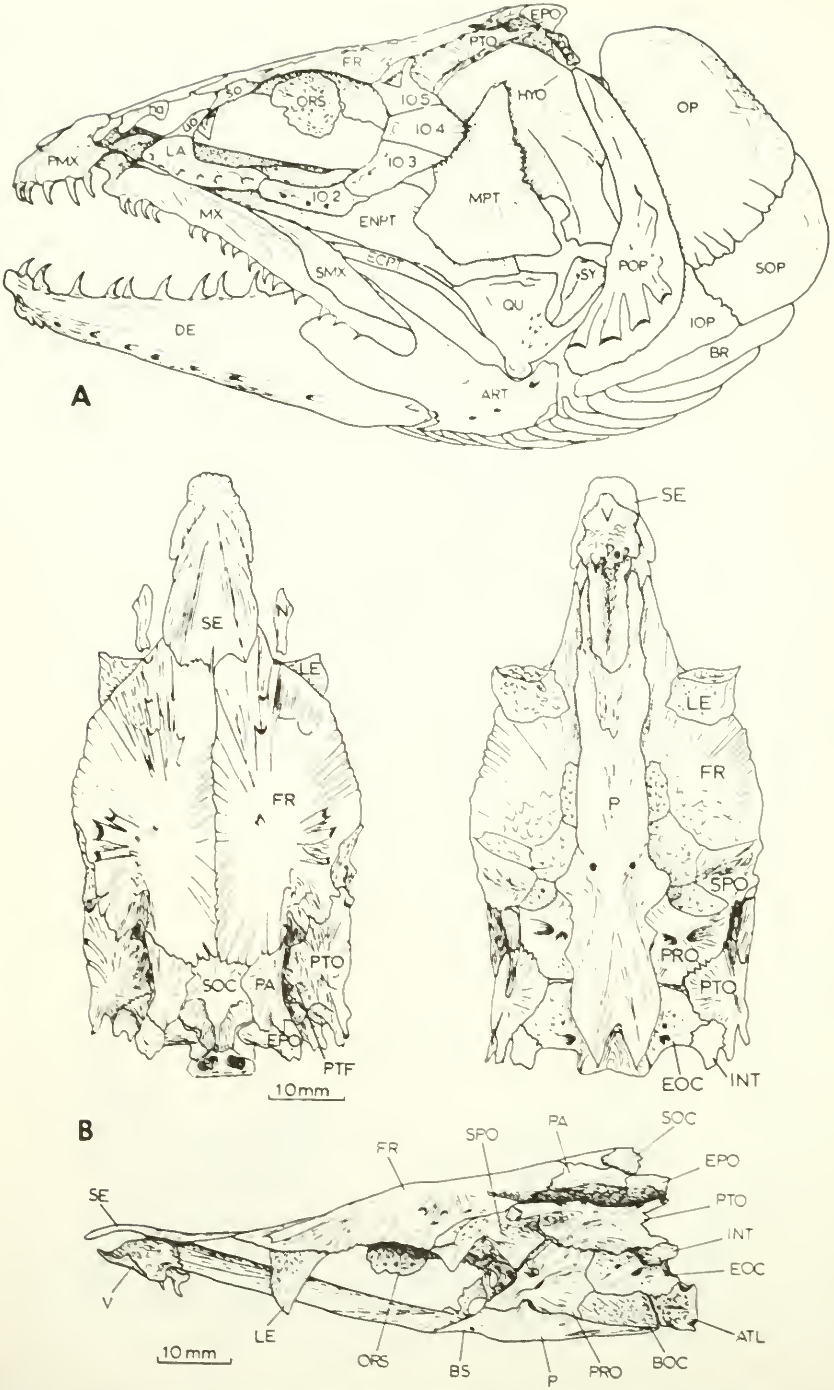

FIGURE 7. (A) Osteocranium of *Salvelinus confluentus*, UMMZ 172458, head length 112 mm, Flathead L., Montana; (B) neurocranium of same individual in dorsal, ventral, and lateral views.

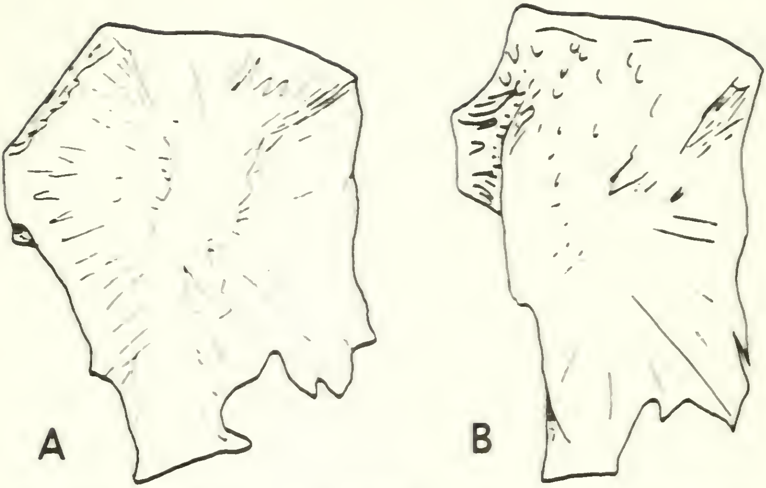

FIGURE 8. Right hyomandibular from (A) *Salvelinus confluentus*, UMMZ 188857, 130 mm, trib. Clearwater R., Montana; (B) *Salvelinus malma*, UMMZ 93829, 140 mm, Soleduck R., Washington.

The opercle is deep and relatively narrow. Its anterior and posterior edges converge slightly toward the top of the bone and the dorsal margin is rounded. The posterior margin is characteristically crenulated in the adult. Similar crenulations are often found on the posterior margin of the subopercle. The laminar parts of the preopercle especially the vertical limb, are weakly developed; thus, this bone has a rather slender, sickle shape. Often an emargination can be found on the lower posterior border of the preopercle. This may also occur in *S. malma*.

The frontal bones are without much ornamentation and with scarcely an elevation of the midline (Figure 7B). In *S. malma* the frontals are typically gabled as in a barn roof. The heavy covering of fatty tissue over the frontals in *S. malma* has given rise to many ridges, pits, and cavities, as well as causing the pores of the supraorbital canal to be elevated in bony tubes above the surface.

As with the hyomandibular, the supraethmoid is also highly diagnostic for the bull trout (Figure 9). Instead of being sharply divided into two parts (head and posterior extension) by a pronounced constriction, as in *S. malma*, the lateral margins of the bone are nearly parallel posteriorly and then taper gradually toward the anterior end. The head of the bone is marked by just a slight lateral expansion about halfway along the lateral margin. Both the head and posterior extension of the supraethmoid in *S. confluentus* are more elongated than in *S. malma* and in this respect they approach the condition in *S. namaycush*. The anterior margins of the ascending processes of the premaxillae attach along the supraethmoid head and are correspondingly lengthened in *S. confluentus*. Again, this is a character also found in the lake trout.

The neurocranium is depressed in comparison to that of other *Salvelinus*, with the parasphenoid only slightly flexed (Figure 7B). *S. malma* possesses a well-

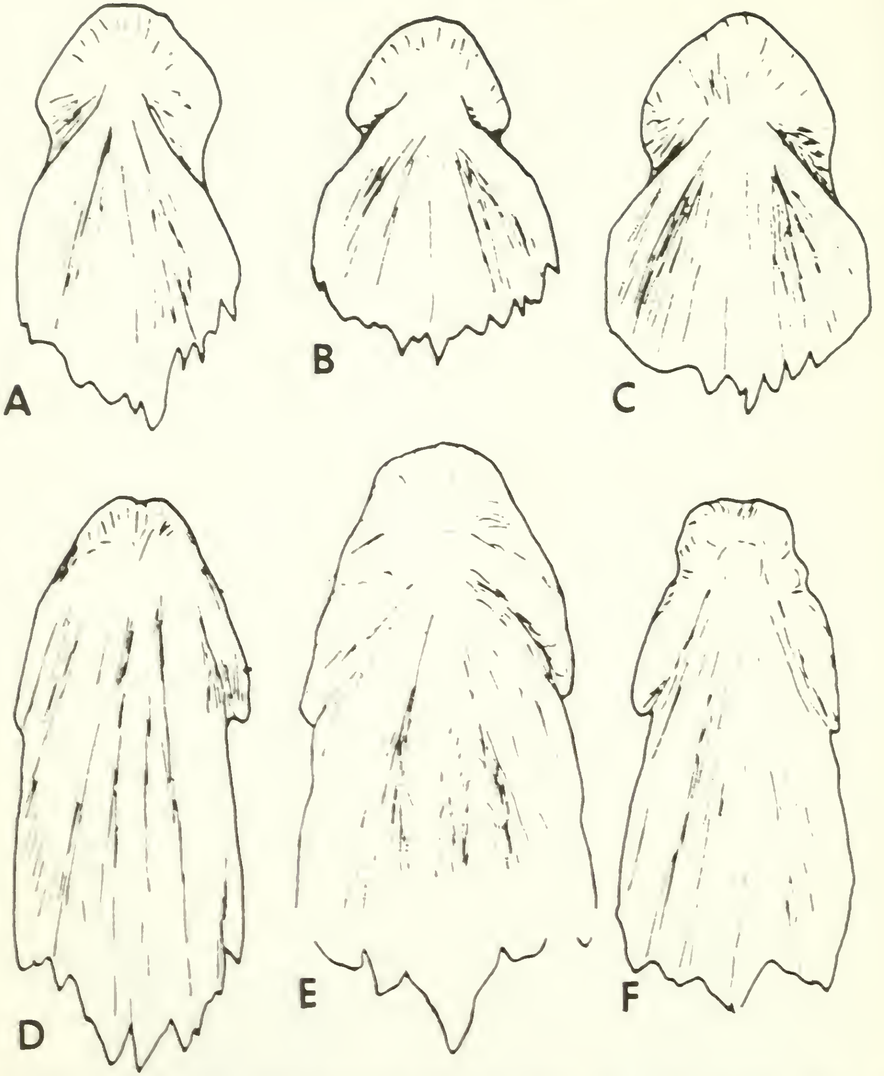

FIGURE 9. Comparison of supraethmoids in *Salvelinus malma* (A–C) and *Salvelinus confluentus* (D–F); not drawn to same scale: (A) UMMZ 126507, 286 mm, female, Karluk R., Kodiak I., Alaska; (B) UMMZ 106259, 383 mm, female, Unalaska I., Alaska; (C) UMMZ 106259, 485 mm, female, Unalaska I., Alaska; (D) UMMZ 159333, 227 mm, male, Morrison L., Brit. Col.; (E) UMMZ 172458, est. 490 mm, Flathead L., Montana; (F) UMMZ 172458, est. 420 mm, Flathead L., Montana.

developed flexure in the parasphenoid which is consistent with its deeper neurocranium. The lateral profile of the neurocranium showing these characteristics can usually be seen in radiographs taken with the specimens lying flat on their sides.

When observing the palate in *S. confluentus,* this species, like *S. malma* (Morton and Miller 1954), does not show a well-developed toothed platform on the vomer. The form of vomerine teeth usually is a shallow "V." Sometimes these teeth are arranged in a single transverse row. There is always a well-developed gap between the palatine and vomerine tooth rows. This is a consistent feature of *S. confluentus* whereas in *S. malma* it is variable.

HYBRIDS

Two of nine specimens of bull trout (UMMZ 188852) taken from Long Creek, Lake Co., Oregon, in the upper Klamath basin were identified by me as hybrids with brook trout, *Salvelinus fontinalis* (Figure 10). The hybrids had much darker pigmentation over the head, body, and fins than the other seven specimens, the dorsal fins were mottled, and the lower fins were tricolored. Light spots on the flanks were uniformly smaller than those on the flanks of the bull trout. The maxillary bones of the upper jaw were long and straight, a characteristic of the brook trout. Vertebral counts for the hybrids were intermediate (both with 62), whereas the Long Creek bull trout ranged from 64 to 66, with a mean of 65. According to Vladykov (1954), brook trout have 58 to 62 vertebrae with a mean of 59.5. The branchiostegal ray count was high, 13 and 14 on the left side, like that of the bull trout, whereas brook trout usually have 11 on the left side (Vladykov 1954). All of the Long Creek specimens, including the two hybrids, possessed basibranchial teeth.

Hybridization between the bull trout and the brook trout has also been mentioned by Paetz and Nelson (1970) to occur in the Clearwater River drainage of Alberta.

Two possible hybrids between *S. malma* and *S. confluentus* were identified from lakes in the Skeena River basin, British Columbia. The first individual (UMMZ 159328, 203 mm, female) was taken from Swan Lake. It resembles *S. confluentus* in the number of branchiostegals (27), and vertebrae (66) but is more like *S. malma* in number of gill rakers (20) and mandibular pores (13). Gill raker charateristics are intermediate between *S. malma* and *S. confluentus*. In head form and maxillary shape, the hybrid also resembles *S. malma*. The second specimen (UMMZ 159333, 188 mm, female) from Morrison Lake is very similar in appearance to the Swan Lake individual, especially in its head morphology. It has 24 branchiostegals, 67 vertebrae, 20 gill rakers, and 15 mandibular pores. Like the first specimen, the gill rakers are also intermediate in shape and structure between those of *S. malma* and those of *S. confluentus*.

DISTRIBUTION

Salvelinus confluentus is distributed in a north-south belt along the Rocky Mountain and Cascade ranges of northwestern North America (Figure 1). The area stretches from lat 41° N to lat 60° N or slightly beyond. Localities plotted are about equally distributed on both sides of the Continental Divide between lat 50° and 60° N. Major river drainages involved in the distribution pattern on the Pacific slope are: The McCloud in the upper Sacramento River basin of California; the upper Klamath in Oregon; the Snake in Oregon, Idaho, and Nevada; the Columbia River throughout its length; the Pend Oreille; the Clark Fork of Idaho and Montana, including the Flathead; the Kootenay River of British Columbia; the Fraser River of British Columbia, plus Puget Sound in Washington and the Skeena and Taku rivers of British Columbia. In the Bering Sea drainage they are found in the headwaters of the Yukon at the boundary between British

FIGURE 10. Two hybrid *Salvelinus confluentus* × *S. fontinalis* (below) compared with two *S. confluentus* (above); all from same catch by W. Seegrist, Long Cr., Lake Co., Oregon. *Photograph by the author.*

Columbia and the Yukon Territory. No specimens were examined from the Nass, Stikine, or Alsek drainages of the Pacific slope of Canada. McPhail's (1961) data indicate bull trout are in Bowser Lake of the Nass drainage.

On the east side of the Continental Divide, *S. confluentus* is found in the headwaters of the South and North Saskatchewan rivers of the Hudson Bay drainage in Alberta and in headwater areas of the Athabaska, Peace, and Liard rivers of the MacKenzie system in Alberta and British Columbia, the latter draining to the Arctic Ocean.

The distributional pattern of *S. confluentus* is largely the result of headwater migration and drainage crossover by stream capture. In the northern half of its range this has occurred following the retreat of the last continental ice sheet. Stream capture of the upper Columbia tributaries by those of the Saskatchewan enabled the bull trout to cross to the east side of the Continental Divide along with *Salmo clarki* and *Prosopium williamsoni.* Lindsey (1964) has explained transfer of fishes from the upper Fraser to the Peace River by a drainage block at the time the continental ice sheet was retreating from northern British Columbia. It is possible that *S. confluentus* entered the Taku River by means of migration along the coastal waters, but other species entered the Taku from the east through the Liard tributaries or from the Liard via the Yukon headwaters without any coastal connections (McPhail and Lindsey 1970). *S. confluentus* is known from collections prior to 1900 to have entered coastal waters in Puget Sound, Washington.

Because the bull trout is so generally distributed throughout the Columbia River basin and because this basin borders others where the bull trout is found, it is likely that this species originated there. Transfer to drainage basins in the southern part of its range, such as the Klamath and Sacramento, may have occurred during or following the last glaciation, but it is possible this distribution follows an older pattern, as suggested by the isolated occurrence of *S. confluentus* in the upper reaches of the Sacramento, Klamath, and Snake rivers. However, according to R. Behnke (Colorado State Univ., pers. commun.) the occurrence of *S. confluentus* in the Snake River drainage above Shoshone Falls (Hubbs and Miller 1948) is most likely the result of headwater transfer from the Salmon River drainage.

The distribution of the bull trout corresponds in many ways to that of the mountain whitefish, *Prosopium williamsoni.* The latter species differs in having reached the headwaters of the Missouri drainage in northwestern Wyoming and western Montana. It also has crossed into the Bonneville and Lahontan basins. The mountain whitefish is not known from the headwater tributaries of the Yukon drainage where the bull trout is present (Scott and Crossman 1973).

There is a possibility that *S. confluentus* was present at an earlier time in the Bear River of the Bonneville basin. Rostlund (1951) indicates a species of *Salvelinus* was known in these waters before 1850. If this is true, it may also have entered the Lahontan basin, as did *Prosopium williamsoni,* but has since disappeared. The retreat of *S. confluentus* from the southern extremes of its range is occurring today as it probably has in the past. The gradual change in climate since Late Pleistocene with subsequent loss of water once supplied from mountain glaciers and snowfields has been a major factor in eliminating habitats where the bull trout can survive. Once a prominent species in the McCloud River of the Sacramento system in California, the bull trout has gradually declined since the late 1800's and is now close to extirpation. Modifications of the river by man may have accelerated the rate of decline.

Since Livingston Stone first called attention to the bull trout of the McCloud River in 1872, very few specimens from the McCloud have been deposited in museums. Fifteen are known to me, including one probably taken on Stone's initial tour of the McCloud. The old USNM specimens were originally preserved in alcohol without fixation in formalin; several are in such a poor state of preservation that they cannot be removed from their glass container. Two specimens (USNM 15549) labeled Wye-dai-deek-it, the original Indian name for the bull trout in the McCloud Valley, were collected by Stone in 1874. Seven (including one skeleton) were sent by Stone to the USNM between 1875 and 1881. Five specimens were taken singly between 1938–1975; one came from the Mt. Shasta Hatchery at Mt. Shasta in 1956; three small individuals, taken on hook and line between 1938 and 1950, are housed in the California Academy of Sciences; a larger adult taken on hook and line July 19, 1975, is in the collection of the California Department of Fish and Game (CDFG 0513). The exact locations of capture of Stone's bull trout are not known, although they were probably taken in the vicinity of the trout hatchery on Green's Creek (Wales 1939) where set lines were placed to catch rainbow trout.

Wales (1939) presented testimony that the bull trout formerly occurred in the upper Sacramento River in the vicinity of Dunsmuir, Siskiyou Co., and in the Pit River near the mouth of Squaw Creek, Shasta Co. Jordan (1907) listed upper Soda Springs on the Sacramento River as a locality, but Evermann and Bryant (1919) stated the McCloud River is the only stream in California in which the bull trout is known to be native.

Campbell (1882) reported bull trout occurred in the McCloud River from its mouth upstream to Big Springs. Big Springs is a source of melt water from snowfields on Mt. Shasta, which yields a nearly constant flow of 7 C (45 F) water (Wales 1939). Although Campbell had fished the entire McCloud River, he never took bull trout above Lower Falls (3.2 km above Big Springs) where he reported water temperatures from 15.5 C to 21 C (60 F to 70 F). Downstream at the fish hatchery on Greens Creek (now inundated by Lake Shasta), Campbell reported water temperatures of 13 C to 15.5 C (55 F to 60 F) at midday in the hottest weather, and from the hatchery up to the Big Springs the river got "one degree colder about every 10 to 12 miles for the distance of 65 or 70 miles."

The early records from Oregon and Washington indicate the bull trout was once more widely distributed on the Pacific side of the Cascade and Coast ranges than it appears to be today. Specimens taken from Puget Sound by Jordan and others in the 1880's are assignable to either *S. confluentus* or *S. malma*. The head of Suckley's (1858) type of *Salmo confluentus* is a bull trout taken from a Coast Range drainage (Pullayup River) that empties into Puget Sound. Cope (1879) reported one of the earliest records for *Salvelinus confluentus* from the Klamath basin; this is the only previously published record based on an actual specimen from that basin. The earliest confirmed record for *S. confluentus* is the specimen collected in 1854 from The Dalles on the lower Columbia River. In contrast, this species was not collected from the Snake River drainage of Nevada until much later (Miller and Morton 1952).

DISCUSSION

I have attempted to provide evidence for the separation of *S. confluentus* from *S. malma*, particularly in that part of the range of *S. malma* southward from southern Alaska on the eastern side of the Pacific basin in North America. The systematics of *S. malma* throughout its range, including Alaska and the North Pacific basin, is lengthy and complicated and will be treated elsewhere.

There are valid reasons for considering the bull trout a full biological species: 1) The character states investigated which separate *S. confluentus* from *S. malma* are constant throughout a broad geographical area occupied by *S. confluentus*. 2) Stability is further indicated by the fact that variation of all characters investigated is minimal when compared to other recognized species of *Salvelinus*. 3) Even though the ranges of *S. malma* and *S. confluentus* overlap in the Pacific slope drainages from northern California to southern Alaska, there is no evidence of introgression in the material studied.

Sympatry

Sympatry of *S. malma* and *S. confluentus* occurs in the Puget Sound of Washington, the Skeena Basin of British Columbia, and the Taku Basin of southern Alaska and northern British Columbia. Information available at this time on Livingston Stone's incompletely cataloged USNM specimens indicates that sympatry between *S. malma* and *S. confluentus* may also have occurred in the Sacramento basin of California. Both *S. malma* and *S. confluentus* were identified from the Yukon Basin; however, *S. malma* came from the Tanana drainage of central Alaska and *S. confluentus* from the extreme headwaters in British Columbia, Canada. A complete understanding of how *S. confluentus* and *S. malma* maintain sympatry will probably come from a study of these species in the Skeena Basin of British Columbia. Both appear to be disseminated throughout these waters, where considerable study of the "Dolly Varden" has already taken place.

In the Skeena drainage (Figure 1, insert), specimens of *S. confluentus* were studied from the following lakes: Lakelse, Damschilgwit (Cabin), Morrison, Morice, Slamgeesh, Bear, and Sustut. Specimens of *S. malma* came from Johanson and Alastair lakes. Two suspected hybrids came from Swan and Morrison lakes. Although the hybrids indicate both species probably occur in some lakes, it is possible that certain of the lakes may contain only one of the species pair. Larger samples from these lakes may be helpful in determining to what extent hybridization is taking place. In the Taku River, *S. malma* was taken 22 km (14 miles) upstream from the mouth at Canyon Island where Meehan and Siniff (1962) reported downstream migration of juvenile Dolly Varden in 1961. *S. confluentus* was taken further inland in Flannigan Slough, a small tributary to the Taku River. The Taku River collections suggest that *S. malma* and *S. confluentus* may be ecologically separated, with anadromous *S. malma* occupying most of the lower drainage, especially Twin Lakes, the lower main channel, and the river mouth, and *S. confluentus* restricted to certain small tributaries, such as Flannigan Slough and perhaps the headwaters.

Of nine specimens examined from Puget Sound, five were *S. malma* taken near Port Townsend, Washington in 1884. Labeling, as well as their silvery pigmentation, indicated they were sea run individuals. The other four specimens are *S. confluentus*. Two of these were taken by D. S. Jordan in 1880, and labeled "Puget Sound." The third was taken in Elliot Bay at Seattle in 1889 and the fourth was captured in a freshwater tributary to Puget Sound near Ft. Steilacoom in 1856. Jordan's specimens are two of ten sent to the United States National Museum and may have been collected during his work on the fishes of Puget Sound (Jordan and Starks 1895).

S. confluentus appears to be distributed throughout the MacKenzie basin in British Columbia and Alberta. Unfortunately, no material was available from the Nahanni River, part of the Liard drainage in the Northwest Territories, and only one specimen of *S. malma* was found in samples from the MacKenzie (USNM 147661).

McPhail (1961) demonstrated the existence of northern and southern forms of *S. malma* in North America. The northern form occurs in the coastal drainages of the Bering Sea north to Seward Peninsula. Specimens corresponding to the northern form have been examined for this study from the Yukon basin of central Alaska. These specimens also resemble the *S. malma*-like char described as

Salvelinus anaktuvukensis by Morrow (1973) from the north slope of the Brooks Range, Alaska. Data from these *Salvelinus* were not used in making comparisons with *S. confluentus*. McPhail (1961) stated that head size would not distinguish the form which Jordan, Evermann, and Clark (1930) called *Salvelinus malma spectabilis*. However, if McPhail's data (1961) on head size are reexamined in light of the present work, it can be seen that the samples shown to have the longest heads (Cottonwood River, Sage Creek, Glacier National Park, and probably also Bowser Lake in the Nass drainage) are from localities where *S. confluentus* is found. Except for the Taku River, where *S. confluentus* and *S. malma* may have been present in a mixed sample, the other samples represent *S. malma* and show an average smaller head size. Much of McPhail's material was reexamined for this study. The samples of *S. confluentus* from the Taku River drainage were found to be smaller-headed with respect to samples of *S. confluentus* from other localities, including the adjacent Yukon basin. Taku River basin *S. confluentus* live at the extreme end of the northern dispersal route. Transfer to this basin probably took place from the Liard via the Yukon headwaters or directly from the western reaches of the Liard.

Variability

At the end of the southern dispersal route in the Sacramento basin, the McCloud River *S. confluentus* possess the largest head size and are also distinguished in having a greater percentage of individuals (50% of those examined) lacking basibranchial teeth. Only one specimen outside of the McCloud River was found to lack basibranchial teeth. Jordan (1879) at one time recognized the McCloud River population as a separate species, (*Salvelinus bairdii*), on the basis of this character.

Two specimens collected sometime prior to 1877 are part of Livingston Stone's material sent to the USNM, most of which came from the McCloud River or Sacramento River drainage. Small head size identifies them as *S. malma*. In other characters, such as number of gill rakers, compressed body, straight maxilla and supraethmoid, they resemble *S. malma*. Silver pigment on their sides indicated they may have been anadromous individuals. In the shape of their gill rakers and head form they are not typical of *S. malma* but the deteriorated condition of these specimens prevented further study.

Of the coastal collections, *S. malma* from Puget Sound, Washington and the Soleduck River of Washington's Olympic Peninsula are geographically closest to the McCloud River specimens. Those taken from Puget Sound in the 1880's were anadromous and compared closely with *S. malma* from further north along the coast of British Columbia. The Soleduck River specimens represent a population isolated above a high falls. The largest individual measured 135 mm. They differed from anadromous *S. malma* in their larger heads and fewer vertebrae and gill rakers. It appears likely that prior to 1900, *S. malma* ranged south along the Pacific Coast to California and may have been fairly common in Washington's coastal waters of Puget Sound (Jordan and Starks 1895; Dymond 1942).

Specialization

Radiographs of 112 *S. confluentus* showed about 13% with whole fish in their stomachs. Sculpins predominated in the stomach contents, but at least two bull trout had eaten salmonids. Fewer *S. malma* had fish in their stomachs. Some *S.*

malma had eaten gastropods, a food also seen in the stomachs of three *S. confluentus.* One 380 mm *S. confluentus* examined from the Finlay River near Ft. Grahame, British Columbia (NMC 66-437), had swallowed a 215 mm individual of its own species. Two bull trout from northern British Columbia had eaten small mammals (one a shrew and the other an unidentified rodent).

Fish eating habits of the bull trout have been noted by Ricker (1941), Godfrey (1955), Jeppson and Platts (1959), Bjornn (1961), and Thompson and Tufts (1967). Armstrong and Morton (1969) summarized other food habit studies of the bull trout. Scott and Crossman (1973) have recently reviewed the food habits of the bull trout under their section on the Dolly Varden. According to Brown (1971), the principal food of the adult bull trout is fish, although it will utilize other vertebrates of suitable size, such as frogs, snakes, mice, and ducklings.

Characters of the jaws, teeth, and head of *S. confluentus* which differ from those of *S. malma* are best explained as adaptions to a piscivorous habit. The large area for jaw muscle insertion, large jaws and teeth, the curved maxilla, the elongate hyoid bar with numerous branchiostegal rays, the high number of mandibular sensory pores, and the elongated head of the supraethmoid for articulation of the extended premaxillary ascending processes, are features paralleled in the lake trout, *S. namaycush,* a species well-known for its piscivorous diet.

The direction of evolution in *S. confluentus* has been away from a diverse predator, such as anadromous *S. malma* toward a more specialized fish-eating mode of existence entirely in fresh water. The changes in the head and component bones are the easiest to document, but there are probably marked behavioral and ecological differences between *S. confluentus* and *S. malma* that have not yet been studied. Most of the similarities pointed out above between the bull trout and the lake trout are considered as parallel developments and are not considered to be evidence of a close phyletic relationship.

SUMMARY AND CONCLUSIONS

The bull trout was first described as *Salmo spectabilis* in 1856 by Girard from a specimen collected at The Dalles, Oregon, on the lower Columbia River. Girard's specific name "spectabilis" does not stand because of the rules of zoological nomenclature pertaining to homonyms. The name *campbelli* was substituted by Suckley, who described the bull trout three more times under the names "*confluentus*", "*bairdii*", and "*parkei*." In 1882 Jordan and Gilbert included the above names except *confluentus* in the synonymy of *S. malma,* where they have remained to the present. With formal species recognition for the bull trout, its scientific name becomes *Salvelinus confluentus* (Suckley); the common name, Dolly Varden, applies to *Salvelinus malma* (Walbaum).

Evidence for specific distinction of the bull trout is found in a series of osteological, morphometric, and meristic characters that remain relatively constant throughout its distributional range including areas of sympatry with *S. malma.* The size and shape of the head and jaws, head length, the number of branchiostegal rays, and the morphology of the gill rakers are the easiest characters to use in separating the bull trout from *S. malma.* The shape of the supraethmoid bone is also highly diagnostic for the bull trout, but it must be exposed through removal of overlying tissue. The shape of the neurocranium and hyomandibular are also distinctive. Additional osteological characters are found in the maxilla, premaxilla, ceratohyal, opercle, and frontal bones.

The cranial structures in the bull trout that differ from those of the Dolly Varden are interpreted as modifications toward a more piscivorous existence in freshwater. The changes are genetic and have occurred through the long process of selection and adaption. By no means can they be construed as environmentally-induced somatic changes.

The life history of the bull trout differs significantly from that of the Dolly Varden in being almost completely nonanadromous throughout its known range. Ecological and behavioral differences between the two have not been studied in detail.

The bull trout is widely distributed in montane lake and stream habitats on both sides of the Continental Divide between lat 50° and 60° N. It appears to have an affinity for cold waters fed by mountain glaciers and snowfields. In the deglaciated part of its range in western Canada, the bull trout has dispersed from the Columbia River basin through headwater transfer and crossover following the retreat of the Cordilleran ice sheet in Late Wisconsin time. The distribution pattern to the south of the ice sheet may be older. Populations of bull trout in the Sacramento, Klamath, and southern Snake River drainages all show signs of depletion.

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REPRODUCTION AND SPAWNING OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, IN SAN PEDRO BAY, CALIFORNIA [1]

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The gonosomatic index (GSI) was computed for samples of adult northern anchovy collected from the Los Angeles-Long Beach Harbor live-bait fishery during 1973 and 1974. GSI values were highest in February and March of both years and declined to the lowest values in September. The abundance of anchovy eggs and larvae in plankton samples taken from San Pedro Bay during the same period was also highest in February and March and lowest during August and September.

Field and laboratory data suggest that within an environmental temperature range of 13 to 18 C (55 to 66 F), northern anchovy have the potential to breed all year, but are constrained to a seasonal reproductive cycle by dietary requirements that exceed available production of zooplankton.

INTRODUCTION

Environmental investigations of the Los Angeles-Long Beach Harbor and San Pedro Bay by the Allan Hancock Foundation, University of Southern California, recognized the northern anchovy, *Engraulis mordax* Girard, as a key species, both ecologically and economically, in southern California nearshore waters (Soule and Oguri 1972–1976). This understanding prompted a summary of the biology and fishery of *E. mordax* (Brewer 1975*a*) and a study on the thermal tolerance and resistance of the fish (Brewer 1976). This paper is an outgrowth of those studies. Data are given on the reproductive cycle and spawning of the anchovy in nearshore waters off southern California. The results are discussed in relation to environmental factors which may control anchovy spawning throughout the fish's geographic range.

The northern anchovy is probably the most abundant fish in the California Current (Mais 1974). A dramatic increase in anchovy biomass during the past decade (Smith 1972) has led to an intensive effort to understand the biology and population dynamics of this relatively unexploited resource (Calif. Dept. Fish and Game 1971).

Comprehensive data on the reproduction of commercial fishes is a prerequisite for intelligent fishery management. Understanding the environmental factors that influence spawning seasons and regulate fecundity in fishes is necessary if fishery stocks are to be predicted and exploited wisely. Such information on northern anchovy was, in part, detailed by Bolin (1936), Ahlstrom (1959, 1966, 1967), MacGregor (1968), Leong (1971), and Mais (1974). While Ahlstrom's studies have compiled an enormous data bank on the seasonal occurrence and distribution of anchovy spawning in offshore waters, California's bays, harbors, and estuaries have been neglected. In light of man's increasing alteration of shallow marine habitats for various industrial and recreational pursuits, it is essential to understand the role that these areas play as spawning and nursery grounds for fishes.

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MATERIALS AND METHODS

Samples of adult *E. mordax* were obtained from the Long Beach, California, live-bait fishery between February 1973 and September 1974. The anchovy live-bait fishery was described by Wood and Strachan (1970). Fish were measured to the nearest millimeter of standard length (SL) and weighed to the nearest 0.01 g after being lightly blotted. The left gonad of each fish, which is generally larger than the right, was excised, blotted lightly, and weighed to the nearest 0.01 g. The gonosomatic index (GSI) was computed for each individual according to the following formula: wet gonad weight/wet specimen weight $\times 10^4$. Variations of the GSI have been used for a number of species as a measure of reproductive maturity (Moser 1967; Khanna and Pant 1967; McInerney and Evans 1970; Haydock 1971; Kaya 1973). By following monthly changes in the weight of the testes and ovaries, as expressed by the GSI, reproductive maturation can be estimated without time-consuming histological examination of the gonads.

Bimonthly plankton collections for anchovy eggs and larvae were initiated in February 1973 at 15 stations in the outer Los Angeles-Long Beach Harbor. Later, more stations were added within the main channels of the inner harbor as well as adjacent areas outside the harbor. Eventually, 22 stations were monitored (Figure 1, Table 1). Each of the 561 plankton collections was standardized. Samples were taken with a 0.5-m (1.7-ft), 222μ mesh (nylon) conical net, towed at about 2 knots at a depth of 4 m (13 ft) (calculated by wire angle) for

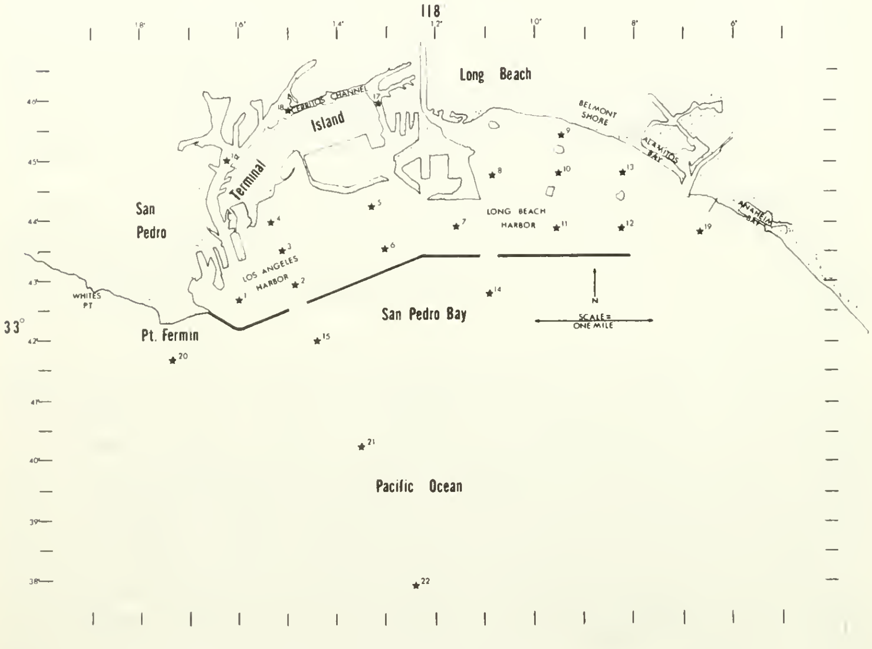

FIGURE 1. Los Angeles-Long Beach Harbor and San Pedro Bay with plankton tow station locations.

TABLE 1. Plankton Tow Station Data.

Station no.	*Bottom depth (m)*	*Inclusive trawl dates*
1	12	Feb. 1973–May 1974
2	12	Feb. 1973–Sept. 1974
3	9	Feb. 1973–Sept. 1974
4	6	Feb. 1973–Sept. 1974
5	11	Feb. 1973–May 1974
6	20	Feb. 1973–May 1974
7	16	Feb. 1973–May 1974
8	12	Feb. 1973–May 1974
9	7	Feb. 1973–May 1974
10	11	Feb. 1973–May 1974
11	16	Feb. 1973–May 1974
12	12	Feb. 1973–May 1974
13	7	Feb. 1973–May 1974
14	19	Feb. 1973–May 1974
15	19	Feb. 1973–May 1974
16	11	Apr. 1973–Aug. 1974
17	11	Nov. 1973–Aug. 1974
18	11	Jan. 1974–Aug. 1974
19	7	Mar. 1974–Aug. 1974
20	21	Mar. 1974–Aug. 1974
21	23	July 1974–Sept. 1974
22	36	July 1974–Sept. 1974

5 min. A calibrated rotometer, located inside the mouth of the net, was used to determine the volume of water filtered during 40 of the standardized tows. The mean volume of water strained was calculated to be 50.5 m^3 per tow (range, 43–57; standard deviation, 5.1; standard error of mean, 0.8). All samples were taken during daylight hours, with the exception of one complete series. Samples were preserved in 5% formalin solution and later sorted with the aid of a dissecting microscope. Large samples were aliquoted with a Folsom Splitter.

RESULTS

Standard lengths, weights, and gonosomatic indices were computed for 359 female and 280 male *E. mordax* sampled during 1973 and 1974. The female-male ratio of 1.28:1 is close to the estimate by Clark and Phillips (1952) for the 1947–1951 live-bait fishery (1.2:1), and the statewide estimate of 1.27:1 given by Miller et al. (1955). However, Klingbeil (1977) suggests spatial and temporal segregation of the sexes in anchovies which may lead to sampling bias when specimens are obtained from commercial or bait fishermen's nets.

The highest individual GSI values (male, 524; female, 751) and the highest mean GSI values occurred in February and March of both years and gradually declined to the lowest values in September (Figure 2). A very rapid increase in the GSI values occurred between January and February. Although fish with seemingly ripe gonads (large, yolked eggs plainly visible in ovaries; testes enlarged and cream-colored) were found throughout the year, the proportion of fish with ripe gonads was highest in February and lowest in late summer. Female anchovies as small as 81 mm (3.2 inches) SL were found with well developed ova, and males as small as 78 mm (3.1 inches) SL were found with enlarged testes. Anchovies within this size range are probably 1 year old (Collins 1969).

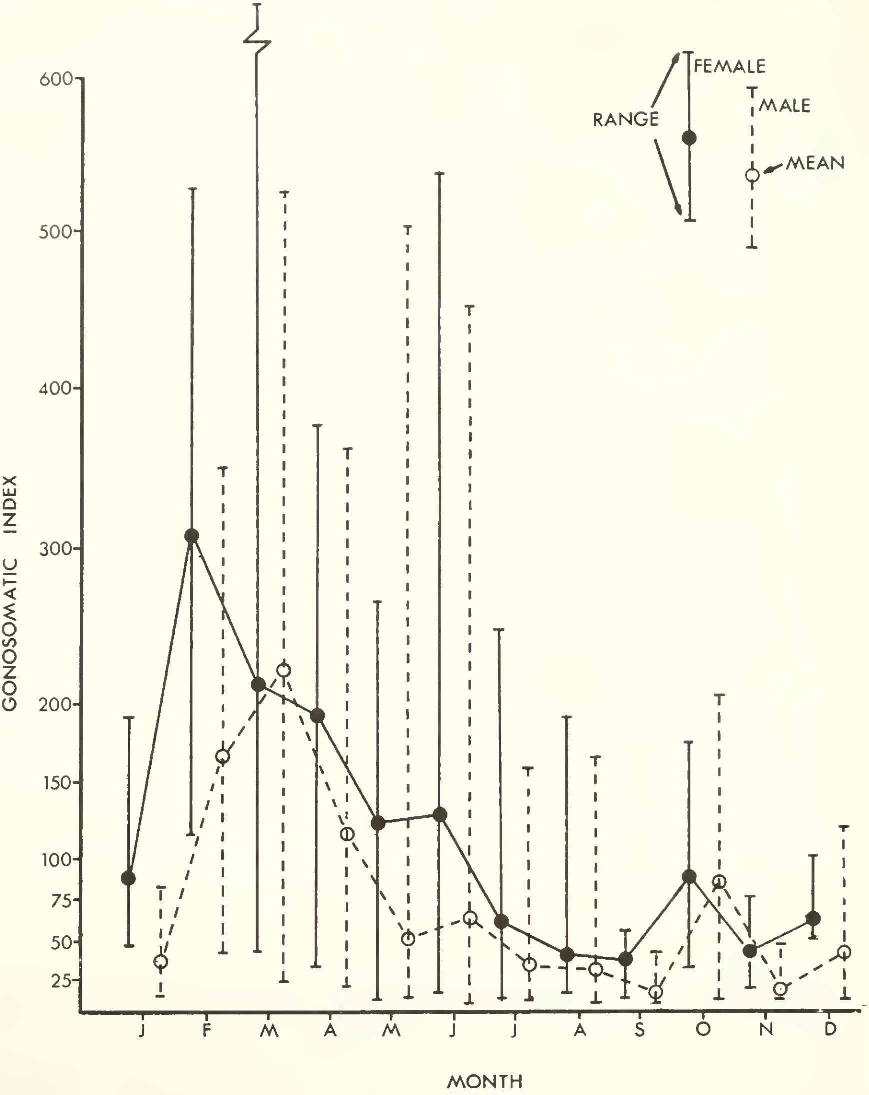

FIGURE 2. Gonosomatic indices for *Engraulis mordax* sampled from the Los Angeles-Long Beach Harbor live-bait fishery (original data in Brewer 1975*b*).

Although spawning was recorded in every month, eggs and larvae occurred most frequently and were most numerous in February and March when 61.5% of all eggs and 68.6% of all larvae were taken (Tables 2 and 3; Figure 3). Tows made during the period between February and May captured 80% of all eggs and 81.4% of all larvae. This same period included 50.5% of all trawls taken. The greatest number of anchovy eggs taken during one trawl was 1720 (May 1974, station 20), equivalent to 34,059 eggs per 1000 m^3 of water filtered. The greatest number of larvae taken during one trawl was 812 (March 1974, station 14), or 16,079 larvae per 1000 m^3 of water filtered. During the entire 20-month towing period, San Pedro Bay yielded 536 eggs and 128 larvae per 1000 m^3 of water filtered.

TABLE 2. Eggs and Larvae of *Engraulis mordax* taken in Los Angeles-Long Beach Harbor and San Pedro Bay, California, February 1973–September 1974, Summarized by Month.

Month	*No. of tows*	*No. of occurrences* *Eggs*	*Larvae*	*No. of specimens* *Eggs*	*Larvae*	*Mean No. per 1000 m^3* *Eggs*	*Larvae*
January	36	2	2	4	2	2	1
February	51	31	24	4054	1098	1574	426
March	68	60	60	5189	1471	1511	428
April	72	42	37	863	377	237	104
May	92	45	35	3214	258	692	56
June	30	1	0	1	0	1	0
July	37	13	5	326	15	174	8
August	37	11	6	980	151	524	81
September	38	18	12	403	22	210	11
October	32	12	1	20	1	12	1
November	34	6	23	129	155	75	90
December	34	5	16	7	68	4	40
TOTALS	561	246	221	15190	3618		

TABLE 3. Eggs and Larvae of *Engraulis mordax* taken in Los Angeles-Long Beach Harbor and San Pedro Bay, California, February 1973–September 1974, Summarized by Station.

Station	*No. of tows*	*No. of occurrences* *Eggs*	*Larvae*	*No. of specimens* *Eggs*	*Larvae*	*Mean No. per 1000 m^3* *Eggs*	*Larvae*
1	32	10	12	128	79	79	49
2	35	18	16	466	209	264	118
3	35	14	14	434	229	246	130
4	35	14	10	361	122	204	69
5	32	15	9	267	105	165	65
6	31	15	13	370	175	236	112
7	32	10	14	272	62	168	38
8	32	10	10	736	70	455	43
9	31	10	14	247	105	153	65
10	32	15	14	192	127	119	79
11	32	13	14	417	98	258	61
12	32	19	19	1246	293	771	181
13	32	14	14	846	153	523	95
14	30	20	20	2927	930	1932	614
15	35	19	19	3101	614	1754	347
16	29	5	5	8	11	5	8
17	15	5	8	42	22	55	29
18	11	4	4	7	10	13	18
19	6	5	4	94	23	310	76
20	6	5	5	2195	130	7244	429
21	3	3	2	348	29	2297	191
22	3	3	2	486	22	3208	145
TOTALS	561	246	221	15190	3618		

Some of the increase in the number of eggs spawned during the summer months resulted from increased effort during July, August, and September 1974, with the initiation of off-shore stations 21 and 22 (Figure 1). Some 49% of all eggs collected during the summer months of 1973 and 1974 were taken from a

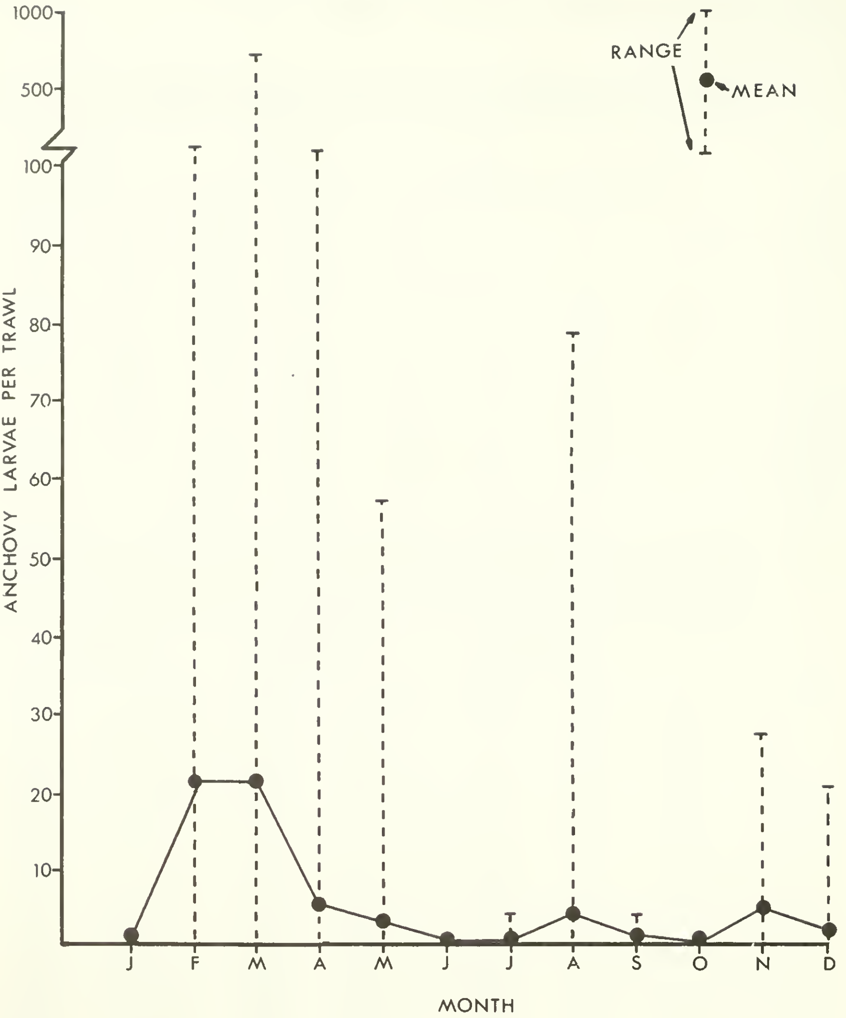

FIGURE 3. *Engraulis mordax* larval abundance in Los Angeles-Long Beach Harbor and San Pedro Bay based on number of larvae captured per tow per month.

total of only six trawls at stations 21 and 22. Mature, reproducing fish may move to deeper waters offshore to escape warm waters nearshore.

DISCUSSION

Data on seasonal occurrence and distribution of *E. mordax* larvae from a large area influenced by the California Current is available. According to Ahlstrom (1967), the northern and southern extent of anchovy spawning fluctuates from year to year in response to varying oceanic conditions and no average distribution of abundance of larvae could be found. However, the spawning distribution is closely tied to water temperatures. During California's "warm water years" in 1957, 1959, and 1964 (Jones 1971), Ahlstrom (1966) recorded a northward shift in anchovy spawning off California. Similarly, during 1956, an abnormally cold year for waters off California, an unusually high number of anchovy larvae were captured off southern Baja California. While anchovy eggs have been taken in water temperatures (at 10-m depth) ranging from 9.9 to 23.3 C (50 to 74 F), over 90% were taken in water 13.0 to 17.5 C (55 to 64 F) (Ahlstrom 1956). Ninety-six percent of all larvae captured during the period 1951 to 1964 were taken between Point Conception, California, and Magdalena Bay, Baja California, with the highest yields between January and May and the lowest yields between August and October (Ahlstrom 1967). Water temperatures (at 10-m depth) between Point Conception and Magdalena Bay from January through May range between 12 and 18 C (54 and 66 F). Maximum temperatures in the same area occur in the months of August, September, and October (Lynn 1967).

Within restrictive temperature limits, other subtle environmental factors control reproduction of *E. mordax*. In San Pedro Bay, surface water temperatures are generally between 13 and 18 C (55 to 66 F) throughout the year (Soule and Oguri 1972–1976); nevertheless, most spawning occurs in the late winter and early spring.

Day length influences gonad maturation in some fishes. Wiebe (1968) found that spermatogenesis would proceed in *Cymatogaster* (Embiotocidae) in cold water (10 C) if day lengths were long; high temperatures (20 C) and short photoperiods inhibited gonad maturation, while high temperatures and long photoperiods hastened gonad maturation. Kaya (1973) observed that ". . . long and increasing photoperiods and elevated temperatures of spring . . ." induced rapid gametogenesis in *Lepomis* (Centrarchidae). At first sight, anchovy reproduction off southern California seems to fall within a similar pattern of regulation, with intensive spawning occurring when water temperatures and day lengths are increasing. However, other data discount the importance of photoperiod or changing water temperatures as stimuli for reproduction.

Richardson (1973) has shown that spawning of *E. mordax* is delayed off Oregon until June, July, and August when water temperatures are above 14 C (57 F). Day lengths are maximum in June and are decreasing in July and August.

Leong (1971) maintained a spawning stock of *E. mordax* at the La Jolla Fisheries-Oceanography Center throughout the year, under laboratory conditions, which included a short day length (4 hr) and constant temperatures of 15 C (59 F). Adult anchovy held at temperatures between 12 and 18 C (54 and 64 F) in the laboratory by Brewer (1975*b*) developed and maintained relatively high GSI values regardless of the photoperiod. GSI values for acclimated laboratory fish were higher than those sampled from nature at the same time during the summer and fall when the laboratory fish were maintained under photoperiods of 8, 12, or 16 hr of light.

Indirect evidence suggests that the seasonal reproductive cycle of the anchovy may be imposed by limited availability of food.

Gametogenesis requires the storage of large amounts of lipids and proteins in the gonads. The caloric requirements of reproductive fish must be substantially above maintenance levels; these levels may not be available to the anchovy throughout the year (Leong and O'Connell 1969). Clemens and Reed (1967) and de Vlaming (1971) have induced gonadal regression in *Carassius* (Cyprinodontidae) and *Gillichthys* (Gobiidae), respectively, by food deprivation. Scott (1961) found that insufficient diet caused reduction in fecundity in *Salmo* (Salmonidae). On the other hand, well fed northern anchovy in the laboratory maintain high GSI values throughout the year (Leong 1971; Brewer 1975*b*).

Data on zooplankton densities lend support to these speculations concerning limited food availability. Surface zooplankton densities from San Pedro Bay were recorded each month in 1972 (Harbors Environmental Projects 1975 and unpublished data). Assuming that station 15 (Figure 1) is representative of San Pedro Bay waters and the dominant zooplankter *Acartia tonsa*, which comprise 57.9% of all zooplankters is representative of the adult anchovy's food (Loukashkin 1970), trends in food availability coincide with the relative abundance of anchovy larvae (Table 4). Interestingly, 81.5% of all anchovy larvae were captured in the first 5 months of the year and 82.1% of all *Acartia* were captured during the same monthly period. Quarterly surveys of zooplankton in 1973 and 1974 by the Harbors Environmental Projects show similar trends in zooplankton abundance.

TABLE 4. Abundance of *Acartia tonsa* in Relation to Abundance of Anchovy Larvae and Mean GSI Values in San Pedro Bay.

Month	*Percentage of Acartia captured*	*Percentage of larvae captured*	*Mean GSI values*	
			female	*male*
January	46.7	0.0	84	33
February	21.4	30.4	308	167
March	4.4	40.7	210	218
April	1.4	10.4	189	116
May	8.2	7.1	124	54
June	2.3	0.0	127	64
July	2.4	0.4	61	34
August	0.5	4.2	44	29
September	0.9	0.6	42	16
October	2.3	0.0	86	80
November	7.6	4.3	43	18
December	1.5	1.9	62	47

E. mordax may have the potential to breed all year, but is constrained to a seasonal reproductive cycle by high and low temperatures (e.g., above 18 C and below 13 C). Within this temperature-regulated cycle, the maximum expression of the anchovy's fecundity may be limited by nutritional requirements that outweigh the available environmental production.

This view holds that the number of spawnings per year and the number of eggs spawned are variable. Within the geographical range of anchovy spawning, multiple spawnings are possible only as long as temperatures are not restrictive, and the number of eggs spawned is maximal only if the fish's diet is not limiting.

Data on larval abundance in San Pedro Bay (Table 4) where temperatures generally are not limiting suggest a trimodal abundance of larvae (i.e., three unequal batches of eggs spawned annually). Low GSI values and repeat spawnings during the second half of the year correspond to a period of low zooplankton densities. Low zooplankton availability, combined with increased water temperatures (and hence, increased metabolic requirements) during August, September, and October, may not allow the increase in gonad weights necessary for heavy spawning. The resorption of ovarian eggs noted by MacGregor (1968) may be a manifestation of the anchovy's inability to obtain an adequate diet during part of the year. Careful temperature and photoperiod controlled laboratory experiments on anchovy fed various rations could resolve these suppositions.

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HOOKING MORTALITY OF JUVENILE LARGEMOUTH BASS, *MICROPTERUS SALMOIDES*[1]

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Mortalities of juvenile largemouth bass due to hooking were studied as part of an overall assessment of the value of minimum length limit regulations. Significant mortality occurred only among fish hooked in the esophageal area. Results indicate that direct mortality due to hooking is not a factor which materially reduces the value of size limit regulations.

INTRODUCTION

In 1972 the California Fish and Game Commission imposed an experimental 305-mm (12.0-inch) size limit on largemouth bass at Merle Collins Reservoir, Yuba County. This action was based on high angler harvest rates recorded by Rawstron and Hashagen (1972) and length frequency of sport catch as determined from census (Hashagen 1973). Subsequently, size limits have been imposed at several reservoirs to control overharvest of largemouth bass. Other states also use size restrictions for retaining desirable predator-prey structure and to control bass harvest (Funk 1974).

Hooking mortality will diminish the effectiveness of size restrictions and it is essential that the magnitude of immediate and delayed mortality of sublegal fish be determined. The effects of hooking on largemouth bass less than 305 mm (12.0 inches) were investigated by Rutledge (1974) with inconclusive results. Therefore, as part of an evaluation of the size limit at Merle Collins Reservoir, a companion study was initiated in January 1976 to assess hooking mortality of sublegal largemouth bass.

METHODS AND MATERIALS

The experimental design of this study involved the hooking (by hand) of hatchery-reared bass held in tanks on the grounds of the Department's experimental management facility (Field Station) in Sacramento. To determine the degree of pull on embedded hooks under actual fishing conditions, anglers caught fish of test size on tackle that included a spring scale between the rod tip and the hook. Anglers caught the fish, played them for 30 seconds, and lifted them waist high. During the course of this action, an attachment to the spring scale recorded the maximum reading. The mean of these readings (24 observations) was doubled and this value, 346 g (12.2 oz), was applied as pressure to all experimental fish hooked by hand. All hooking experiments (angling and by hand) were conducted over the period January 15 through March 21, 1976.

A No. 4, medium-shanked "Compac" hook was embedded to the depth of the barb at designated locations within the fish's mouth cavity. The cavity was separated into six major areas, each of which was further divided into subareas.

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The number of subareas within each major area was positively correlated with the size of the area and ranged from two to 12 (Figure 1). Individual hookings were randomized by subarea within each area. Generally, 50 fish per area were hooked.

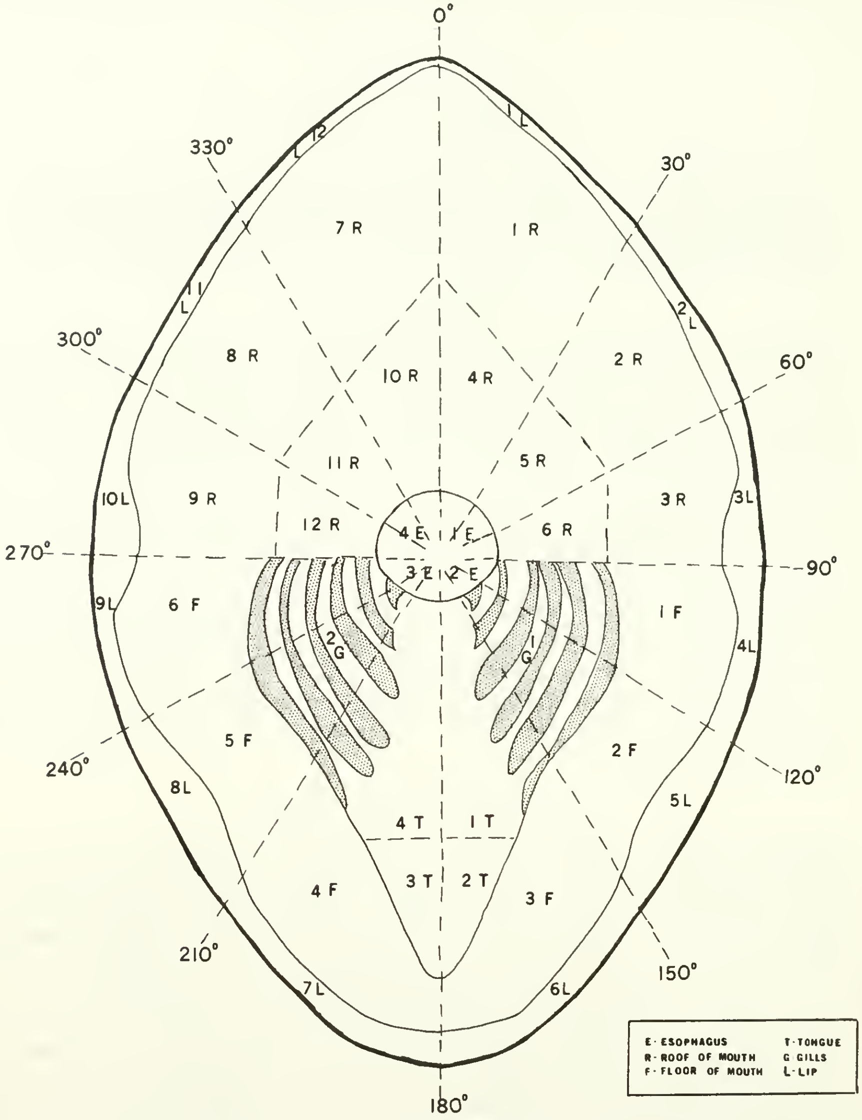

FIGURE 1. Mouth cavity of largemouth bass divided into six major hooking areas (E,R,F,L,G,T) and numbered subareas within each area.

Test fish were differentially fin punched by major hooking area and an additional group (also fin punched) served as a control. All fish were weighed and measured. Following hook placement and the application of 346 g (12.2 oz) of pressure in line with the hook shank, the fish was allowed to move about the test tank for 30 seconds. It was then lifted to waist level by a monofilament line attached to the hook. The hook was usually removed by hand although the use of needle-nosed pliers was occasionally required. Fish were tossed back into the tank and observed (i) continuously for the first hour, (ii) at the end of each hour for the next 6 hours, (iii) at the end of the first 24 hours, and (iv) daily for a 60-day interval. All expired fish were examined by a pathologist to determine cause of death.

Deaths were segregated according to hooking area by identifying fin punches. Since no two fish of a given group were the same size, hooking positions by subarea were determined from length-weight measurements. Immediate mortality was defined as death occurring during the first 24 hours. Death thereafter was considered delayed.

Fish were handled like the average angler might. Rough treatment, such as jerking the hook from the fish's mouth, was avoided. However, the few fish that fell to the ground during handling were used, since anglers often drop fish.

Study fish, subyearling largemouth bass ranging in total length from 139.8 (5.5 inches) to 264.3 mm (10.4 inches) and averaging 193.0 mm (7.6 inches), were obtained from the Department's Imperial Valley Warmwater Hatchery, Imperial County. These pond-reared fish were fed as many golden shiners, *Notemigonus crysoleucas,* as they would consume every other day of the study. Temperatures in the 6,800 liter (1,800 gal) test tank ranged from 9.4 C (49 F) to 15.0 C (59 F). Water in the tank was exchanged weekly to remove metabolic wastes.

RESULTS

Fifty-six percent (95% C.I.; 41.0%–70.0%) of esophageally-hooked bass died as a result of hooking. Mortalities among groups hooked in other areas were not significantly different from the 2% (95% C.I.; 0.0%–14.0%) loss in the control group (Table 1). Twenty-one of 35 fish hooked in the ventral surface of the esophagus died. In these cases, death resulted from hemorrhaging in the pericardial cavity. The hook cut through the esophagus and pericardium and ruptured the heart in the aortic area. According to Donald R. Manzer, examining pathologist from the Department's Fish Disease Laboratory, the relative anatomy of the largemouth bass makes it likely that death will often result when a hook embeds in the esophagus with the barb oriented ventrally. In his opinion, similar results would likely be recorded if the hook were left in the fish.

Seven of the 15 fish hooked in the dorsal surface of the esophagus also died. These deaths were attributed to excessive stress associated with the comparatively difficult job of hook removal since they could not be related directly to physical damage.

Of a total of 32 hooking mortalities, 20 were immediate and 12 were delayed (Table 1). One death was attributed to bacterial gill disease.

Over 88% of the test fish survived both the stress from being crowded in the tank for 60 days with at the most 22.7 liters (6 gal) per fish, and stress and physical damage associated with hooking. Five of the gill-hooked fish bled profusely, but all survived. Of the fish hooked in the roof of the mouth, the hook penetrated an eye cavity in fourteen cases. None of these fish died.

There was no correlation between size of test fish and hooking mortality. The mean length of the expired esophageally-hooked fish was the same as that of the control group ($Z=0.96$, $P>0.05$).

TABLE 1. Mortality by Hooking Area and the Control Group

	Hooking area						*Control group*
	Lip	*Roof of mouth*	*Gills*	*Tongue*	*Floor of mouth*	*Esophagus*	*(50 Fish)*
No. of fish hooked	50	50	50	35	50	50	0
No. of immediate mortalities ($\leq$ 24 hours)	0	0	0	0	0	20	0
No. of delayed mortalities ($>$ 24 hours)	2	0	1	0	1	8	1
Total mortality	2	0	1	0	1	28[1]	1
Percent mortality	4.0	0.0	2.0	0.0	2.0	56.0	2.0
95% C.I. for percent total mortality	0.0–19.0	0.0–7.0	0.0–14.0	0.0–7.0	0.0–14.0	41.0–70.0	0.0–14.0

[1] Does not include one mortality attributed to disease.

DISCUSSION

While anglers using certain types of small baits (worms, salmon eggs, etc.) hook fish in areas of the mouth unlikely to cause death, they are more likely to deep-hook small bass than anglers using lures or minnows. However, the resultant mortality is probably minor since anglers using these baits catch comparatively few small bass. Of the sublegal largemouth bass hooked and released at Merle Collins Reservoir during 1974 and 1975, only 12.0% were caught by anglers using small baits exclusively. Conversely, anglers using lures or minnows released 58.9% of their catch during the same period (unpublished data).

The size of the hook used in this study represents the average hook size used by most anglers. It is probably larger and more damaging to fish than hooks normally used by anglers fishing small baits. Recorded losses of esophageally-hooked fish under study conditions may, therefore, be greater than those which normally occur.

I did not test the effects of summertime temperatures on hooked fish. Results of this study strongly suggest, however, that hooking mortality is not a factor which materially reduces the value of size limit regulations.

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CATCH-PER-UNIT-OF-EFFORT STUDIES OF NORTHERN CALIFORNIA DUNGENESS CRABS, *Cancer magister*[1]

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Northern California commercial Dungeness crab fishermen were interviewed to determine their catch-per-unit-of-effort. The data were used to calculate population size and mortality rates of legal sized crabs and to predict season landings. Generally, the mean catch per trap increased as the number of fishing days increased. As the season progressed, fishermen tended to fish their traps for longer periods. The calculated weight of legal male crabs at the beginning of the season ranged from a low of 1.1 Mg (2.4 million lb) in November 1971 to a high of 7.5 Mg (16.5 million lb) in November 1969. Instantaneous total mortality rates (z) ranged from −0.00490 during the 1966–67 season to −0.18300 during the 1971–72 season. The fishermen probably harvest a greater percentage of the available crabs during seasons of high abundance.

INTRODUCTION

Accurate and consistent catch-per-unit-of-effort data are vital to population dynamics studies. California Dungeness crab fishermen are not required to submit records of daily catch and effort. In December 1964 we initiated interviews with commercial crab fishermen in Eureka to determine the number of traps fished and the weight of crabs caught. A similar study was undertaken at Crescent City in January 1966 (Gotshall and Hardy 1969). Data were collected from both areas through the 1971–1972 season. Originally, these data were used to obtain estimates of the abundance of legal sized crabs and to predict season landings. It soon became apparent from the data that population size estimates and mortality rates of legal sized crabs could be calculated. We also distributed log books (voluntary) to cooperative fishermen beginning in 1966. Unfortunately, very few of the fishermen kept consistent data and this experiment was terminated during the 1968–69 season.

METHODS

Commercial fishermen were interviewed whenever possible as they were unloading the day's catch at the dock. Eureka interviews were conducted by Department of Fish and Game biologists and seasonal aids.

Crescent City interviews were conducted by the Pacific Marine Fisheries Cooperative Port Sampling Project biologists (Public Law 88-309) from January 1966 through May 1968. From December 1968 through February 1972 these interviews were conducted by Department biologists from Eureka.

The information collected during each interiew included: number of traps pulled that day, number of days traps had fished (1 day equals approximately 24 hr of fishing), location, depth traps were fished, and weight of crabs landed.

RESULTS

From December 1964 through February 1972, 1,460 interviews were con-

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[1] Accepted for publication March 1978.

ducted at Eureka, and 1,230 at Crescent City (Tables 1 and 2). These numbers do not include interviews where the fishermen had pulled traps fished for two or more different time periods. Generally, the Eureka fishermen fish an area bounded on the south by Cape Mendocino and on the north by Dry Lagoon (Figure 1). Crescent City fishermen do most of their fishing between Big Lagoon and the Oregon border. Monthly mean catch per trap for one day's fishing at Eureka ranged from a high of 9.8 kg (21.7 lb) per trap in May 1966 (one interview) to a low of 0.4 kg (0.9 lb) per trap in February 1972. These figures represent 14.3 and 0.5 crabs per trap, respectively, based on mean weight data (Table 3).

TABLE 1. Number of Crab Fishermen Interviewed and Mean Catch (Kg) of Crabs Per Trap by Days Fished, Cape Mendocino to Big Lagoon, December 1964 – February 1972.

	Days fished									
	1		*2*		*3*		*4*		*5*	
Month	*No. of Inter-views*	*Kg/ trap*	*No. of Inter-views*	*Kg/ trap*	*No. of Inter-views*	*Kg/ trap*	*No. of Inter-views*	*Kg/ trap*	*No. of Inter-views*	*Kg/ trap*
1964 – 65 Season										
December	23	5.3	–	–	1	10.1	–	–	–	–
January	13	3.8	12	5.6	2	4.6	2	5.1	3	9.6
February	4	3.1	9	4.1	2	3.7	2	2.8	10	4.5
March	13	4.4	4	2.6	2	1.7	–	–	1	3.9
1965 – 66 Season										
December	–	–	11	10.8	–	–	–	–	1	–
January	7	9.5	4	10.7	5	12.8	2	12.7	4	11.8
February	3	7.8	9	9.8	1	9.4	1	7.8	4	11.0
March	3	6.5	7	5.6	6	6.5	6	8.9	1	5.8
April	1	7.9	1	10.9	–	–	–	–	1	19.1
May	1	9.9	4	12.2	–	–	–	–	–	–
1966 – 67 Season										
December	80	6.9	21	7.8	4	7.0	–	–	2	6.6
January	17	4.4	5	6.9	1	10.9	1	8.5	2	4.7
February	7	3.8	2	6.2	1	1.6	1	7.6	1	8.1
March	4	5.9	1	3.2	–	–	–	–	–	–
April	5	3.3	5	2.7	1	8.4	–	–	1	6.7
May	1	1.0	3	3.5	–	–	–	–	1	5.4
1967 – 68 Season										
December	20	7.6	3	6.6	5	8.9	1	6.0	4	8.1
January	31	5.6	6	8.5	2	6.5	–	–	3	7.3
February	23	4.7	4	4.3	3	4.0	–	–	3	6.5
March	15	3.4	7	3.1	4	3.7	1	1.7	3	2.8
April	10	2.1	9	5.1	5	5.0	10	5.6	10	3.7
May	5	2.6	7	3.3	4	2.6	1	3.2	8	5.6
1968–69 Season										
December	27	6.0	15	11.7	4	9.8	–	–	2	7.7
January	65	5.9	42	5.5	11	6.0	4	4.4	5	4.5
February	10	3.5	8	3.0	8	2.5	9	2.8	14	3.2
March	19	2.3	20	2.0	22	2.3	4	2.0	5	2.8
April	–	–	5	3.6	6	4.0	–	–	8	2.2
May	8	3.9	2	8.6	1	11.4	–	–	6	13.6
June	–	–	1	3.9	1	1.5	–	–	–	–
*1969–70 Season **										
January	120	8.8	1	9.0	–	–	–	–	–	–
February	71	4.6	48	5.3	7	5.5	4	5.3	2	1.9
March	17	4.3	29	3.2	21	3.1	4	3.2	12	2.7
April	3	1.5	2	2.9	5	2.7	–	–	8	2.5

*1970–71 Season ***										
February	48	5.5	17	5.7	1	9.4	–	–	–	–
March	25	2.6	16	2.5	10	2.9	7	2.8	5	2.1
April	–	–	5	1.6	–	–	1	1.5	4	1.2
May	–	–	–	–	1	2.7	–	–	–	–
1971–72 Season										
December	20	3.2	13	3.9	14	5.0	2	5.6	7	3.3
January	2	1.0	3	1.3	3	1.7	2	0.7	6	1.5
February	2	0.4	1	0.8	–	–	–	–	1	0.3

* Season opened December 1, fishing did not begin until January.
** Season opened December 1, fishing did not begin until February.

TABLE 2. Number of Crab Fishermen Interviewed and Mean Catch (Kg) of Crabs Per Trap by Days Fished, Dry Lagoon to Oregon Border, December 1966–December 1971

	Days fished									
	1		*2*		*3*		*4*		*5*	
Month	*No. of interviews*	*Kg/ trap*	*No. of interviews*	*Kg/ trap*	*No. of interviews*	*Kg/ trap*	*No. of interviews*	*Kg/ trap*	*No. of interviews*	*Kg/ trap*
1966–67 Season										
December	38	6.1	9	6.3	6	8.5	3	6.8	1	10.7
January	9	9.4	26	6.4	10	6.0	10	6.1	12	6.4
February	36	6.5	25	5.5	10	6.0	6	6.0	6	8.9
March	18	5.9	13	4.3	15	6.6	2	6.5	4	11.0
April	1	0.8	1	1.1	1	2.8	1	1.9	1	0.9
May	–	–	–	–	–	–	–	–	–	–
June	–	–	–	–	–	–	–	–	3	2.8
1967–68 Season										
December	49	9.3	17	11.7	7	10.8	1	25.0	31	12.5
January	40	7.6	24	9.8	9	12.2	8	11.8	11	11.0
February	25	3.6	55	5.0	18	5.3	9	7.9	20	9.2
March	1	4.3	6	4.9	4	3.6	4	3.4	10	5.6
April	–	–	4	2.8	8	4.1	2	3.7	13	4.1
May	–	–	1	1.4	1	1.4	3	2.9	9	3.5
1968–69 Season										
December	41	9.5	9	9.4	1	12.5	2	11.9	6	12.0
January	26	6.3	12	5.8	8	4.8	4	5.8	7	5.4
February	4	2.0	4	3.1	5	2.5	2	3.4	13	4.4
March	3	1.8	14	2.5	16	2.4	5	3.5	18	3.9
April	–	–	3	3.3	7	2.9	4	2.4	9	4.0
May	3	2.2	4	7.1	1	1.7	2	7.2	18	7.0
June	–	–	–	–	–	–	–	–	1	6.4
*1969–70 Season **										
January	46	10.5	16	15.2	10	15.8	2	22.1	8	17.4
February	17	4.9	12	3.4	4	5.5	3	4.7	7	5.3
March	1	1.3	4	3.6	8	1.5	3	1.7	7	3.5
April	4	4.3	9	4.1	5	3.3	–	–	9	5.8
May	–	–	1	3.0	–	–	–	–	1	5.7
*1970–71 Season ***										
February	43	10.9	2	7.4	3	17.4	2	17.2	1	19.1
March	31	5.7	9	6.1	3	5.1	2	4.3	–	–
April	2	4.5	1	5.6	–	–	1	4.3	–	–
May	–	–	1	5.4	–	–	–	–	–	–
June	–	–	1	4.2	–	–	–	–	–	–
1971–72 Season										
December	16	8.9	15	2.7	6	3.1	2	3.7	3	0.4

* Season opened December 1, fishing did not begin until January.
** Season opened December 1, fishing did not begin until February.

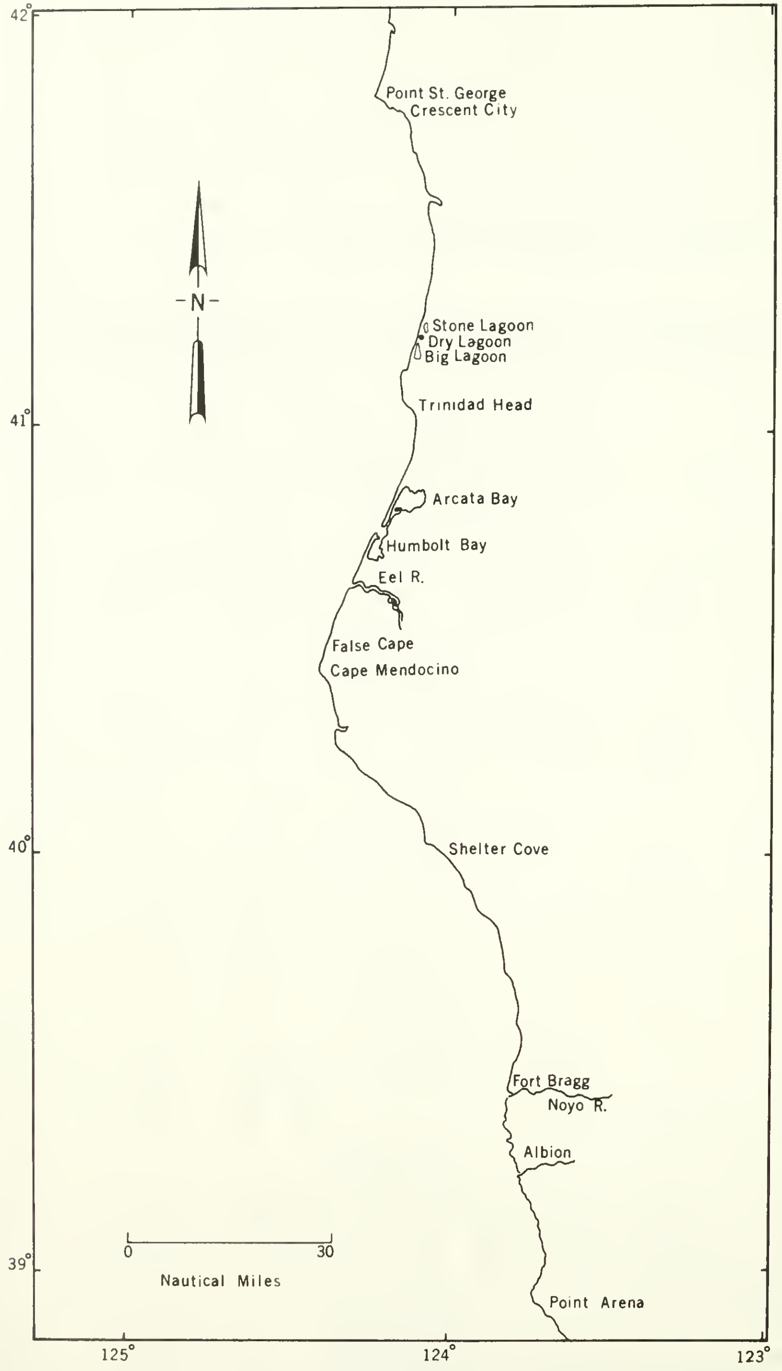

FIGURE 1. Northern California fishing areas and landmarks.

TABLE 3. Monthly and Seasonal Mean Weights (Kg) of Dungeness Crabs Landed at Crescent City and Eureka, 1964–1972

Month	*Season* 1964–65	1965–66	1966–67	1967–68	1968–69	1969–70	1970–71	1971–72
Eureka								
December	–	0.91	0.94	0.85	0.91	–	–	0.82
January	0.88	0.91	0.94	0.74	0.91	0.73	–	0.83
February	0.86	0.88	0.98	0.84	0.93	0.80	0.92	–
March	–	0.89	–	0.78	0.90	0.73	0.86	–
April	–	–	0.99	0.71	0.94	0.77	0.83	–
May	–	0.69	0.91	0.82	0.94	–	–	–
June	–	–	–	–	–	–	–	–
Mean for Season	0.87	0.86	0.95	0.78	0.92	0.75	0.86	0.83
Crescent City								
December	–	–	0.94	0.83	0.89	–	–	0.77
January	–	0.94	0.99	0.84	0.92	0.89	–	0.81
February	–	0.77	0.94	0.82	0.91	0.85	0.96	–
March	–	0.84	0.93	0.78	0.93	0.84	0.94	–
April	–	0.78	0.89	0.79	0.86	0.84	0.92	–
May	–	0.76	–	–	0.84	–	0.94	–
June	–	0.75	0.84	–	–	–	–	–
Mean for Season	–	0.81	0.94	0.79	0.90	0.86	0.94	0.78

The highest monthly mean recorded by Crescent City fishermen for 1 day's fishing occurred in February 1971 and was 10.8 kg (23.9 lb) or 11.3 crabs per trap (Table 3).

Generally, the monthly mean catch per trap increased as the number of fishing days increased, particularly during the first month of the season. During most seasons the catch-per-unit-of-effort declined steadily each month and then increased again in March, April, or May.

As the season (December 1 to July 15) progressed, fishermen tended to fish their traps for longer periods. Approximately 70% of the fishermen pulled their traps every day during the 1st month of the season (Figure 2). However, by the 5th month this figure dropped to 12.3% and increased slightly to 19.1% during the 6th month. Conversely, only 8.1% fished their traps 5 or more days during the 1st month but, by the 7th month, this figure increased to 66.7%. It appears that the fishermen could have caught more crabs had they pulled their traps every day, particularly after the 1st month of the season. For example, in March 1969 Eureka fishermen averaged 2.3 kg (5.1 lb) or 2.6 crabs per trap overnight and 2.3 kg (5.1 lb) per trap after three nights. If they had pulled their traps every day, they could have averaged 6.9 kg (15.3 lb) or 7.7 crabs; assuming, of course, that weather conditions permitted fishing every day.

Population Size

A population size estimate of legal sized crabs at the start of the fishing season was calculated from the combined Eureka and Crescent City catch per trap data for 1 day of fishing, and cumulative landing data (Table 4).

The following equations were used, based on Leslie's least square method (Ricker 1975):

$$Y = a + bX$$

and

$$\hat{N}_o = \hat{a}/\hat{c}$$

and $\hat{c} = -b$

TABLE 4. Dungeness Crab Cumulative Landings (Lb) (Cape Mendocino to Oregon Border) and Catch (Kg) Per Trap Data (1-day sets) Used to Calculate Population Size at the Beginning of the Fishing Season

	Season											
	1966–1967		*1967–68*		*1968–69*		*1969–70*		*1970–71*		*1971–72*	
Week	*Cumulative landings*	*Kg/ trap*	*Cumulative landings*	*Kg/ trap*	*Cumulative landings*	*Kg/ trap*	*Cumulative landings*	*Kg/ trap*	*Cumulative landings*	*Kg/ trap*	*Cumulative landings*	*Kg/ trap*
1	864	8.9	0	9.0	200	17.5	0	10.2	15,896	10.1	0	7.9
2	400,554	5.4	501,185	9.0	110,282	7.0	360,727	8.4	285,551	4.8	332,632	4.0
3	911,289	5.1	995,718	6.4	975,384	7.5	1,152,228	9.0	608,563	6.1	673,147	3.8
4	1,023,500	8.8	1,226,683	9.6	2,156,945	8.7	1,442,890	10.3	897,243	6.3	713,869	0.8
5	1,445,247	5.4	3,114,818	5.3	4,832,925	11.7	2,308,941	11.8	1,554,859	12.9	1,207,478	1.3
6	1,921,936	5.8	3,545,810	8.4	5,897,597	6.9	3,160,913	6.6	1,849,655	5.4	1,259,718	5.0
7	2,477,794	4.3	4,205,240	7.0	6,211,416	6.0	4,147,876	7.9	2,919,950	3.5	1,601,983	3.0
8	3,038,634	9.0	4,532,345	6.0	6,877,951	5.3	4,867,998	8.0	3,117,825	8.2	1,690,966	2.1
9	3,418,249	4.4	5,271,468	11.2	7,402,128	4.7	5,596,269	6.8	3,485,464	3.4	1,973,297	1.2
10	3,658,664	5.2	5,671,732	8.2	8,244,794	4.1	5,869,864	5.6	3,624,971	2.2	2,006,636	0.4
11	4,080,178	4.2	6,379,980	5.9	8,489,587	4.3	6,820,740	5.0	4,134,233	2.8		
12	4,295,258	5.9	6,555,446	4.9	8,971,512	4.0	8,490,261	4.7	4,336,692	4.9		
13	4,907,682	8.4	7,117,576	3.4	9,226,525	3.2	8,989,825	5.5	4,685,040	6.0		
14	5,484,917	8.1	7,564,417	3.7	9,419,762	3.3	9,453,660	3.9	4,733,447	1.2		
15	5,919,965	5.2	7,644,672	4.9	9,877,190	2.8	10,032,507	3.0	4,828,089	1.2		
16	6,572,003	5.8	7,891,500	2.6	10,153,489	1.6	10,902,083	4.5	5,059,929	3.6		
17	8,726,446	0.8	8,313,966	4.0	10,270,088	3.7	11,409,995	4.9	5,131,401	1.4		
18	8,824,793	1.8	8,674,202	5.3	10,397,656	3.4	11,652,343	2.5	5,230,101	3.5		
19			8,979,738	3.8			12,039,298	1.5	5,954,482	4.5		
20			9,475,358	3.3			12,248,072	3.3				
21			9,610,584	3.9								
22			9,851,743	3.4								
23			10,136,793	2.8								
24			10,246,795	2.8								
25			10,427,896	0.9								
26			10,652,284	2.4								
27			10,816,943	2.6								

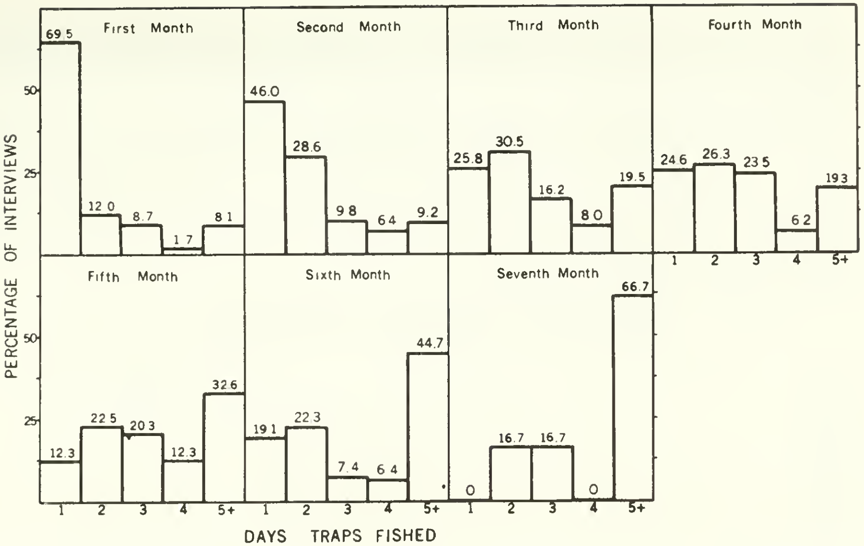

FIGURE 2. Percentage of crab fishermen interviews and number of days traps were fished, Crescent City and Eureka dates combined, 1964 through 1972.

Where:

Y = mean catch in pounds per trap for 1 day of fishing
a = intercept of line on Y axis
b = slope of line
X = cumulative landings
$\hat{a}$ = product of the original population, N_o and the catchability, c
$-\hat{b}$ = catchability, $\hat{c}$
N_o = estimated population in pounds of legal sized crabs at the start of the fishing season

Population estimates were calculated for the 1966–67 through the 1971–72 season (Table 5). The largest calculated population estimate, 7.6 Mg (16.7 million lb), was present at the beginning of the 1969–70 season, the lowest population estimate, 1.1 Mg (2.4 million lb), was obtained from data collected during the early part of the 1971–72 season.

TABLE 5. Calculated Population Estimates of Northern California Dungeness Crabs by Weight (Kg) at the Beginning of the Fishing Season, Cape Mendocino to Oregon Border.*

Season	*Intercept (a)*	*Slope (b)*	*Population (mean no.)*	*Lower 95% confidence limit*	*Upper 95% confidence limit*	*Total catch Mg*	*Exploitation rate (u)*
1966–67	16.34318	0.00000102	7,274,318	3,257,893	41,044,989	4.597	63.2
1967–68	20.85992	0.00000140	6,764,575	4,624,158	10,504,761	4.859	71.8
1968–69	25.29165	0.00000185	6,206,707	3,625,982	11,863,158	5.321	85.7
1969–70	22.40918	0.00000134	7,592,363	6,684,943	8,962,693	6.118	80.6
1970–71	17.84373	0.00000217	3,733,205	1,674,335	7,153,291	3.258	87.3
1971–72	12.29002	0.00000505	1,104,886	793,287	3,120,111	0.804	72.8

* Fort Bragg area landings not included.

Based on these population estimates, fishermen were harvesting between 63 and 87% of the available crabs during the seasons considered (Table 5). Jow

(1965) estimated that fishermen harvested 85% of the available crabs during the 1962–63 season. He also speculated from tag recovery data that fishermen harvested a higher percentage of the population during years of low abundance than during years of high abundance. From my data it appears that fishermen are harvesting a higher proportion of the legal males during years of high abundance, and a year or so after the population begins to decline, than during years of low abundance and years when the population is increasing. Fishing effort (numbers of boats) follows a similar pattern, thus supporting catch-per-trap data, assuming that a relationship exists between fishing effort and the percentage of crabs harvested (Table 6).

TABLE 6. Number of Boats Per Season Landing Dungeness Crabs at Ports Between Cape Mendocino and Oregon Border.

Season	*Boats*	*Mean number of months boat made landings*
1966–67	198	–
1967–68	213	–
1968–69	244	3.3
1969–70	264	3.4
1970–71	257	2.7
1971–72	189	2.8

Mortality Rates

In the calculation of weekly instantaneous mortality rates during the fishing season, the following equation was used. (Calculations by Eugene Witeck).

$$ln\ Y = a + b\,X$$

Where:

$ln\ Y$ = natural log of weekly mean catch in pounds per trap (Table 7).

a = intercept of line on Y axis.

$-b$ = monthly instantaneous total mortality rate (Z)

X = week number of fishing season.

TABLE 7. Weekly Mean Catch (Lb and Kg) Per Trap of Northern California Dungeness Crabs Used to Calculate Weekly Instantaneous Mortality Rates.

Week number of season	*1966–67*		*1967–68*		*1968–69*		*1969–70*		*1970–71*		*1971–72*	
	Lb/ trap	*Kg/ trap*	*Lb/ trap*	*Kg/ trap*	*Lb/ trap*	*Kg/ trap*	*Lb/ trap*	*Kg/ trap*	*Lb/ trap*	*Kg/ trap*	*Lb/ trap*	*Kg/ trap*
1	19.6	8.9	19.0	8.6	16.8	7.6	22.4	10.2	20.3	9.2	15.9	7.2
2	11.6	5.3	20.9	9.5	19.2	8.7	20.3	9.2	14.9	6.8	3.8	1.7
3	16.6	7.5	18.8	8.5	–	–	15.2	6.9	14.1	6.4	6.4	2.9
4	12.8	5.8	–	–	25.7	11.7	17.9	8.1	8.0	3.6	–	–
5	9.4	4.3	17.4	7.9	15.8	7.2	12.1	5.5	11.6	5.3	5.4	2.4
6	14.9	6.8	14.9	6.8	10.9	4.9	10.2	4.6	7.0	3.2	–	–
7	11.5	5.2	19.0	8.6	8.7	3.9	9.6	4.4	–	–	–	–
8	–	–	11.2	5.1	16.4	7.4	7.6	3.4	–	–	–	–
9	9.3	4.2	7.5	3.4	8.8	4.0	10.0	4.5	–	–	2.6	1.2
10	13.1	5.9	7.7	3.5	7.5	3.4	10.9	4.9	–	–	0.9	0.4
11	18.4	8.4	10.3	4.7	10.3	4.7	5.7	2.6	–	–		
12	17.9	8.1	8.3	3.8	14.1	6.4	4.8	2.2	10.0	4.5		
13	11.4	5.2	7.3	3.3	5.3	2.4	10.3	4.7				
14	12.7	5.8	8.7	3.9	–	–	3.3	1.5				
15			5.3	2.4	3.2	1.4	2.3	1.0				
16			6.2	2.8	3.1	1.4	6.0	2.7				
17			6.2	2.8	10.0	4.5						

18	2.0	0.9	10.8	4.9
19	–	–	4.5	2.0
20	–	–	–	–
21	5.1	2.3	–	–
22	5.5	2.5	–	–
23	7.0	3.2	10.0	4.5
25	4.8	2.2	–	–
26			8.6	3.9
27			4.2	1.9

Instantaneous rates of fishing mortality (F) and natural mortality (M) were calculated from the following (Notation from Ricker 1975).

$u = L/N_o$

Where:

u = annual expectation of death from fishery (rate of exploitation from Table 5).

L = season landings in pounds (Table 4).

N_o = population in pounds at start of season (Table 5).

and:

$$A = 1 - e -^{z}$$

$$Z/A = F/u$$

Thus: $F = uZ/A$

Since: $Z = F + M$

Then: $M = Z - F$

Where: Z = instantaneous total mortality rate.

A = total annual expectation of death.

F = instantaneous fishing mortality rate.

M = instantaneous natural mortality rate.

These calculations were based on the assumption that the calculated population estimate at the beginning of each season was truly representative. The data yielded significant correlation coefficient estimates for only three seasons, 1967–68, 1968–69, and 1969–70, at the 5% level or less.

The weekly instantaneous total mortality rates (Z) varied considerably from season to season (Table 8). The highest rate occurred during the 1971–72 season (−0.18300) and the lowest rate during the 1966–67 season (−0.00490). These rates correspond to seasonal survival rates (S) of less than 0.01% and 86%, respectively.

TABLE 8. Mortality Rates and 95% Confidence Intervals for Northern California Dungeness Crabs * (Cape Mendocino to Oregon) During Fishing Season.

					*Seasonal rates ***				
Season	*−i (weekly rate)*	*Lower confidence limit*	*Upper confidence limit*	*Fishing season (weeks)*	*−Zt*	*A*	*u*	*Ft*	*Mt*
1966–67	−0.00490	−0.00943	+0.00037	30	−0.15	0.14	0.63	0.68	–
1967–68	−0.07710	−0.07794	−0.07626	32	−2.47	0.92	0.72	1.93	0.54
1968–69	−0.04900	−0.04990	−0.04810	32	−1.57	0.79	0.86	1.71	–
1969–70	−0.11550	−0.11745	−0.11355	32	−3.70	0.98	0.81	2.94	0.76
1970–71	−0.05740	−0.06663	−0.04817	26	−1.49	0.77	0.87	1.68	–
1971–72	−0.18300	−0.20602	−0.15998	37	−6.77	0.99	0.73	4.99	1.78

* 159 mm carapace width and larger.

** Notation from Ricker 1975.

The amount of interview data (40 interviews) used to calculate rates for the

1971–72 season was small when compared to other seasons (i.e. 149 during 1970–71); this, plus the fact that most of the interviews were conducted in the Eureka area thus biasing the data, might explain in part the high mortality rate for that season (Table 8).

The calculated seasonal instantaneous fishing mortality rates (F) ranged from 0.68 during the 1966–67 season to 4.99 during the 1971–72 season.

The highest calculated instantaneous natural mortality rate (1.78) occurred during the 1971–72 season; the lowest rate (0.54) occurred during the 1967–68 season. If these rates are representative, we might expect the range of survival during a 6-month closed season to be 17 to 58%, disregarding seasons where natural mortality rates could not be calculated because of the low calculated total mortality rate and corresponding high fishing mortality rate. Jow (1965) calculated a bi-monthly survival of 27% from tagged crabs released in Pelican Bay.

The preceding calculated population estimate and mortality rates yield valuable insights into the condition of crab stocks off northern California and therefore should be helpful in estimating change in yield due to changes in legal sizes. However, the estimates are no better than the data used to calculate them. Unfortunately, the catch-per-trap interviews contain two basic weaknesses: they were neither consistent nor random. These two factors probably account for most of the variation and inconsistencies. A third factor involved is the increase in mean pounds per trap that occurred during most seasons in March, April, or May. At present, it is unclear whether this increase is due to the small number of interviews, a sudden influx of crabs from some other area, or a new molt. There is some evidence that some sublegal crabs undergo ecdysis during the later winter as shown by an increase in the number of soft crabs during this period.

The Leslie population estimate relies on three assumptions:

1) the population vulnerability must not change during the experiment,
2) the entire population must be available for capture,
3) there should not be an excess of recruitment and immigration, over emigration and natural mortality.

The crab population estimates were for legal-sized males only, thus, the first assumption was met. The second assumption presents little problem during the first 2 or 3 months of the season; but the increase in the catch per trap in and during early spring might indicate that either a new segment of the population has moved into the area, or a molt of sublegal males has increased the number of legal males. From our tagging studies we speculate that there is very little movement of crabs into or out of the area.

We do not have sufficient natural mortality data to determine whether it is excessive or not. The natural mortality rates in Table 8 are based, in part, on the catch-per-unit-of-effort data. Therefore, they are subject to the same weaknesses as the population estimates.

One method of obtaining truly representative catch-per-trap data would be a mandatory log book system. Such a system would provide data for the entire fishery throughout the season. At present, it is costly, primarily in terms of man-days, to obtain sufficient interviews to be meaningful during the latter part of the season when only a few boats are operating out of each port. However, a log book system might prove more expensive than the interview system because of the large number of boats in the fishery and the number of man-days that would be required to process the logs. Utilization of port samplers hired only for the season to conduct interviews could be less expensive and they might obtain more accurate data. A log book might prove to be a valuable aid to the fishermen, particularly new, inexperienced fishermen, in following trends in crab behavior from year to year.

ACKNOWLEDGMENTS

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SEX RATIOS OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, OFF SOUTHERN CALIFORNIA [1]

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Sex ratios for the northern anchovy, *Engraulis mordax*, were calculated from samples taken from the southern California commercial reduction fishery and California Department of Fish and Game Sea Survey cruises for the period 1966–1975.

Sex ratios calculated on a seasonal, monthly, and daily basis for the commercial fishery seldom approached the expected 1:1 ratio. Only a few ratios slightly favored males, whereas females were frequently dominant. Although sex ratios for sea survey cruises were most always close to the expected 1:1 ratio, there were a large number of samples that showed extreme dominance of either females or males for those cruises occurring during the period February to June. Sex ratios calculated by area of capture for this same time period suggested a spatial segregation of the sexes.

INTRODUCTION

Sex ratio data for the northern anchovy has been recorded routinely since the California Department of Fish and Game began continuous sampling of the southern California commercial reduction fishery in 1966. The female to male sex ratio calculated from samples taken during the 1968–69 season was 1.42:1. For the next six seasons the ratio varied between 1.14:1 and 2.02:1 (Table 1).

TABLE 1. Calculated Sex Ratios (F:M) of Anchovies Taken at San Pedro, 1968–69 Through 1974–75 Reduction Seasons.*

	Calculated from	
Season	*Actual numbers sampled*	*Estimated numbers sampled **
1968–69	1.45 : 1	1.42 : 1
1969–70	1.14 : 1	1.14 : 1
1970–71	1.60 : 1	1.60 : 1
1971–72	1.52 : 1	1.52 : 1
1972–73	1.99 : 1	1.98 : 1
1973–74	2.02 : 1	2.02 : 1
1974–75	1.57 : 1	–

* Using correction factors.

Whether or not these data reflect the actual sex composition of the anchovy population off southern California is of importance to fisheries management. Anchovy biomass estimates, calculated by the National Marine Fisheries Service from California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larval surveys, assume a 1 : 1 sex ratio (Smith 1972). If, however, the sex ratio is not 1 : 1, then biomass estimates should be adjusted.

The mechanisms of meiosis and fertilization tend to dispel the concept of a pelagic fish population consistently exhibiting a sex ratio other than 1 : 1. Accepting this premise raises the question of why anchovy fishery sex ratios vary so much and seldom approach the 1 : 1 ratio expected.

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[1] Accepted for publication March 1978.

METHODS

Data for this paper were taken from two principal sources, the southern California reduction fishery and California Department of Fish and Game Sea Survey Project cruises. Mais (1974*b*) summarized the scope of these survey cruises. Estimated sex ratios of the commercial catch from 1968–69 to 1972–73 seasons were published in age and length composition reports (Collins 1971; Spratt 1972*b*, 1973*a*, 1973*b*; Sunada 1975). Computer compilations and individual sample sheets were obtained for these seasons and for the 1973–74 and 1974–75 seasons from Department of Fish and Game files. Sex ratio data from Sea Survey cruises were taken from individual sample sheets for the years 1966 to 1975. Station data for these cruises were available from CalCOFI Data Reports 16–24 (Mais 1969*a*, 1969*b*, 1971*a*, 1971*b*, 1971*c*, 1972, 1973, 1974*a*, 1975).

Sex ratios calculated for an entire commercial season were based on an estimate of total numbers of females and males landed. These ratios involved a correction for any differences in average weight of the sexes. In most cases, the correction factors were small and the sex ratios obtained from the actual numbers of females and males sampled were in close agreement with corrected ratios (Table 1). Sex ratios reported by month or area of capture for the commercial season and all sex ratios reported from sea survey data were calculated directly from numbers sampled. All sex ratios reported here represent the female to male (F : M) ratio.

In some cases, samples contained a varying number of fish whose sex were reported as unknown, usually because of immaturity of the sex organs. These fish were ignored in calculating the sex ratio.

The numbers of fish used to calculate the sex ratios represented an extremely small portion of the total population and the standard deviations were high when using these figures to estimate the sex ratio of the entire central anchovy population (Spratt 1972*a*; Vrooman and Paloma 1975).

In general, sex ratios were compared as they related to both time and space. Date and location of capture were available on most sample sheets. For Sea Survey data, actual coordinates of stations were available. For the commercial fishery, location of capture was reported by the captain of the fishing vessel on logs collected by the Department of Fish and Game.

RESULTS

Sex ratios calculated from sampling the fishery daily varied considerably. Monthly sex ratios (Figure 1) calculated for 1968–69 through 1974–75 seasons twice were as high as 3 : 1 and frequently were higher than 2 : 1. No month showed a preponderance of males in the samples and only three times did the monthly sex ratio favor males. The combined numbers for all seasons resulted in a sex ratio of 1.60 : 1. In contrast, sex ratios from Sea Survey cruises (Figure 1) conducted during the same period varied to a lesser degree and combined numbers for all cruises resulted in a sex ratio of 1.09 : 1. Consistent seasonal or cyclic trends were not apparent from either set of data.

The monthly sex ratios for the fishery also were collated by Fish and Game block number (Pinkas 1951) or area of capture to determine if the location of capture by the fishing fleet reflected any geographical differences (Figures 2 and 3). The San Pedro Channel was the most frequent and consistently fished area. Landings often occurred from areas northwest, east, and southeast of the chan-

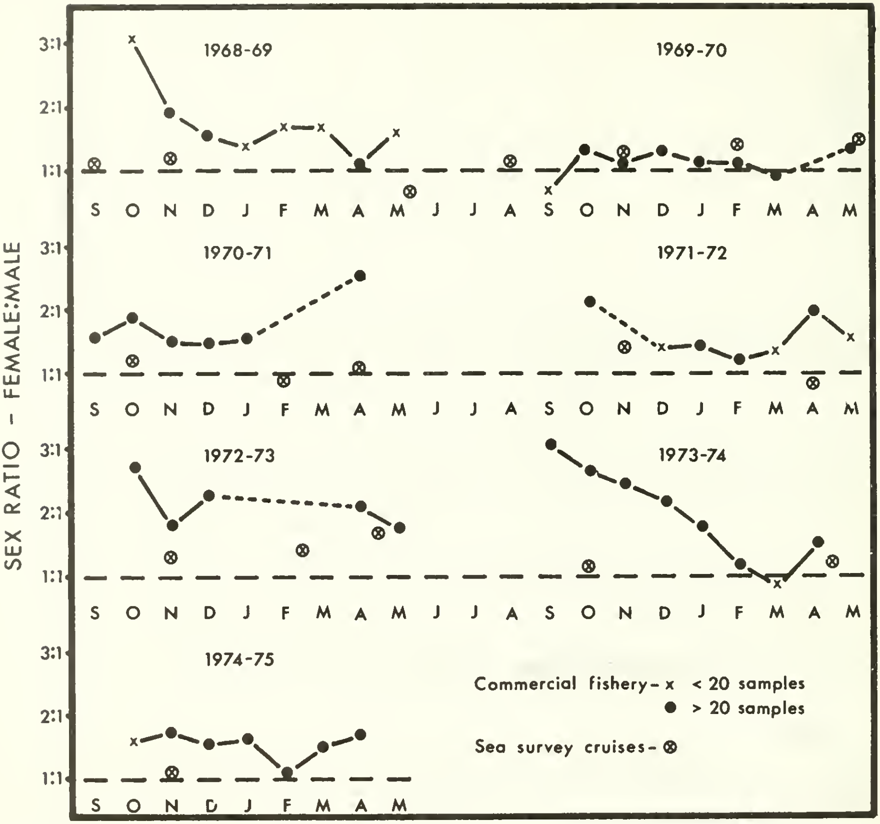

FIGURE 1. Sex ratios (F:M) of anchovies by month computed from samples taken from the commercial fishery (1968–69 through 1974–75 seasons) and from California Department of Fish and Game Sea Survey cruises.

nel. In a majority of months there was one area where the sex ratio was high with adjacent areas exhibiting lower values. Notable landings were made from the Santa Barbara Channel only occasionally, but the sex ratio was often high in samples from these landings (6.40 : 1, 4.23 : 1, 1.92 : 1, 1.28 : 1, 3.03 : 1). In April 1973, landings arrived from a fairly large area ranging from just northwest of Palos Verdes Peninsula to east of San Clemente Island. The sex ratios for this month exhibited a declining trend from north to south.

Data from Sea Survey cruises were better suited than commercial fishery data for studying the possibility of spatial differences in the sex ratio. Samples, obtained by mid-water trawl at night (Mais 1974*b*), were taken over a much larger area than those from the commercial fishery. The reported location of capture for these samples was also more reliable. The duration of cruises in the Southern California Bight normally was less than 1 month, reducing the problem of movement of portions of the population. The sample size was standardized by number (25 fish) and, as a rule, all fish were sexed (samples from the commercial fishery seldom contained more than 17 fish) (Figure 4). The principal disadvantage of these data was the relatively small number of samples from each cruise, which necessitated grouping the data. Since 1966, most cruises took place during five

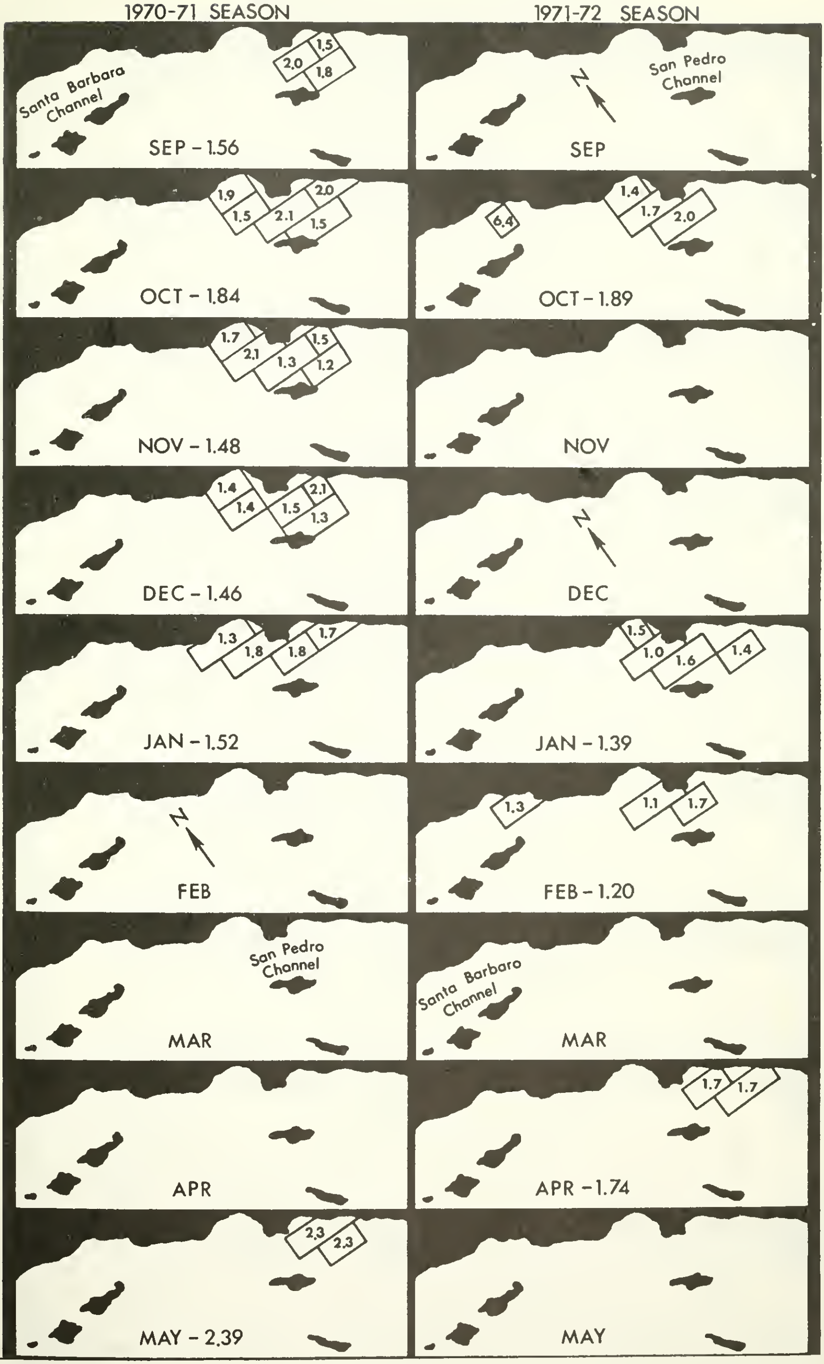

FIGURE 2. Sex ratios (F:M) of anchovies computed by month and block number (area of capture) from samples obtained from the San Pedro reduction fishery in the 1970–71 and 1971–72 seasons.

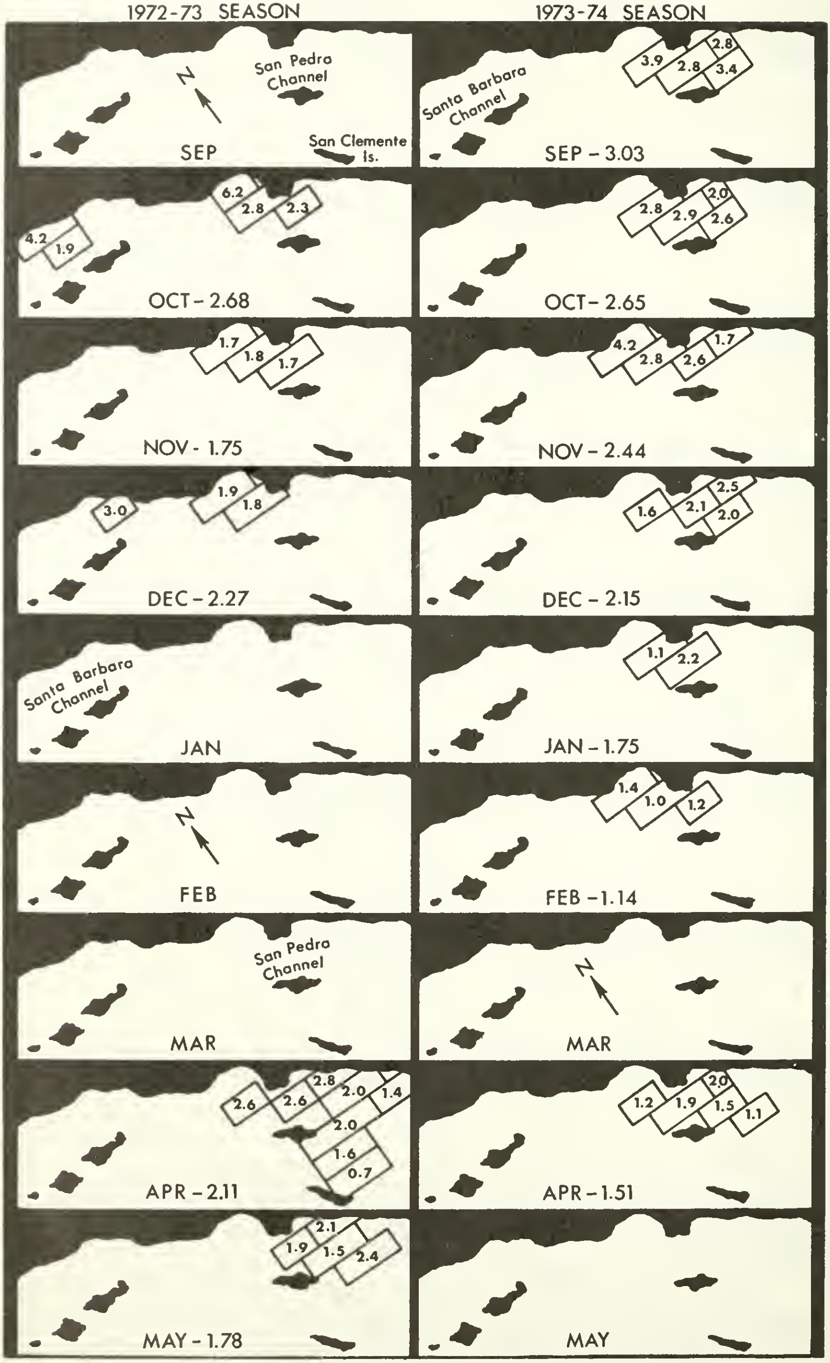

FIGURE 3. Sex ratios (F:M) of anchovies computed by month and block number (area of capture) from samples obtained from San Pedro reduction fishery in the 1972–73 and 1973–74 seasons.

periods of the year, "February", "April", "May–June", "October", and "November." An examination of sex ratio data for these periods produced some interesting results (Figure 5).

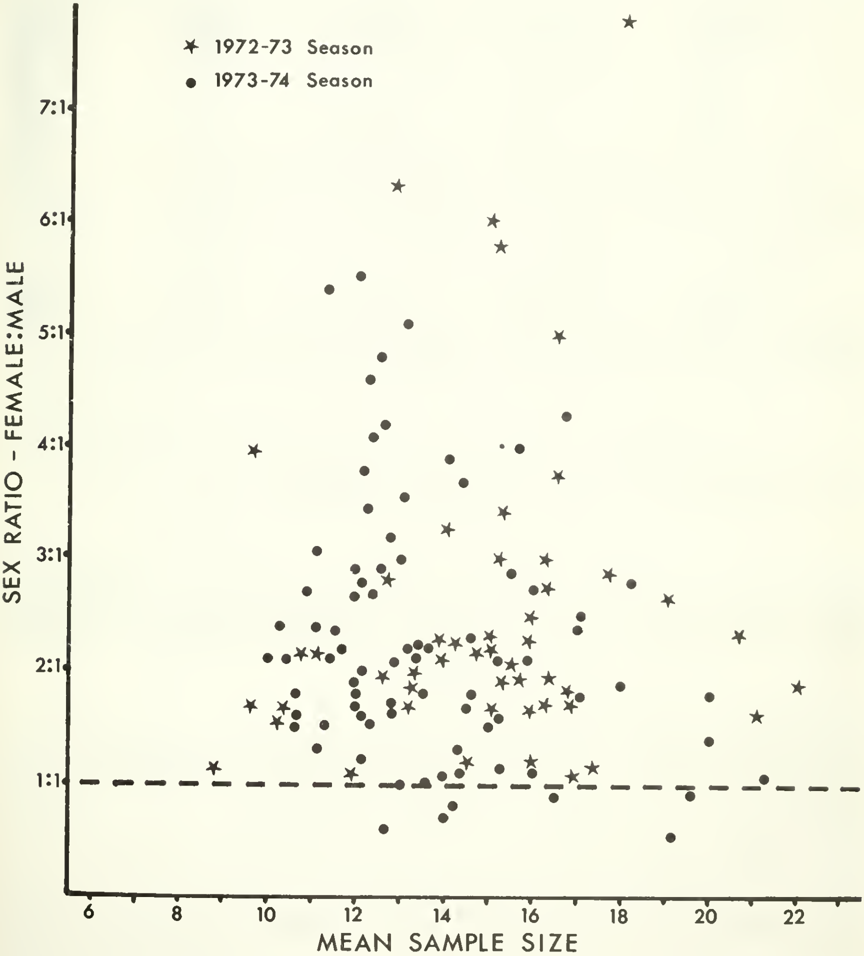

FIGURE 4. Comparison of daily sex ratios (F:M) for two commercial seasons with the mean number of fish occurring in samples.

For the "February", "April" and "May–June" cruises, there were areas which showed significant differences between sex ratios. The delimiting of these areas for which separate sex ratios were calculated was more or less arbitrary, especially for "October" and "November" cruises. However, the task was made somewhat easier for the earlier cruise periods by the occurrence of a large number of samples that were predominantly either female or male (i.e., 24 : 1, 2 : 23, 0 : 25). One area, southeast of San Clemente Island, showed a consistent dominance of males, a phenomenon which was not noticed in commercial fishery samples. Just to the north, there is a smaller area which was predominant-

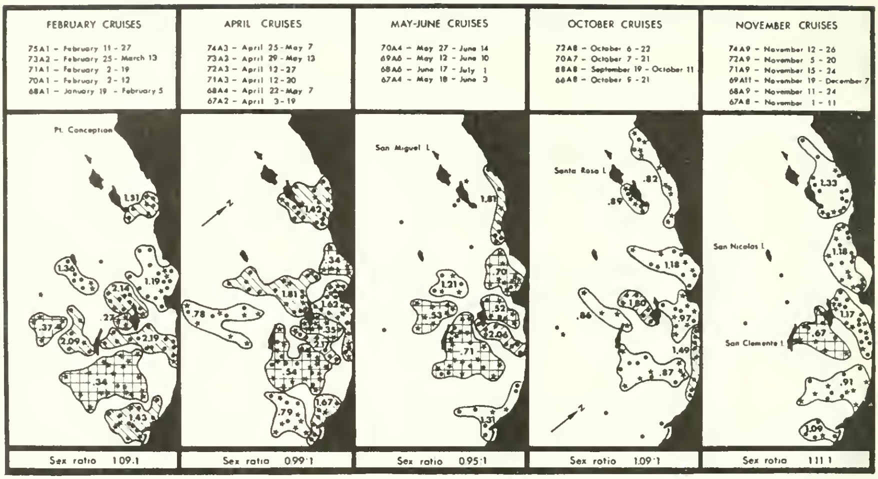

FIGURE 5. Sex ratios (F:M) of anchovies computed from samples taken by midwater trawl on California Department of Fish and Game Sea Survey cruises. Stars represent samples with a majority of males. Circles represent samples with a majority of females. Hatched areas indicate strong male or female dominance in samples. Cruise designations (i.e. 75A1, 69A6) refer to the chronology of the cruise (first and sixth) on the research vessel ALASKA (A) during a calendar year (1975 and 1969).

ly female for the first three cruise periods. In the Channel Islands-Port Hueneme area the sex ratio consistenty favored females. During "April" and "May–June" cruises, males were dominant in the vicinity of Santa Monica Bay. During the "October–November" cruises, there was a breakdown of this pattern with few areas showing large differences in sex ratios.

The observed female distribution in samples of 25 fish for "October–November" and "February–April" were radically different (Figure 6). For the "February–April" period, 34% of the samples fell beyond the 2% probability zone of the expected binomial distribution, while 13% fell beyond this zone in "October–November". Of the two distributions, the "October–November" data fitted the expected distribution more closely. The expected distribution assumed a 1 : 1 sex ratio with no sampling bias and was smoothed for comparison.

The dominance of females in commercial fishery samples could be explained by assuming that differential mortality or growth rates affected females and males. If males did not live as long, more females would be expected in landings as the older year classes were harvested. Conversely, the sex ratio would be expected to drop when recruitment of younger fish occurred. One might expect the same trend, if females grew faster or larger than males (Collins 1969) and the anchovy tended to school by size.

To test the assumptions of a differential mortality or growth rate, a correlation was attempted using the number of fish in a sample as a quick and easy indicator of the mean length of fish in the sample. Samples were taken by weight and, in this respect, were approximately equal, but there was an increase in the number of fish in the samples when smaller fish were being landed and when recruitment occurred. For either assumption, there should be a trend apparent in the sex ratio as the size of the sample varies. The correlation of mean sample size to sex ratio

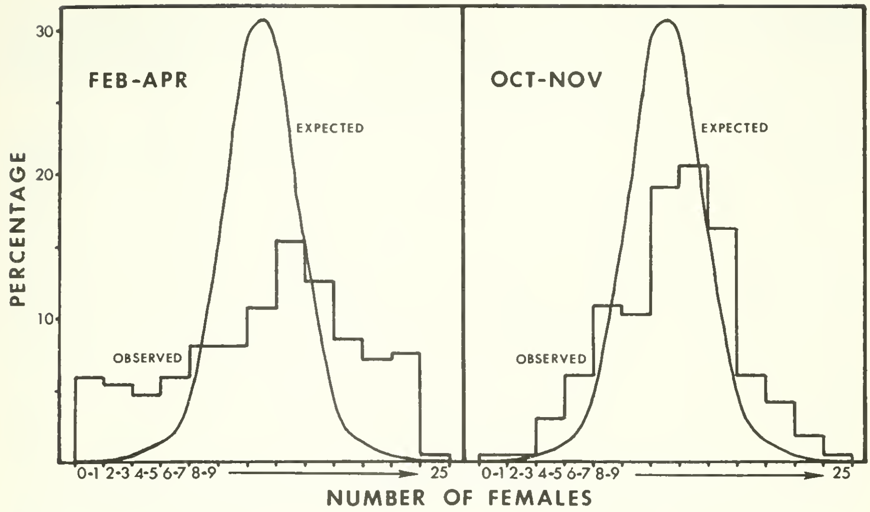

FIGURE 6. The expected and observed distribution of the number of females in samples of 25 fish for two different periods of sampling. Samples were collected on Sea Survey cruises over 8-year period. The expected binomial distribution assumes a 1:1 sex ratio with no sampling bias and is smoothed for comparison. The distributions are grouped by increments of two.

for two seasons on a daily basis (Figure 4) indicated no such trend. However, these data showed that the sex ratio for any day of sampling was often higher than 2 : 1 and seldom favored males.

DISCUSSION

If I were to assign a sex ratio as a population parameter based on the sampling of the commercial fishery, it would be higher than the 1 : 1 (female : male) expected. Through a seven season period, the sex ratio seldom approached the expected value. However, a sex ratio of 1.03 : 1 was derived from 9 years of Sea Survey data. The most important difference in sampling appeared to be that Sea Survey cruises covered a more extensive area than the commercial fishery. Data from Sea Survey cruises during "February", "April", and "May–June", included many samples with a preponderance of one sex (Figure 6). These same cruises provided information which suggested a temporal and spatial difference in the sex composition of the population (Figure 5).

Whether anchovies segregate by sex over large areas or within schools or loose aggregations is difficult to ascertain. Continued occurrences of high female to male ratios from the fishery support a theory of a wide spatial difference in the sex composition. Because of the effectiveness of the purse seine, fishermen often captured the major portion, if not all, of the anchovy school they were setting on. It is assumed then that the samples from the fishery reflected the sex ratio of the anchovy schools in the areas fished. The ratios of these samples most often favored females and indicated the fishery was harvesting primarily portions of the population that exhibited a dominance of females.

The possibility exists that the sexes only loosely segregate and that they have a differential vulnerability to gear at different times and places. Concentrations containing mostly males may not form the large dense schools necessary for effective purse seining. Acoustic surveys found very few commercial size schools in the area southeast of San Clemente Island where males dominated. Also, schools with more females may have been easier to locate because of some difference in activity or density within a school.

Sampling bias may explain female dominance in fishery samples. For example, did the sampler tend to select larger (female) fish? There is no evidence, at this time, which either supports or rejects this suggestion. Did females have a higher fat content and segregate either in the vessel's hold or in the net after it was pursed alongside the vessel? Anchovies were sampled using a stratified random sampling plan with subsampling without replacement. Some mixture occurred in the offloading process because of the use of a wet pump. It would be difficult even to try to sample from the same portion of each vessel's load and, if we assumed that segregation occurs after capture, then dominance of males in samples would be more evident.

For some reason there may have been more than a loose segregation by sex. Evidence included the seemingly unexpected but frequent occurrence of 24:1, 23:2 and 0:25 type samples from Sea Survey cruises and less frequent occurrences of daily sex ratios as high as 6:1 (Figure 4) from the commercial fishery. One additional bit of evidence was a personal observation of the sexing of more than 350 anchovies from one mid-water trawl, of which only two were females.

I believe the sex ratio of the anchovy population off southern California is reasonably close to the 1:1 ratio expected, but that at times spatial segregation of sexes occurs. How and why this segregation occurs is mostly a matter of conjecture at this time. The seasonal appearance of abnormally high sex ratios for sea survey samples at a time when spawning was known to be occurring (MacGregor 1968) suggests some behavioral mechanism. Any further suppositions based on available data seem fruitless at this time. However, the commercial fishery as a sampling mechanism of the anchovy population off southern California is clearly biased. Additional supporting evidence (other than sex ratios) is the fact that the age composition of the landings and of Sea Survey samples differ markedly with a relatively weak representation of older year classes from the former (Mais, Calif. Dept. of Fish and Game, pers. commun.). Although fisheries biologists have maintained for years that the anchovy could sustain a much larger harvest, they seldom concerned themselves with the possibility that the sampling data from the commercial fishery presents a distorted picture concerning year-class strengths, mortalities, etc. These implications are no doubt important to population dynamicists and deserving of their attention.

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THE ORIGINS OF RAINBOW TROUT, *SALMO GAIRDNERI* RICHARDSON, IN NEW ZEALAND[1]

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The origins of the rainbow trout in New Zealand have long been the subject of controversy. The Baird Station on the McCloud River and the Russian River in California have been popularly named as principal sources. A search of records and literature in both New Zealand and America reveals rather conclusive evidence that the 1883 shipment of trout eggs to New Zealand originated from steelhead rainbow trout in Sonoma Creek, a tributary to San Francisco Bay. Progeny from this 1883 shipment were widely distributed throughout New Zealand, resulting in many self-sustaining populations. The Russian River as a source for these eggs is refuted. An earlier shipment of eggs in 1878 could well have been from cutthroat trout, the common native species of Lake Tahoe (California) from which the eggs were reportedly shipped. Other shipments in the late 1800's from the McCloud and Shasta rivers and in 1930 from Lake Almanor in California are discussed but are not considered to be as important as the 1883 shipment.

INTRODUCTION

The origins of the successful rainbow trout in New Zealand have long been the subject of controversy among trout anglers and fishery biologists. It is well known that they were shipped in 1883 from California via San Francisco and were received by the Auckland Acclimatisation Society, but the records were not clear in respect to the waters from which they originated.

The importance of genetically distinct stocks in relation to acclimatization has been recognized by several workers (Pautzke and Meigs 1940, Neave 1949, Shapovalov and Taft 1954, Ricker 1954, Needham and Gard 1959, MacCrimmon 1971, and Ricker 1972). Both migratory and non-migratory populations exhibit the genetic diversity necessary for speciation (Mottley 1954). Loss of rainbow stocks by seaward migrations has caused Tasmanian authorities to abandon stocking rainbow trout in rivers with access to the sea. (Lynch, Commissioner Inland Fish, Tasmania, pers. comm.)

With few exceptions, American fisheries literature has perpetuated the belief that Baird Station on the McCloud River in California was the source of nearly all exports of rainbow trout eggs to other countries, including New Zealand. Dollar and Katz (1964) put it typically: "From these McCloud River trout have been developed most of the hatchery trout stocks used today in U.S., Europe,

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New Zealand, and other countries".

The tendancy to rely on the primacy of the Baird Station may be due to the fact that it represented the first government supported effort to obtain rainbow trout ova for hatchery purposes in the U.S.A. Since the Baird Station was the major fish cultural operation at the time and was gathering, hatching, and distributing McCloud River trout eggs as well as chinook salmon, *Oncorhynchus tshawytscha,* in the late 1800's, it was logical for later workers to look upon it as a probable source of rainbow trout egg shipments to New Zealand, especially in the absence of any information to the contrary.

When New Zealand sources are examined there is no mention of the Baird Station and only oblique references to the McCloud River as a source for later shipments. Hobbs (1948) cited a reference which indicated that these eggs came from the Russian River, a coastal stream in California. A further treatment of this view is provided later in this paper. Another New Zealand view is that expressed by Stokell (1955), who believes that at least one source of New Zealand rainbows was Lake Almanor, California.

NEW ZEALAND RECORDS

The earliest record of a relevant importation was in 1878 by the Auckland Acclimatisation Society (A.A.S.). The Minute Book of June 10, 1878 notes the arrival of 10,000 eggs of trout from Lake Tahoe (California/Nevada, U.S.A.), a gift from Mr. T. Russell. Mortality was high, however, and by July 1, 1878 only 350 young fish were alive for distribution. The Minute Book of July 1, 1878 records the resolution that these fish were to be distributed in Lake Takapuna, some of the Waikato lakes, and Lake Omapere.

The Minute Book of August 5, 1878 records the arrival of 5,000 healthy ova from the same source as the previous shipment and the minutes for September 2, 1878 state that 2,000 young trout were available for distribution. The distribution of this second lot was left to the chairman and no locality is given. No further mention of this stock occurs in the records and it is not possible to say whether any individuals survived. Of the localities mentioned, Lake Takapuna was suitable for trout, as rainbows from a later shipment released in this water appeared to survive and grow (Ann. Report., A.A.S., 1888). Survivors of the Tahoe stock could have been overlooked with the success of later shipments.

The uncertainty extends also to the species comprising the 1878 consignment. The Lahontan cutthroat trout, *Salmo clarki henshawii,* was native to Lake Tahoe, and a rainbow trout, *Salmo regalis,* was reputed to be the native rainbow trout of Lake Tahoe (Snyder 1933). The status of *Salmo regalis* is now in doubt and it is now believed not to have been indigenous to Lake Tahoe (Behnke 1972).

The identification of trout species and the use of common names was sometimes a rather informal process among the fish culturists of the 1870's and 1880's. Common names were often applied as a matter of personal or local preference. Some early fish culturists attached little importance to species separation and some were known to change the common names on shipping labels so that the receiver would be "guaranteed" satisfaction. Thus, the common names under which many of these early shipments were made cannot always be relied upon.

Since the native trout of the Lake Tahoe area was the Lahontan cutthroat, it is possible, although not certain, that the 1878 shipment was of this species rather than rainbow. If, in fact, they were cutthroat trout, it raises a question of possible hybridization in the New Zealand waters where they were planted and where subsequent stocking occurred with rainbow trout. Where this has happened in America the rainbow usually dominate, and the cutthroat gradually disappear through the processes of competition and hybridization.

The 1883 Shipment

The most widely recognized importation, that of 1883, has been referred to frequently (Ayson 1908, Thomson 1922, 1926, Hefford 1926, Hobbs 1948). It is interesting to note that the Auckland Acclimatisation Society showed no intention of importing rainbow trout and was not aware of the correct identity of the shipment for several years. How this anomalous situation actually occurred will probably never be determined but the details are worth examining.

The Society was interested in developing the char or brook trout, *Salvelinus fontinalis,* and attempted to obtain some from California:

> "An order was also forwarded to San Francisco for ova of the well known brook trout (*Salmo fontinalis*) but for various causes it was unable to obtain any."
>
> (Ann. Report, A.A.S., 1881–82)

The order must have stood for it is recorded (Minute Book, February 13, 1883) that 10,000 brook trout ova from San Francisco had arrived but all were dead.

In late February or March, 1883 two successful shipments arrived:

> "The Secretary announced the arrival of 10,000 brook trout ova from San Francisco by the "City of New York", from which 500 healthy young fish had been hatched, and also of 12,000 ova of the same fish by the "Zealandia", about 5,000 or 6,000 of which appeared to be in good condition."
>
> (Minute Book April 3, 1883).

A further shipment of 30,000 ova was received from California in March 1884 (Minute Book April 8, 1884) but all were dead on arrival.

No useful comments can be made on the identity of the two unsuccessful shipments, but the two shipments in 1883 resulting in live fish were the subject of some confusion. The two shipments resulted in 4,000 to 5,000 fish, some of which were distributed in the Auckland area and some retained in the Auckland Domain to form a breeding stock (Ann. Report, A.A.S., 1884). In 1886 some of the fish retained in the ponds were sexually mature and eggs were obtained from them (Ann. Report, A.A.S., 1886) but doubts as to their identity were apparent. In the Minute Book (September 7, 1886) the fish are referred to as "black spotted Brook Trout". By February 1887 the fish were recognized as rainbow trout (Minute Book February 1, 1887), and are so identified after this date. The correction is referred to in Volume VI of the bound annual reports (1931–1938) and the secretary for that period, T. F. Cheeseman, is credited with the hand written alterations which appear in the annual reports of the period.

Hugh Craig of San Francisco, an honorary secretary to the Auckland Society, was instrumental in shipping a variety of plants and animals to Auckland and was directly involved in the 1883 shipment. Whether he was responsible for the identification problem is not known.

With this revised identification, the 1883 eggs became the first successful source of rainbow trout in New Zealand.

Information on the origin of the 1883 shipment was provided in a memorandum dated October 22, 1924 addressed to the Secretary, New Zealand Marine Department, from L. F. Ayson, Chief Inspector of Fisheries for the Marine Department. Part of this memorandum reads:

> "I believe that the first rainbow eggs (so called) were imported by the Auckland Acclimatisation Society from California about 1877 and two more small consignments were imported in 1883. These shipments were arranged for by Mr. Hugh Craig of San Francisco (an ex-New Zealander) and from inquiries I made on one of my visits to California, I was informed that the eggs were procured from a private hatchery on the Russian River owned by Mr. La Motte. Later I visited Mr. La Motte at Ukiah where he was managing a hatchery for the Great Western Railway Company. In speaking about rainbow trout in New Zealand, he stated that at the hatchery on the Russian River he handled only steelhead trout and the eggs he supplied to Mr. Craig were from steelhead trout so that the first so-called rainbow trout which were liberated in streams in the Auckland district, including those in the Rotorua and Taupo Districts, were hatched from these eggs."

Ayson's memorandum gave rise to the often held belief that the source of the 1883 shipments was the Russian River. As will be shown later, this was an incorrect assumption. However, the indication by La Motte that the eggs supplied to Hugh Craig were from steelhead trout is significant and is supported by later evidence. It also suggests that the eggs were not supplied to Craig as anything other than from steelhead trout.

The McCloud and Shasta Shipments

In the same memorandum, given in part above, Ayson states that further shipments of rainbow trout were imported:

> "Several shipments of rainbow eggs collected from the McCloud and Shasta Rivers were brought to New Zealand later, but I cannot say whether any of the fish hatched from these eggs were liberated in streams in the Auckland District or not. Some of the later shipments were brought out by the late Mr. Johnson of Opawa, Christchurch, and from his hatchery there he supplied eggs of these fish to different Acclimatisation Societies in the South Island. The South Island Acclimatisation Societies also procured rainbow eggs from the Auckland Society so that it is impossible to say whether the rainbow trout in Lake Hawea, Otago, are from eggs received from Auckland or from Mr. Johnson's stock fish at Opawa."

It should be noted here that there may have been confusion regarding the McCloud and Shasta rivers. The Baird Station was located near the town of Mt. Shasta, but not on the Shasta River. It seems likely that any rainbow trout eggs shipped from Baird Station came from the McCloud River.

Ayson's statement is confirmed in part by G. M. Thomson, a Dunedin naturalist who had made a particular study of faunal introductions to New Zealand. Thomson (1926, p. 88) states in discussing the origins of rainbow trout:

> "In later years, Mr. A. M. Johnson of Opawa, Christchurch, imported some more ova and the fry were probably distributed mostly in Canterbury."

Johnson maintained a private fish breeding establishment from 1875 to some time this century but unfortunately no records of his activities are known to exist (Scott 1964). If Ayson's statement on the origin of this stock can be accepted, then it appears that some time after 1883 Johnson was distributing this stock in the South Island.

The 1930 Shipment

The Annual Reports of the Auckland Acclimatisation Society indicate that a further successful shipment of rainbow trout eggs was made in 1930. The report for the year ending March 31, 1930 (Ann. Report, A.A.S. Vol. VI) states:

> "Advice has now been received that 100,000 ova derived from the non-migratory form of rainbow trout from the inland waters of California will be shipped about April or May. The ova, if received, will be hatched at the Internal Affairs Department's hatchery at Rotorua."

The shipment is confirmed in an historical survey entitled "The introduction of rainbow trout" in Volume VI (1931–1938) of the Annual Reports, where it is stated:

> ". . . it was not until the rainbow in the Rotorua Lakes were showing signs of worms in the lining of the stomach that Mr. Ayson imported a consignment of rainbow eyed-ova together with quinnet ova from California, some of the rainbow consignment going to the Rotorua hatchery."

Further details of the distribution are given by Ashby (1967) in a history of the Auckland Acclimatisation Society. On page 124 he states that in the last 3 months of 1930, 75,000 fry were hatched from the California eggs and were released at Mangatangi (30,000) and in the Waihou River.

It is possible that the remainder of the shipment was sent to Rotorua, but there is no information on the release of this part of the shipment.

A possible origin for this shipment is indicated in a letter of July 27, 1936 from J. O. Snyder, Chief, Bureau of Fish Conservation, California Division of Fish and Game, to G. Stokell, Canterbury:

> "Sometime ago at the request of some New Zealand authorities, I tried to determine the origin of the trout which were shipped to that country and found that I could not do it with any degree of certainty. The fish might have been the descendants of what we may determine are coast steelheads or they may have been taken from fishes that perhaps never reached the sea, having been blocked off through some natural or artificial means. For instance, I am quite certain that the last shipment of fish eggs to New Zealand came from Lake Almanor, an artificial reservoir now completely separated from the sea."

The date of the letter and the inland location are both consistent with the New Zealand statements on this shipment, and it is proposed to regard Lake Almanor as the probable source of the 1930 shipment.

CALIFORNIA RECORDS

As already mentioned, when the origins of foreign rainbow trout populations are considered in America they are generally assumed to have been the McCloud River and the old Baird Station. The history of Baird Station is well known, and the work of Livingston Stone, who operated the station for the U.S. Bureau of Fisheries, has been described by Stone (1883), Wales (1939), and Leitritz (1970). At one time there was controversy over the types of rainbow trout handled at the station which was operated primarily to obtain ova of chinook salmon. Needham and Behnke (1962) consider that ova were obtained from both migratory and resident forms.

Little or no evidence can be found in U.S. sources to support the Baird Station as the origin of the New Zealand rainbows. The only mention found was a brief comment in the U.S. Commissioner's Report (1887) that the New Zealand fishery is one of the best examples of a Baird Station success. However, this may well have been a reference to the successful introduction of chinook salmon, the eggs of which came from the Baird Station. Livingston Stone (First Report to Commissioners 1872–1873) mentioned that both New Zealand and Australia had requested rainbow trout ova from the California Acclimatisation Society. No records could be found to indicate any shipments from the Baird Station to New Zealand, but such records exist for consignments to England, Germany, Ireland, and Japan.

The paucity of evidence of any officially sponsored scheme by California authorities to ship ova to New Zealand tends to confirm the New Zealand view that arrangements were made to obtain ova from a private trout hatchery.

New Zealand authorities considered that California's Russian River provided the ova for the 1883 shipments. This view was based on the previously cited statements of L. F. Ayson in his memorandum of October 22, 1924. Although there was confirmation that a private hatchery had operated on the Russian River and that A. V. La Motte (whose name was associated with the 1883 shipments) was its operator, there seemed to be no confirmation of its operation in 1883. In fact, available records indicate the hatchery at Ukiah functioned between 1897 and 1927 (Leitritz 1970).

A search of old records revealed no evidence of a hatchery on or near the Russian River at Ukiah until 1897. The evidence showed clearly that La Motte commenced construction of the hatchery in March of that year (Ukiah Republican Press newspaper, 1897). Ukiah had no rail service until 1887; it seems unlikely that the 1883 shipment would have been sent from Ukiah by stagecoach.

A. V. La Motte operated a private hatchery in Sonoma County (Smiley 1883) and our further search produced a description of the formation of the Lenni Fish Propagating Company by A. V. La Motte in 1878 on Sonoma Creek, near the mouth of Graham Creek, in Sonoma County (Munro-Fraser 1880).

From this information we can piece together some of the possible reasons for the confusion which led to the belief that the Russian River was the source of the 1883 eggs. A. V. La Motte operated the Lenni Fish Propagating Company on Sonoma Creek from 1878 to sometime after 1883. He became associated with the North Pacific Game and Fish Club and was active with that organization in 1890 when his name was mentioned in a table of trout distribution by private hatcheries appearing in the Biennial Report of the California State Board of Fish Commissioners for the years 1888–1890. This table also indicates the North Pacific Game and Fish Club was active in taking eggs from trout trapped in Sonoma Creek and in planting trout in Sonoma County. It seems reasonable to assume that La Motte was active at Sonoma Creek from 1878 to at least 1890.

In 1897, La Motte had left the Sonoma Creek area to construct and operate a hatchery on Gibson Creek, a tributary of the Russian River. At the time he was contacted by L. F. Ayson he was operating that hatchery near Ukiah, and this led to the mistaken assumption that the 1883 eggs came from the Russian River.

But did the 1883 eggs come from the Sonoma Creek operation? Direct evidence of this was found in the following newspaper excerpt from the Sonoma Weekly Index for July 21, 1883:

> "Mr. A. V. La Motte, Superintendent of the Lenni Fish Propagating Company, informs us that the Company sometime since shipped 30,000 trout eggs to the Auckland, New Zealand, Acclimatisation Society, and have received the report from them that they arrived in better order than any prior lot they had received from other parties. This we consider another feather in Sonoma's cap, and a big, bright one, too."

In view of the foregoing and because Sonoma Creek had a run of steelhead which could be easily trapped, we consider it highly unlikely that the 1883 eggs came from anywhere but Sonoma Creek.

Our thoughts in this regard are reinforced by entries in the Biennial Report of the State Board of Fish Commissioners of the State of California for the years 1888–1890 (p. 51) which indicate that trout were being trapped in Sonoma Creek by permission of the California State Fish Commission and were listed as "native trout".

Sonoma Creek flows directly into the northern part of San Francisco Bay and has always had a good run of steelhead, although extensive development in the drainage and heavy fishing pressure have taken their toll in recent years. Other strains of rainbow trout and perhaps other species of trout have been planted in Sonoma Creek since 1883, but it is unlikely that it was subjected to such activities before that date. As far as is known, the only trout in Sonoma Creek today are steelhead.

The small difference between the New Zealand records (32,000 eggs in three shipments) and the American information (30,000 apparently in one shipment) is not viewed as significant. The numbers are reasonably close, considering fish cultural practices of those days, and La Motte could have simply omitted specific references to more than one shipment when he informed the newspaper of his success.

We conclude from this new evidence that the 1883 shipment of rainbow trout eggs were from steelhead originating in Sonoma Creek, California and not from the McCloud or Russian rivers as previously supposed.

No evidence can be found in American records for the 1878 shipment of eggs from Lake Tahoe. I.C. Frazier, a recognized fish culturist who was associated with some of the acclimatization societies in the early 1870's (Leitritz 1970), established a hatchery with rearing ponds on the Truckee River below Lake Tahoe. During this same period the Comer brothers operated a hatchery on the Truckee River and obtained their eggs from fish caught in the tributaries to Lake Tahoe (California Commissioners of Fisheries Report, 1870 and 1871). Either of these operations might have been the source of the 1878 shipment but, if so, the species was very likely Lahontan cutthroat trout, *Salmo clarki*, rather than rainbow trout.

Other than the previously cited letter of July 27, 1936 from J.O. Snyder, no records could be found regarding the source of the 1930 shipment of rainbow trout eggs. Snyder stated that he was quite certain that the eggs came from Lake Almanor, an artificial reservoir without access to anadromous fish. The State's Lake Almanor hatchery, operated at the town of Chester from 1931 to 1933, handled brown, *Salmo trutta*, brook, *Salvelinus fontinalis*, and rainbow trout. The

Mud Creek Egg Collecting Station which was operated at Lake Almanor from 1928 to 1931 to collect rainbow trout eggs may have been the source of the 1930 shipment, but this could not be confirmed.

Unfortunately, no records can be found of the shipments to A.M. Johnson of Opawa, Christchurch, which, according to Ayson, were from eggs collected on the McCloud and Shasta rivers in California. It is puzzling that the McCloud River is cited as the source of these eggs because shipments to foreign countries from the Baird Station seemed to be well recorded, but there is no mention of a shipment of trout to New Zealand in the available reports.

DISCUSSION AND CONCLUSIONS

The foregoing evidence lends strong support for the significance of the 1883 shipments of eggs from California as the principal source for the acclimatization of rainbow trout in New Zealand. It also refutes previous beliefs that the 1883 eggs came from either the McCloud or Russian rivers but rather conclusively points to a steelhead ancestry originating from Sonoma Creek, a tributary to San Francisco Bay in California.

Progeny from this 1883 shipment were widely distributed throughout New Zealand by the Auckland Acclimatisation Society and many of these liberations resulted in self-sustaining populations. The present day distribution of rainbow trout is detailed by Allen and Cunningham (1957).

Other shipments which must also be recognized, but whose influence on the total acclimatisation of rainbow trout in New Zealand remains in doubt, occurred in 1878, late in the 19th century, and in 1930 (Table 1). The 1878 eggs were reportedly from Lake Tahoe and although possibly from rainbow trout, they were more likely cutthroat trout, the abundant native salmonid in the Tahoe area at that time. The shipment will, for purposes of this paper, be listed as either rainbow or cutthroat trout. Thus, although it might be argued that the 1883 shipment represented a relatively unmixed stock, since transfer of stocks in California then was not yet widespread, it cannot be maintained that present day populations of New Zealand rainbow trout are descended from this shipment only.

TABLE 1. Origin of New Zealand Rainbow Stocks

Date	*No. of lots*	*Source*	*Exporter or supplier*	*Importer*	*Live fish distributed*
1878[1]	2	Lake Tahoe, California	?	Auckland Acclimatisation Society	2,000 +
1883....................	3	Sonoma Creek California	A.V. La Motte	Auckland Acclimatisation Society	4,400 +
Late 19th Century	?	McCloud and Shasta rivers (?)	?	A.M. Johnson (Opawa)	Yes (Number unknown)
1930....................	1	Lake Almanor California	California Division of Fish and Game (?)	Auckland Acclimatisation Society	75,000

[1] The 1878 eggs were more likely to have been from cutthroat trout, but in the absence of conclusive proof they are included in the table.

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THE FIRST EASTERN PACIFIC RECORDS OF BULLEYE, *COOKEOLUS BOOPS* (BLOCH AND SCHNEIDER, 1801), (PISCES, PRIACANTHIDAE)

At least 10 specimens of *Cookeolus boops* have been taken in the eastern North Pacific. Eight of these that were saved measured 148–226 mm (5.83–8.90 inches) SL. These are the first valid records of bulleye in the eastern Pacific Ocean. Its previously known range was both sides of the Atlantic and the Indo-west Pacific (Caldwell 1962) but even there, the bulleye is a relatively uncommon fish. Anderson *et al.* (1972) described six specimens from the western North Atlantic, bringing the total number of specimens recorded from that region to 13.

My material consists of two specimens in the collections of Scripps Institution of Oceanography (SIO 74-72, 169 mm or 6.65 inches SL, from 320 km or 200 miles west of Gulfo de Tehuantepec, Mexico, and SIO 74-80, 148 mm or 5.83 inches SL, from lat 17°04′ N, long 104°23′ W) and four specimens from the Natural History Museum of Los Angeles County (LACM 30505-1, 189 mm or 7.44 inches SL, from 560 km or 350 miles SW of Acapulco, Mexico; LACM 30506-1, 171 mm or 6.73 inches SL, from off Gulfo de Tehuantepec; LACM 31796-2, 180 mm or 7.09 inches SL, from 64 km or 40 miles off Islas Tres Marias, Mexico; and LACM 31999-1, 226 mm or 8.90 inches SL, from 80 km or 50 miles outside Islas Tres Marias).

The specimens collected from the eastern Pacific are smaller than the largest recorded from the western Atlantic (507 mm or 20.0 inches SL) (Anderson *et al.* 1972), or from Hawaii (355 mm or 13.2 inches SL) (Gosline and Brock 1960). For comparison I have included descriptive data on the two specimens housed at SIO (Table 1):

> Dorsal-fin rays IX–X,13; anal-fin rays III, 13; pectoral-fin rays 18; pelvic-fin rays I, 5; principal caudal rays 8+8; lateral line scales 55; gill rakers on lower limb of first arch 17–18. These counts fall within the ranges given by Anderson *et al.* (1972) for western North Atlantic specimens.

TABLE 1. Measurements of Eastern Pacific *Cookeolus boops* in Hundredths of Standard Length.

	SIO 74-72	*SIO 74-80*
Standard length (mm)	169	148
Head length	36	37
Length of upper jaw	18	18
Length of orbit	12	12
Length of longest pectoral ray	20	21
Length of longet pelvic ray	55	57
Length of first dorsal spine	6	–
Length of longest dorsal ray	31	34
Length of longest anal ray	–	28
Body depth	48	48
Depth of caudal peduncle	11	12
Length of preopercular spine	5	5
Length of dorsal base	61	63
Length of anal base	31	33
Length of pectoral base	7	8

The following data on coloration of the 169-mm or 6.65-inch SL specimen (SIO 74-72) (Figure 1) were recorded while the specimen was still frozen: uniform light pinkish red; dusky spotting on tips of jaws and dorsally on head and dorsum posterior to ninth dorsal spine; two or three scattered dusky blotches on caudal peduncle; dorsal fin with light white to yellowish spines and rays, membrane uniformly black overlain with yellowish orange posterior to eighth ray; anal fin with white to yellow rays, membrane with dusky spots becoming uniformly dusky over distal half of fin, after ninth ray becoming light pinkish yellow; caudal fin yellowish with orange membranes; pectoral fins light yellowish; pelvic fins with light rays, membrane with dusky spots becoming uniformly dusky over distal half of fin.

FIGURE 1. Bulleye, *Cookeolus boops,* collected 300 km off Golfo de Tehuantepec, Mexico (SIO 74-72). *Photograph by the author.*

Although the bulleye has been collected previously at or near the bottom, one individual was obtained from the stomach of a yellowfin tuna, *Thunnus albacares* (Caldwell 1962). Since all the eastern Pacific specimens have been collected by purse seiners fishing for tuna, this species is probably more pelagic than benthic. This conclusion is in agreement with that of Fitch and Lavenberg (1975).

Fitch and Lavenberg (1975) state that they believe *Pristigenys* to be the senior synonym of *Cookeolus* rather than *Pseudopriacanthus*. Current studies on the intrarelationships of the family Priacanthidae (Fritzsche and Johnson MS) indicate that there is no evidence to supprt synonymy of the fossil genus *Pristigenys* with any of the extant priacanthid genera.

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A HERMAPHRODITIC CALIFORNIA HALIBUT, *PARALICHTHYS CALIFORNICUS*

A hermaphroditic California halibut was captured February 26, 1970, off Morro Bay, California. The fish was received by Morro Bay Fisheries, bought by Independent Fish Company (San Pedro), and finally sold to Billy's Fish Market (Santa Monica) on February 27. The retail marketman, Mr. Eldon Hardy, notified the Department of Fish and Game of this unusual specimen and the intact gonads were picked up by Department personnel. Though the fish was not observed, biologists familiar with flatfish anatomy identified the gonads as belonging to a halibut.

Mr. Hardy described the halibut's total length to be as long as his cleaning board (61 cm or 24 inches) and weighing 4½ to 5½ kg (10 to 12 lb). The fish was unusually deep bodied and 10 to 11 cm (4 to 4½ inches) thick. Its weight was more than 2½ times that of the average halibut at this length. The gonads were normal in appearance and coloration (Figure 1). The testes had running milt and the ovaries contained maturing granular eggs. The gonads are preserved in Bouins fluid and are available at the California State Fisheries Laboratory, Long Beach.

FIGURE 1. Male and female gonads of a hermaphroditic California halibut (the lower conical portions are the ovaries). *Photograph by author.*

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SPINAL COLUMN DEFORMITY IN A PILE SURFPERCH, *DAMALICHTHYS VACCA*

Damalichthys vacca, a member of the viviparous fish family Embiotocidae, is common to the shallow coastal waters of California (Miller and Lea 1972). On 19 April 1973, California Department of Fish and Game personnel collected a small number of *D. vacca* by beach seine in a small coastal embayment formerly known as Queen's Way Lagoon (Long 118°11′40″W, Lat 33°45′40″N) and presently part of the City of Long Beach's Shoreline Aquatic Park.

One of the *D. vacca* was noticeably stubby when compared to the other pile surfperch collected. The stubby specimen was a female heavily laden with young and measured 175 mm (6.9 inches) standard length (SL). Ten embryos were removed and preserved in a 10% formalin solution with the stubby female and other portions of the catch. A radiograph of the stubby *D. vacca* and another pile surfperch (Figure 1) collected in the same beach seine set was taken to determine if the fish's unusual shape was due to skeletal abnormalities. The 10 embryos also were radiographed (Figure 2), although they did not appear to have any structural deformities.

FIGURE 1. (Above) Abnormally developed *Damalichthye vacca* exhibiting vertebral fusion and malformations of neural and hemal spines. (Below) Normally developed *D. vacca.*

FIGURE 2. Embryos removed from abnormally developed *Damalichthys vacca.*

The radiograph of the stubby *D. vacca* revealed numerous vertebral fusions along the spinal column, particularly in the caudal one-half, and malformed neural and hemal spines along the entire column (Figure 1). Miller and Lea (1972) list the range of vertebrae in *D. vacca* as 34 to 39. The normally developed specimen in the radiograph had 38 vertebrae while the abnormally developed specimen appeared to have 33 to 35 (Figure 1). No lateral or dorso-ventral curvature was evident. The embryos exhibited no skeletal deformities; although one had been damaged in its removal from the parent (Figure 2).

Skeletal anomalies have been reported for many species of fish (Dawson 1964, 1966, 1971, 1975) but to my knowledge none have been reported for *D. vacca.* The possible environmental or genetic causes of the spinal column deformity observed in *D. vacca* are too numerous to discuss here and I refer the reader to Hickey (1972) for appropriate treatment of that topic. However, I believe that the lack of spinal column deformity in the embryos strongly suggests that the cause of the abnormal condition in the parent is environmental in nature.

ACKNOWLEDGMENTS

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A NOTE ON PRODUCTION MODELING OF POPULATION WITH DISCONTINUOUS REPRODUCTION

Production models commonly employ the assumption that reproduction and recruitment are continuous events. However, for many species, reproduction occurs at known intervals; in fish species whose behavior and physiology are closely linked to environmental conditions, reproduction is often annual or semi-annual.

Using the usual assumption of exponential rates of mortality, with no fishing, we have the equation

$$B_t = B_o e^{-(M-G)t} + R \qquad (1)$$

where B_o is initial biomass at time of reproduction,
t is interval between reproductions,
B_t is biomass at time t (the following reproduction),
M is instantaneous coefficient of natural mortality,
G is instantaneous coefficient of somatic growth,
and R is a pulse recruitment, determined by previous reproductions.

If we consider the effects of continuous fishing, we have

$$B_t = B_o\, e^{-(F+M-G)t} + R \qquad (2)$$

where F is the instantaneous coefficient of fishing mortality. Equilibrium fishing intensity (F_e) is that value of F which results in a constant population size ($B_t = B_o$), and we can write

$$B_o = B_o e^{-(F_e+M-G)t} + R \qquad (3)$$

The corresponding equilibrium yield (Y_e) is

$$Y_e = B_o(F_e/(F_e + M - G))\ (1 - e^{-(F_e+M-G)t}) \qquad (4)$$

Potential population growth ($\triangle B_{pot}$) is the increase in population size whic would occur if there were no fishery, and is equal to $B_t - B_o$ in equation (1) However, B_o is also given by equation (3), so $\triangle B_{pot}$ is calculated by (1) minu (3), and recruitment terms cancel:

$$\begin{aligned}\triangle B_{pot} &= B_o e^{-(M-G)t} + R - (B_o e^{-(F_e+M-G)t} + R)\\ &= B_o\,(e^{-(M-G)t} - e^{-(F_e+M-G)t}) \qquad (5)\end{aligned}$$

The above equation allows us to compare potential population growth unde conditions of no fishing (5) with equilibrium yield (4). This comparison is best expressed as a ratio (δ) which is a function of F, M−G and t:

$$\delta = \triangle B_{pot}/Y_e = [B_o(e^{-(M-G)t} - e^{-(F_e+M-G)t})]/[B_o(F_e/(F_e+M-G))(1-e^{-(Fe+M-G)t})]$$

$$= [(F_e+M-G)\,e^{-(M-G)t}(1-e^{-F_e t})]\,/\,[F_e(1-e^{-(F_e+M-G)t})] \quad (6)$$

Example values of δ are given in Table 1. The quantity δ may be thought of as a biological discount factor. When equilibrium yield is not harvested, the population will grow, but by an amount less than the yield which is foregone.

The values in Table 1 indicate that the quantity (M–G)t is much more influential than Ft in determining the value of δ. Therefore, a single value of δ may be sufficient for most modeling purposes, and δ can be treated as a constant for all likely values of F. Since the above calculation is for continuous fishing, seasonal fisheries will give different values of δ. For fisheries occurring just before reproduction, δ will be near 1, and for fisheries occurring just after reproduction δ will be smaller than the values in Table 1.

Table 1. Example Values of δ.

	Ft	
(M − G)t	*0.1*	*1.0*
0.0	1.00	1.00
0.1	0.95	0.94
0.2	0.90	0.89
0.3	0.86	0.84
0.4	0.81	0.79
0.6	0.73	0.70
0.8	0.65	0.61
1.0	0.58	0.54
1.5	0.43	0.38

Consideration of δ is particularly important in catch-transition methods of estimating the parameters of production models such as in the generalized production model of Pella and Tomlinson (1969). Continuous reproduction is a basic assumption in production models, but they are very often empirically applied to fisheries wherein reproduction is distinctly seasonal. Under continuous reproduction, the relationship

$$\triangle B = Y_e - Y \quad (7)$$

where Y is actual harvest, is appropriate. However, when reproduction is discontinuous, the relationship

$$\triangle B = \delta\,(Y_e - Y) \quad (8)$$

should be used. Equation (7) is therefore a special case of equation (8), wherein $t = 0$ and $\delta = 1$. Since production modeling is often applied when biological information is minimal, a reasonable guess for the quantities (M − G) and t should be sufficient, and will certainly be an improvement over use of equation (7). Estimates of the catchability coefficient and the asymptotic maximum population size which are obtained from the catch-transition approach are often considered to be unreliable (Pella and Tomlinson 1969) and this modification should improve accuracy.

Again, the discount factor may be an important consideration in rehabilitating depleted resources. This factor may be a contributory cause of the apparently slow recovery of the Peruvian anchoveta fishery, where $\delta = 0.6$ is a likely value.

Conversely, when the potential rate of growth of a population is known, and equilibrium yield is to be estimated, maximum sustainable yield will be greater than maximum population growth rate by δ^{-1}. Such is the case in the northern anchovy fishery in California, where $\delta^{-1} = 1.54$.

In the case of marine mammals, the appropriate time interval (t) would not be the gestation period, since mortality would result in the loss of offspring as well as the parent. Rather, t would be the interval between the time when the offspring would survive the death of the mother and the time when the mother would next become pregnant. Since this is a relatively short time, and M—G is relatively small, the discount rate for marine mammals may approach 1.0.

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OBSERVATIONS OF AGONISTIC BEHAVIOR IN THE TREEFISH, *SEBASTES SERRICEPS* (SCORPAENIDAE)

On March 9, 1976, while scuba diving near the west end of Santa Catalina Island, Los Angeles County, California, I observed a display of agonistic behavior between two treefish, *Sebastes serriceps* (Jordan and Gilbert). I came upon the treefish at a depth of about 7 m (23 ft) in front of a rocky cave approximately 0.5 m (20 inches) high by 1 m (39 inches) wide, and several meters deep. A 25-cm (10-inch) fish, subsequently identified as the defender of the cave, had the head of a 20-cm (8-inch) treefish to about mid-orbit in its mouth. The two fish slowly moved back and forth in front of the cave for several minutes while interlocked in this manner.

After the two separated, the larger treefish went into the cave and the intruder swam several meters away. When the intruder returned to the cave entrance, he was approached by the larger fish with erect dorsal fin and a widely gaping mouth. The intruder responded by erecting its dorsal fin and opening its mouth. Both fish, facing one another, then made a series of short darts in an attempt to grasp the other's jaw. When one fish did grasp the other's jaw, the attacked fish would bite down on the attacker's snout. In this manner, the two fish again moved back and forth.

During one dart, the attacker missed the lower jaw and its head went completely into the other fish's mouth. On another dart, one fish bit only one side of the lower jaw and the two hovered at right angles for a short period.

The defender did not initiate agonistic behavior until the intruder approached the cave entrance. At no time during any of the described encounters was contact sufficient to cause visible damage to either fish.

This grasping behavior, which might inhibit respiratory efficiency, terminated when the fish with the other's head in its mouth released its grip. This release might be stimulated by reduced blood oxygen levels.

On February 20, 1970, a similar observation was made at the Los Angeles County Fish and Game Commission's Redondo Canyon Artificial Reef by John Duffy and Robert Hardy (Calif. Dept. Fish and Game, pers. commun.). They observed and photographed what they presumed to be one sequence in the mating behavior of the treefish. Two animals oriented head-to-head, grasped each others lips, held on for several minutes at a time, and occasionally shook each other violently. Unfortunately, the photographs they took are not of sufficient quality to be published.

Little information has been published on aspects of treefish life history and behavior. Phillips (1957) and Miller and Lea (1972) gave systematic accounts of the treefish and described the adult color as yellow to olive with five or six black bars along the body. Feder, Turner, and Limbaugh (1974) reported that treefish are aggressive, territorial, and take shelter in rocky crevices.

The behavior exhibited by the treefish on both occasions was not observed to completion, nor was either pair of fish collected; thus it cannot be determined if the behavior was territorial or reproductive. In contrast to their normal adult coloration, the treefish I observed were dark green overall; the black bars were indistinct. However, photographs of the treefish observed at Redondo Canyon show the usual adult coloration.

Leon Hallacher (U.C. Berkeley, pers. commun.) has observed displays similar to those of the treefish in the gopher rockfish, *Sebastes carnatus,* including the facing and grasping behavior. He considers such behavior rare, having observed it only once in 7 years of diving. Kim McCleneghan and James Houk (Calif. Dept. Fish and Game, pers. commun.) observed similar behavior in the kelp rockfish, *S. atrovirens.*

Comparable displays, manifested by two individuals facing each other with mouths agape and dorsal and pectoral fins erect, have been observed in several Californian fishes, including sheephead, *Pimelometopon pulchrum* (T. J. Mueller, Univ. So. Calif. pers. commun.) and the blackeye goby, *Coryphopterus nicholsii* (Wiley 1973). I have seen such displays in the blue banded goby, *Lythrypnus dalli.* Physical contact accompanying such activities has been only a nip, which caused no apparent damage, and not prolonged grasping bouts as in these treefish.

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—Peter L. Haaker, Calif. Dept. Fish and Game, Marine Resources Region, 350 Golden Shore, Long Beach, California 90802. *Accepted for publication March 1978.*

BOOK REVIEWS

Bright Rivers

by Nick Lyons; J. B. Lippincott Co., Philadelphia and New York, 1977; 166p. $8.95.

Bright Rivers is an autobiography. It is a reflection on, and recitation of the successes and failures of Nick Lyons as a fisherman. He uses the qualities developed in his profession of English professor to enliven this work in a "literary" style. None of us could write so lucidly about fish lost and found.

However, Lyons has a tendency to dwell a little too long and often on his fishing skills, or lack of skills. I think Nick Lyons is a better fisherman than he lets on. Close personal contact with the better fishermen of the United States as he has, must sooner or later rub off. One consolation is that our exposure to his troubles reduces the sting of our own.

The book is divided into two parts. The first deals primarily with eastern fishing, focusing especially on a summer vacation spent in the Catskills. The second deals with fishing trips to the west, especially to Montana. He really gets turned on by Montana—it must be heaven to him. It is in this section that his writing seems to be more alive. The western reader may identify better with this section. He may also be thankful there are more waters to fish and larger fish to be found in this part of the country. Apparently 10-inch fish are a prize in many heavily fished waters where Lyons usually fishes. I hope the author fully develops his skills as a fisherman. When he does, his literary training, combined with angling skill, should coalesce to really produce fine quality angling works.—*Ed Littrell*

The Fresh and Salt Water Fishes of the World

by Edward C. Migdalski and George S. Fichter; Alfred A. Knopf, Inc. N.Y., 1976. 316 pp., illustrated in color. $25.00.

This beautifully illustrated book represents another attempt to present to the general reader an up-to-date review of the world's fish families. The very readable text leads off with a short discussion of classification, fossil fishes, fish morphology, anatomy, physiology, age and growth, and migrations. The discussion of the families highlights size, description, and life histories of some of the more well known as well as rare species. Full color illustrations of over 500 species were produced by Norman Weaver and are truly spectacular.

Unfortunately, I found the text to contain many errors or omissions. For example, the record size of the white shark, *Carcharodon carcharias,* is reported to be 36.5 ft. However, a recent paper indicates that this record is invalid; the statement that most chinook salmon, *Oncorhynchus tshawytscha,* are caught as they move upstream to spawn, completely ignores the large ocean catches by sport and commercial fishermen. The statement that the pink salmon, *O. gorbuscha,* "occurs in greater abundances further south than do other species", I assume is a typographical error. Apparently the authors did not refer to Miller and Lea's *Fish Bulletin 157* as there are several mistakes in geographical ranges, size records, and names of California fish.

On the positive side, some of the species descriptions I found to be very informative as well as entertaining, in particular, the narrative on the carp, *Cyprinus carpio.*

Despite the faults in the text, I feel that the excellent color illustrations will make this book very attractive to professionals and non-professionals who never tire of looking at fish.—*Daniel W. Gotshall*

Inland Fishes of California

by Peter B. Moyle; Univ. of Calif. Press, Berkeley, Los Angeles, London, 1976; 405 pp; illustrated $20.00.

Inland Fishes of California is a much needed and valuable reference book for the student, biologist, amateur naturalist, or interested angler. Unfortunately, there are errors throughout the text, which undoubtedly will be corrected in subsequent editions. Meanwhile, Dr. Moyle has indicated that any purchaser may get a three-page list of errors and additions to *Inland Fishes of California* by writing to:

Dr. Peter B. Moyle
Department of Wildlife and Fisheries Biology
University of California, Davis 95616

A significant difference exists in the quality of the drawings and there is a general lack of illustrations of adult fish. In fact, some of the illustrations resemble juvenile specimens recently removed from bottles of formalin or alcohol. When asked why his illustrations were predominately of juvenile specimens, the author replied that it was partly a matter of availability and partly because of his intention to illustrate sizes which might be encountered most often by students using the usual collecting techniques (traps and seines).

I did not test the keys, however they seemed quite simple and probably would be easy to use.

Although I share the author's feelings about the loss or deterioration of populations of native (particularly non-game) species, his preoccupation with this sentiment reduces the objectivity of his presentation. He tends to portray an aura of helplessness and resignation. When discussing the Sacramento-San Joaquin Delta in his chapter entitled "Ecology", he says "Today it hardly seems worthwhile even to devote much time to the interactions among the introduced species since if any stable associations have been established they are likely to be soon upset as the waters of this zone continue to change, and as other new species become established in them." One could argue that in view of gross changes which are occurring, it should be desirable to predict the effect of such changes and to consider the desirability of modifying them.

His strong identification with native species tends to make his "Ecology" chapter more of a description of what the system was, or might have been, rather than the ecology of what now exists. Introduced species seem to be regarded as "noise" to the theoretical system.

In his discussion of the ecology of Clear Lake, he gives a somewhat detailed description of the ecological relationships of the native species which previously inhabited the lake. Although, as he points out, "at least 13 species are now established and only 4 of the native species are still maintaining large populations", he dismisses recent ecological relationships by saying "too little is known about their ecology to make reasonable speculations about their interactions", and that the species composition is still changing. No one can deny that much change has taken place recently, but on the other hand, many ecological studies also have been made recently in Clear Lake. One wonders if the ability to speculate is more constrained in the face of recent "hard", but conflicting data. Certainly, the dynamics of change, itself, is an important facet of ecology, which is glossed-over lightly.

His descriptions of change consistently carry value judgments. In general, changes brought about by man's influence are labeled "bad", while changes which took place without man's influence are considered "good".

Knowing the author, one is aware that this is precisely the message that he is intending to convey. While I appreciate his sentiments, empathize with him in these feelings, and recognize his right to express them, I feel that a more objective treatment of these subjects would have improved the text considerably.

In summary, however, this is an outstanding book and should be included on the bookshelf of any ecologist, student, or angler interested in California's inland fishes or fisheries.—*John Radovich*

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