

Chapter 18 Osmeridae: Smelts

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The family Osmeridae, commonly known as Smelts, consists of 12 species in 7 genera, which are widely distributed within subarctic and temperate coastal waters in the Northern Hemisphere. Smelts are common in the North American Great Lakes and have a Holarctic distribution throughout the cooler northern waters of the Atlantic and Pacific Oceans (McAllister 1963; Nelson 2006). Smelts are small (<40 cm), elongate, silvery fish and have a curious cucumber-odor (the Greek *osme* means bad smelling) (McAllister 1963), which serves as a yet unknown function (McDowall et al. 1993). Like salmonids (Trouts and Salmon), osmerids have an adipose fin and exhibit a diversity of life histories ranging from entirely fresh water to true estuarine to anadromous. Many species have highly flexible migration strategies and a broad range of behavioral plasticity indicating an ability to adapt to different aquatic environments throughout their life history (Hobbs et al. 2006; McDowall 2008; Ohji et al. 2008; Fig. 18.1). Anadromous species of Smelts run in great schools along the coastline during their spring spawning migrations and serve as forage fish for a variety of fish, bird, and mammal predators (Moyle 2002).

DIVERSITY AND DISTRIBUTION

Within North America, six species in four genera have at least one life-history stage taking place in fresh water: *Hypomesus nipponensis* (Wakasagi) (Fig. 18.2); *Hypomesus olidus* (Pond Smelt) (Fig. 18.3); *Hypomesus transpacificus* (Delta Smelt) (Fig. 18.4); *Osmerus mordax* (Rainbow Smelt) (Fig. 18.5); *Spirinchus thaleichthys* (Longfin Smelt) (Fig. 18.6); and *Thaleichthys pacificus* (Eulachon, often pronounced hooligan or ooligan) (Fig. 18.7). Except for

the Rainbow Smelt, these species are generally confined to the northeastern Pacific Ocean and associated drainages. Here, we cover the native distribution of North American Smelts, introductions of native species outside their range in North America, and note non-indigenous species of Smelts introduced into North America.

Genus *Hypomesus*

The genus *Hypomesus* is represented by five species inhabiting fresh, brackish, and coastal marine waters of the northern Pacific Rim (Saruwatari et al. 1997; Ilves & Taylor 2007, 2008). Two of these are native to and widespread in northwestern North America (Fig. 18.8). The Pond Smelt, *H. olidus*, is broadly distributed from the Copper River north to the Kobuk River, Alaska, and eastward into the Peel River (Yukon) and Mackenzie River delta (Inuvik), Canada (Morrow 1980), as well as the Kamchatka Peninsula and northern Japan (Saruwatari et al. 1997). The Delta Smelt, *H. transpacificus*, is a euryhaline species endemic to the upper San Francisco Estuary, including the Sacramento-San Joaquin River basin, California (Moyle 2002). The Wakasagi, *H. nipponensis*, is a native of Japan, which was introduced as a forage fish in several California localities. Subsequent dispersals and transfers allowed Wakasagi to become established in the Sacramento River watershed and several reservoirs in northern California (Moyle 2002). A phylogenetic reconstruction of species within the genus and biogeographical analyses using mtDNA and nDNA data suggest Cenozoic (≥ 2.6 mya) climate changes were an important driver of diversification in the group. Although precise dating of divergences in *Hypomesus* is infeasible because of a lack of fossil information, the best estimates suggest divergences

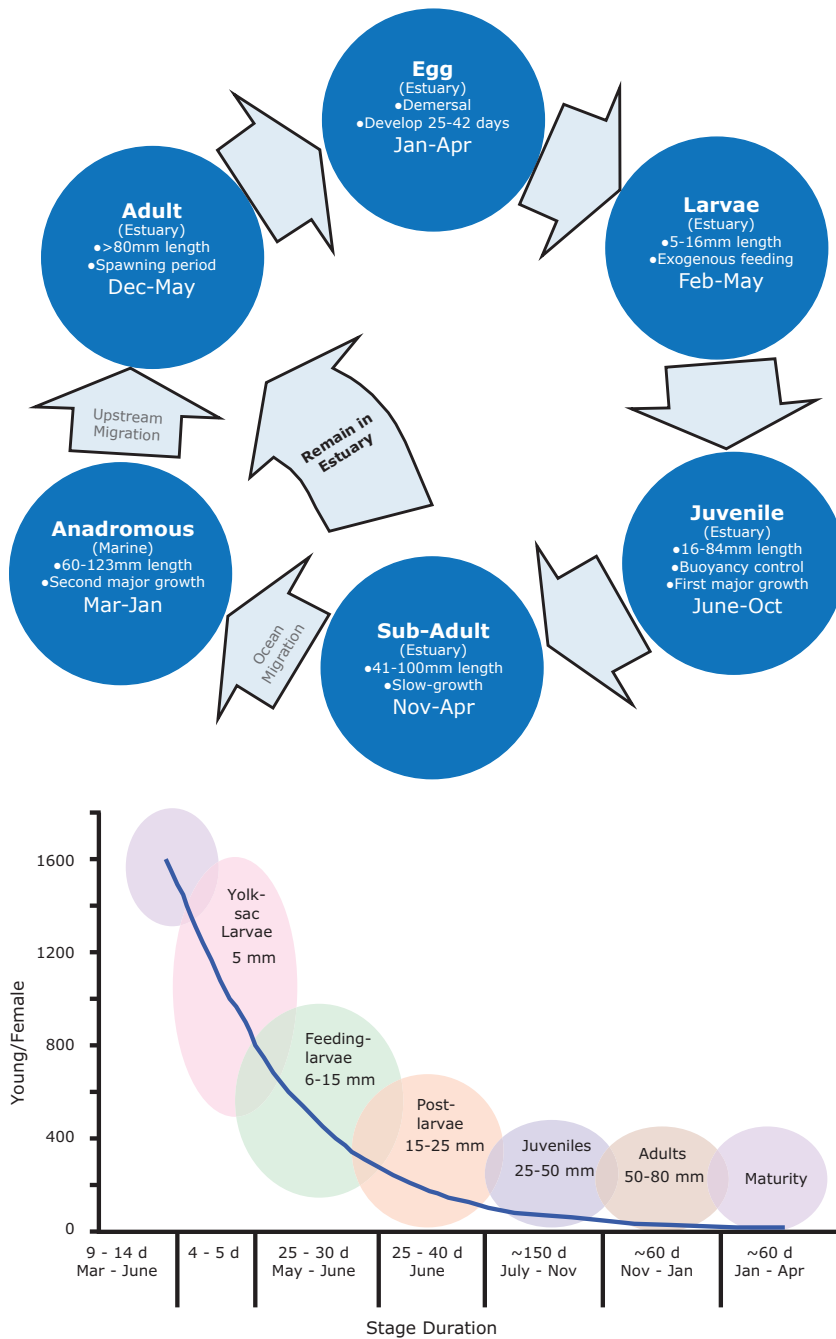


Figure 18.1. Examples of the complex life histories of anadromous Smelts, the Longfin Smelt (*upper*), *Spirinchus thaleichthys*, and Delta Smelt (*lower*), *Hypomesus transpacificus*, in the San Francisco Estuary (redrawn from Merz et al. 2013, Longfin Smelt, and Bennett 2005, Delta Smelt).

predate the climate fluctuations of the Plio- and Pleistocene epochs often invoked to explain the trans-Pacific relationships in many fishes (Ilves & Taylor 2008).

Genus *Osmerus*

The genus *Osmerus* has two North American representatives, the Pacific Rainbow Smelt, *Osmerus dentex*, and the Rainbow Smelt, *O. mordax* (Fig. 18.5). Historically, the two taxa were recognized as subspecies of *O. mordax* (or

by some as subspecies of the European Smelt, *O. esperlanus*); *O. m. mordax*, the Rainbow Smelt, distributed in the North Atlantic Ocean, and *O. m. dentex*, the Pacific Rainbow Smelt, occurring in the North Pacific Ocean (McAllister 1963; Scott & Crossman 1973; Page & Burr 2011). Because these forms (along with the European Smelt) were largely allopatric, the genus has had a long history of systematic, taxonomic, and zoogeographic uncertainty (see summaries by Haldorson & Craig 1984; Taylor & Dodson 1994; Mecklenberg et al. 2011; and references

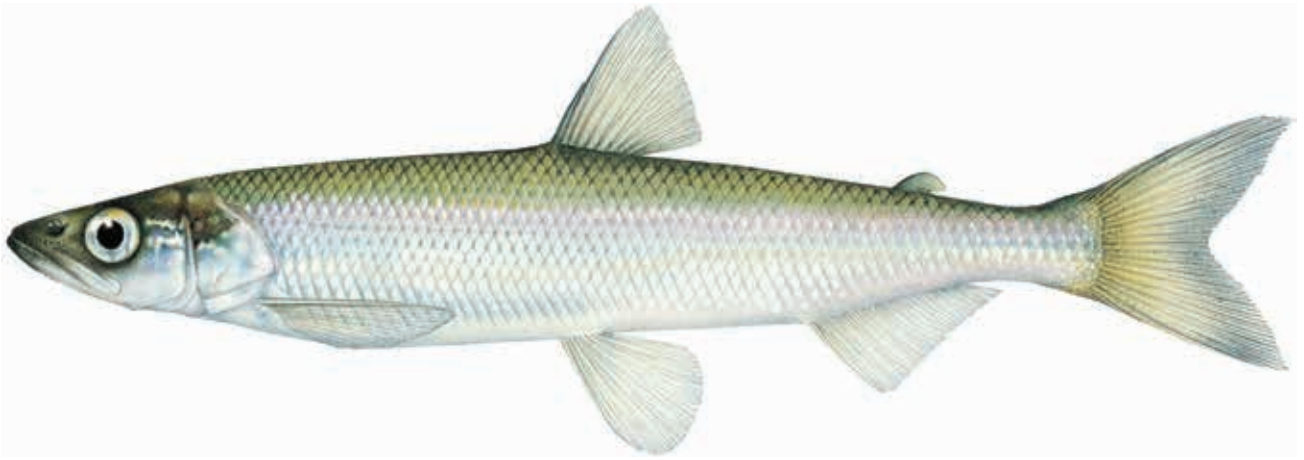


Plate 18.1. Rainbow Smelt, *Osmerus mordax*.



Plate 18.2. Eulachon, *Thaleichthys pacificus*.



Figure 18.2. Adult Wakasagi, *Hypomesus nipponensis*, a species introduced into the western United States (photograph is in the public domain and by and used with permission of René Reyes, Tracy Fish Facility, U.S. Department of the Interior, Bureau of Reclamation, Stockton, California).

therein). Despite morphological and meristic similarity, substantial nuclear and mtDNA variation indicates the two are distinct species with long and separate evolutionary histories (see genetics section; Taylor & Dodson 1994; Mecklenberg et al. 2011; Skurikhina et al. 2013).

Despite a putative marine origin, the Rainbow Smelt has a broad native range in North America (Fig. 18.9) and consists of anadromous as well as natural and introduced

freshwater populations (Bergstedt 1983). Otolith microchemistry and tagging studies on anadromous Rainbow Smelt in Newfoundland demonstrated site-specific population structure maintained by homing to specific estuaries (Bradbury et al. 2008b; see genetics section). Along the Atlantic Coast, the Rainbow Smelt is known from the Delaware River, Pennsylvania, northward to Labrador. In the Pacific and Arctic Ocean regions of North America,

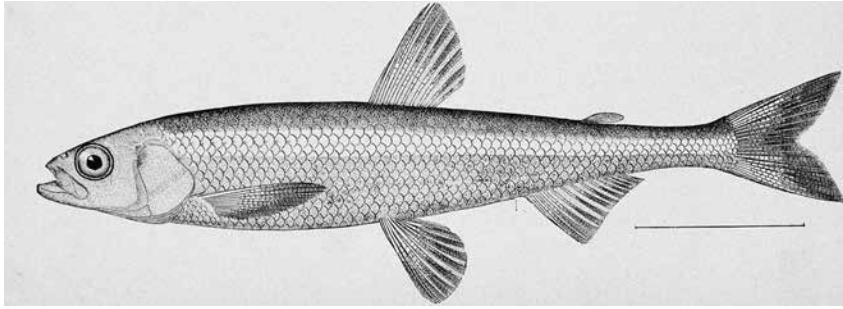


Figure 18.3. The Pond Smelt, *Hypomesus olidus*, drawn by H. L. Todd from a specimen taken at St. Michaels, Alaska, in May 1877 (from Goode 1884) (image is in the public domain; source, NOAA Photo Library).



Figure 18.4. Adult (upper) and juvenile (lower) Delta Smelt, *Hypomesus transpacificus*, that were hatched and reared at the Delta Smelt Culture Facility in the San Francisco Estuary (photograph is in the public domain; source, California Department of Water Resources).



the Pacific Rainbow Smelt is distributed from Barkley Sound, British Columbia, northward around the coast of Alaska and eastward to Bathurst Inlet, Nunavut (and along the Pacific Coast of northern Asia). Interestingly, naturally occurring land-locked freshwater populations of Rainbow Smelt occur in several lakes along the Atlantic Slope of North America in Maine, New Hampshire, and Canada. Morphological and genetic diversity is complexly distributed across the range of the species (see genetics and morphology sections).

Rainbow Smelt were successfully introduced and are established in the Great Lakes, many northern lakes, and some north-central U.S. reservoirs, where they reach population sizes in the tens if not hundreds of millions (e.g., Lake Oahe, South Dakota; Garrison Lake, North Dakota) (Fincel et al. 2016). Subsequent dispersals via spillways

and canals have resulted in the regular occurrence of Rainbow Smelt in several river systems, including the Mississippi, Missouri, Ohio, and Illinois Rivers (Burr & Mayden 1980; Mayden et al. 1987). As a result, Rainbow Smelt are captured as far south as the Gulf of Mexico; however, Rainbow Smelt in these river systems are only winter transients because warm summer water temperatures preclude permanent establishment (Burr & Mayden 1980). Non-native Rainbow Smelt populations, especially those in natural northern lakes, are invasive species reaching large population sizes relatively quickly, and as a result, the species is implicated in the decline of native fishes (e.g., Walleye, *Zander vitreus*; Yellow Perch, *Perca flavescens*; Cisco, *Coregonus artedii*) through competition and predation (e.g., Hrabik et al. 1998, 2001; Mercado-Silva et al. 2007; Gaeta et al. 2015; and references therein).



Figure 18.5. An anadromous, breeding adult male Rainbow Smelt, *Osmerus mordax* (upper), from the Gaspereau River, Nova Scotia, in April. (middle) A freshwater, breeding large-morph female (>300 mm TL) from Hurlbert Brook, Lochaber Lake, Nova Scotia, in April. (lower) A freshwater, breeding dwarf-morph male Rainbow Smelt (about 140 mm TL) from McNab Brook, Lochaber Lake, Nova Scotia, in April. Note the proportional differences in the dwarf and large morphs in dimensions of the heads (e.g., jaw and eye sizes) and caudal fins and both differ in body morphology from the anadromous population (courtesy of Paul Bentzen).



Figure 18.6. Adult Longfin Smelt, *Spirinchus thaleichthys* (photograph is in the public domain and by and used with permission of René Reyes, Tracy Fish Facility, U.S. Department of the Interior, Bureau of Reclamation, Stockton, California).

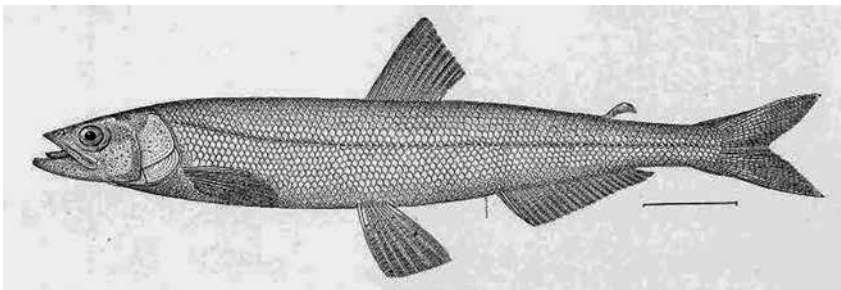


Figure 18.7. The Eulachon, *Thaleichthys pacificus*, drawn by H. L. Todd from a specimen taken at Chilkat River, Alaska, in June 1880 (from Goode 1884; image is in the public domain; source, digital image collection of Freshwater and Marine Image Bank, University of Washington Libraries, Seattle).

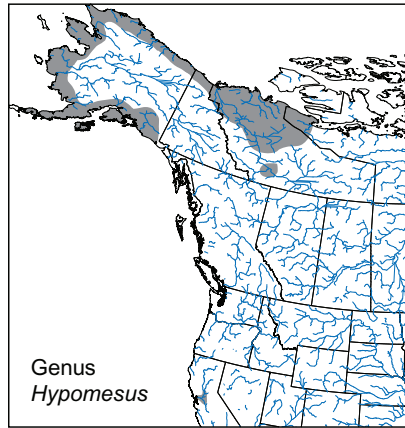


Figure 18.8.
Geographic range
of *Hypomesus* in
North America.

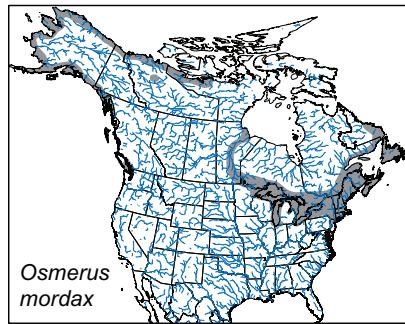


Figure 18.9.
Geographic range
of the Rainbow
Smelt, *Osmerus
mordax*, in North
America,
including some
but not all
introduced
populations (see
text for details).

Genus *Spirinchus*

The genus *Spirinchus* is represented in North America by the Longfin Smelt (*S. thaleichthys*). The Longfin Smelt is an anadromous species, which spawns in coastal rivers and is distributed along the Pacific Coast of North America from the San Francisco Estuary, California, northward to the Gulf of Alaska (Fig. 18.10). Two land-locked freshwater populations are known: one in Lake Washington (Seattle, Washington) and the other in Harrison Lake (British Columbia) (Chigbu & Sibley 1994; Wydoski & Whitney 2003). Populations in Washington and California were once considered separate subspecies, but meristic evaluation suggested the differences were clinal (McAllister 1963). Even so, differences in gene frequencies between the two populations are significant and microsatellite analysis revealed moderate levels of differentiation, suggesting gene flow between them is restricted and the populations warrant treatment as distinct entities (Stanley et al. 1995; Israel & May 2010; see genetics section).

Genus *Thaleichthys*

The anadromous Eulachon, *Thaleichthys pacificus*, is distributed along Pacific coastal and oceanic areas from

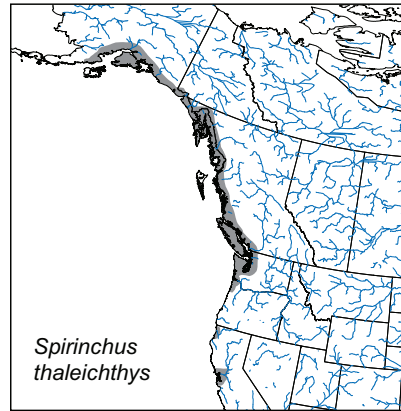


Figure 18.10.
Geographic range
of the Longfin
Smelt, *Spirinchus
thaleichthys*.

Monterey Bay, California, north to Bristol Bay, Alaska. The range extends westward to the Pribilof Islands in the Bering Sea (McHugh 1939; Smith & Saalfeld 1955; Page & Burr 2011; Gustafson et al. 2010, 2012; Fig. 18.11). Genetic differences among populations are evident but complexly arrayed (see genetics section). This species is known in the region as oolichan, ooligan, or hooligan as well as by many variations or unique names applied by Indian Tribes or First Nations peoples (reviewed by Gustafson et al. 2010).

Occasional Freshwater Species

Two additional marine species, *Hypomesus pretiosus* (Surf Smelt) and *Mallotus villosus* (Capelin), spawn along intertidal beaches and occasionally migrate into brackish or fresh waters during spawning periods (McAllister 1963). Fascinatingly, in some populations of Capelin, the freshwater exposure during beach spawning near coastal river mouths (Nakashima & Taggart 2002) may contribute to iteroparity, primarily in females, suggesting that spawning behavior in Capelin is more plastic and complex than originally thought (Vilhjalmsson 2002; Christiansen et al. 2008).

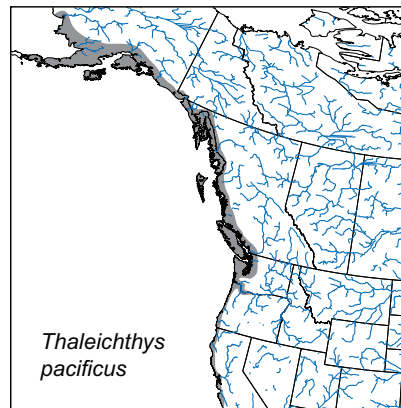


Figure 18.11.
Geographic range
of the Eulachon,
*Thaleichthys
pacificus*, in
North America.

PHYLOGENETIC RELATIONSHIPS

Morphologically Based Hypotheses

Before use of molecular markers in the early 21st century, the taxonomic position of Osmeridae was unresolved and varied considerably based on different morphological datasets and methodologies used to infer phylogenetic relationships. Nelson (2006) considered Smelts part of the superorder Protacanthopterygii within the class Actinopterygii, the Ray-finned Fishes (subclass Neopterygii), and placed osmerids within the order Osmeriformes, the Freshwater Smelts, encompassing a total of 13 families, 74 genera, and 236 species. In contrast, an evaluation of euteleostean relationships prompted Johnson & Patterson (1996) to place osmerids in Protacanthopterygii within the order Salmoniformes, the Trouts, and suborder Osmeroidei. Restriction site maps of nuclear ribosomal DNA in *Osmerus* showed the same distance between *Osmerus* and *Coregonus* as between *Coregonus* and *Thymallus*, implying a close relationship between osmerids and salmonids (Phillips et al. 1995; see also Johnson & Patterson 1996). However, with reconsideration of several morphological characters and use of molecular data, López et al. (2004) challenged the sister-group relationship between osmeroids and salmonoids that was strongly supported in Johnson & Patterson's (1996) study. Springer & Johnson (2004) recognized osmerids as part of the Salmoniformes, including four families (Salmonidae; Osmeridae; Retropinnidae, New Zealand Smelts; and Galaxiidae, Galaxiids) and placed the Salmoniformes with the group Pre-acanthomorpha.

Similarly, much disparity existed in hypotheses of family topology based primarily on morphological data. For example, Nelson (2006) asserted that the monophyly of Osmeridae is contingent on the inclusion of *Plecoglossus* (often assigned to Plecoglossidae, but see molecular-based hypotheses subsection, this section, and Betancur-R. et al. 2013ab). Others also embedded *Plecoglossus* in the osmerid clade (Wilson & Williams 1991; Begle 1991; Johnson & Patterson 1996), but the relative placement varied. In contrast to all previous osmerid work, Johnson & Patterson (1996) suggested that the salangids (Noodlefishes) also are part of the osmerid clade (see molecular-based hypotheses subsection, this section). Earlier works showed a close association of salangids with osmerids, but none recovered them as a monophyletic group.

Morphological studies also failed to consistently resolve basal taxa in the osmerid clade. Several studies indicated the genus *Thaleichthys* as basal (Chapman 1941; McAllister

1963; Begle 1991). However, McAllister's (1963) revision of the family suggested that a clade, including *Hypomesus* + *Mallotus* was basal. This is in partial congruence with other work (Wilson & Williams 1991; Johnson & Patterson 1996) that suggested the genus *Hypomesus* is basal. Johnson & Patterson (1996) postulated that *Hypomesus* may be a paraphyletic taxon, which could explain some of the disagreement about the topological position.

Molecular-based Hypotheses

Molecular sequences have helped resolve inter- and intra-familial relationships and indicate strong support for a monophyletic Osmeridae (Saruwatari et al. 2000; López et al. 2004; Fu et al. 2005; Ilves & Taylor 2008; Near et al. 2012b; Betancur-R. 2013ab, 2017; Fig. 18.12). In an analysis of Ray-finned Fishes using 10 nuclear genes in 579 teleost species, Near et al. (2012b) recovered a highly supported clade within Eutelostei consisting of (*Osmerus* + *Thaleichthys* + *Mallotus* + *Hypomesus*) + (Plecoglossidae, Ayus + Salangidae, Icefishes or Noodlefishes), which they designated as osmeriforms. Osmeriforms were sister to a basal Retropinnidae (New Zealand Smelts). The osmeriforms and retropinnids were sister to the Stomiiformes (Dragonfishes), a relationship also resolved in other less comprehensive molecular analyses (López et al. 2004). An expanded analysis using 21 molecular markers, 1,410 fish taxa, and including the Near et al. (2012b) data, recovered the same relationships (Betancur-R. et al. 2013ab, 2017). Betancur-R. et al. (2013ab, 2017) recognized Osmeriformes as containing four families: Osmeridae, Plecoglossidae, Retropinnidae, and Salangidae.

From an intergeneric perspective, molecular data based on sequences from 3 mitochondrial and 3 nuclear gene regions generated a well-resolved phylogeny dividing the group into 14 species in 6 genera (Fig. 18.13). Clearly, the topology is somewhat different from those hypothesized based on morphology with Salangidae being placed more basally with *Plecoglossus*. Such discrepancies may be caused by several homoplasious traits used in Johnson & Patterson's (1996) morphological analyses. Ilves & Taylor (2009) discovered the homoplasies by mapping the morphological traits onto the molecular phylogeny. Combined molecular and morphometric data showed that 28 characters unambiguously supported the intergeneric relationships inferred from molecular analyses, and 26 characters were autapomorphic for individual genera.

Even with molecular analyses some relationships among the Smelts remain unresolved. Additional molecular data

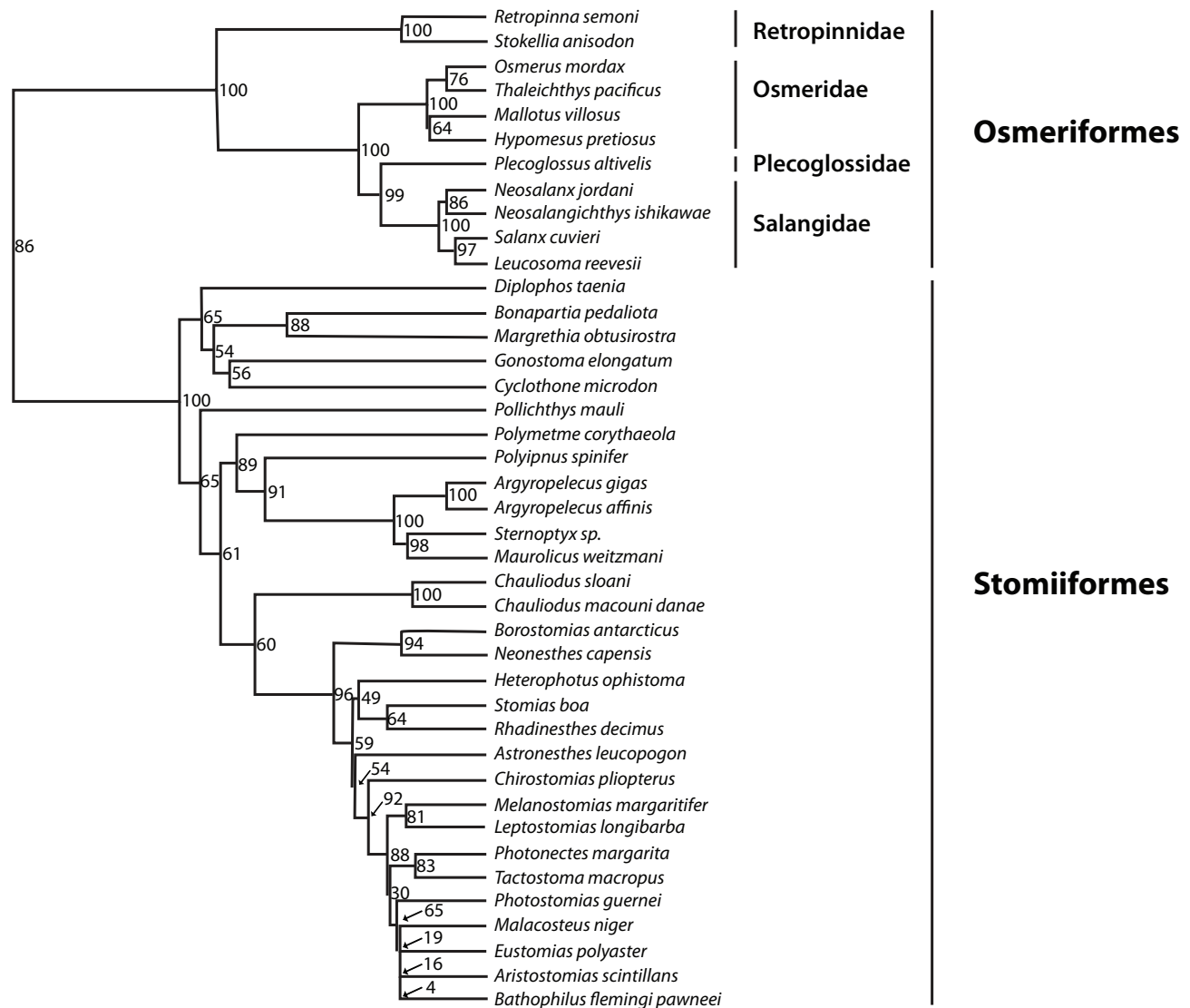


Figure 18.12. Phylogenetic relationships of the Smelts, Osmeriformes, as determined by analysis of 20 molecular markers across 1,410 fish taxa. Only relationships among osmeriform families and their sister order, the Dragonfishes, order Stomiiformes, are shown (redrawn from Betancur-R. et al. 2013ab).

using different nuclear genes may further clarify the phylogenetic position of *Mallotus villosus* (e.g., Skurikhina et al. 2013) and several remaining interspecific uncertainties in *Spirinchus*, *Osmerus*, and *Hypomesus* (Ilves 2007; Ilves & Taylor 2008). Although historical hybridization between species could have resulted in unresolved intrageneric molecular relationships, Ilves & Taylor's (2009) analyses were not restricted to mtDNA (lacking recombination) but also included nuclear genes. Alternatively, the short time available for divergence within these genera may be obscuring molecular relationships among species, leading to discontinuities between species and gene trees (Degnan & Rosenberg 2006). Additional genetic sampling of nuclear genes and

broader within-species phylogeographic coverage may help resolve problematic intrageneric relationships in Osmeridae.

FOSSIL RECORD

The fossil record for osmerids is scant; the fragility of the musculature and skeletal systems of Smelts precludes fossilization under most circumstances (Cavender 1986). However, four taxa are represented by fossils: two extinct genera, †*Enoplophthalmus* and †*Speirsaenigma* (Wilson & Williams 1991); and two extant genera, *Osmerus* (Smith 1981; Cavender 1986) and *Mallotus* (McAllister 1963). All

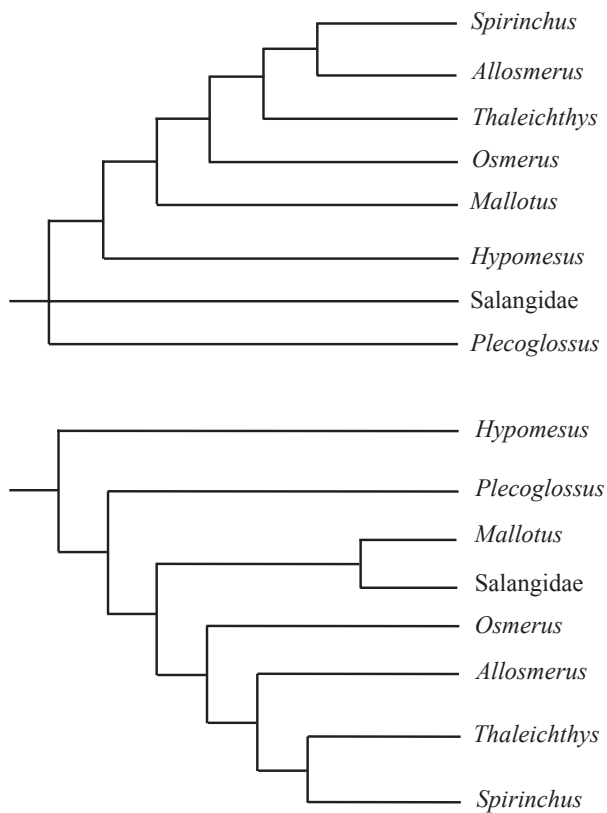


Figure 18.13. (upper) Intergeneric systematic relationships of Smelt (Osmeridae) genera based on molecular sequence data (*Plecoglossus* and Salangidae, Icthyofishes or Noodlefishes, as outgroups) (redrawn from Ilves & Taylor 2009). (lower) Intergeneric systematic relationships of Smelt genera based on morphological characters (redrawn from Johnson & Patterson 1996).

osmerid fossils are from the Cenozoic (65 mya); the oldest fossils, representing the genus †*Speirsaenigma*, are from the Paleocene (65–55 mya), and the others are more recent (Late Oligocene, 34–23 mya and Pleistocene 2.6–0.01 mya). Of these, fossils of †*Speirsaenigma* and *Osmerus* occur in North America.

Only a single fossil of *Osmerus* is known from North America (Smith 1981), but several species of †*Speirsaenigma* are known. The single specimen of *Osmerus* was discovered in a marine stratum (Champlain Sea deposits, Ontario, Canada) and was identified as *O. mordax* from the late Wisconsin or early post-glacial period (about 12,000 years ago) (McAllister et al. 1981). Several specimens of †*Speirsaenigma*, the only other North American osmerid fossils, were found in the Paleocene-aged Paskapoo Formation (about 58 mya) in Alberta, Canada. The specimens occurred in a freshwater fluvial deposition as part of a mass fish kill layer (Wilson & Williams 1991). One species of †*Speirsaenigma*,

†*S. lindoei*, from the Paskapoo Formation was represented by 45 specimens (40–60 mm TL).

Identification of †*Speirsaenigma* as an osmerid was warranted by the presence of several distinct osteological features: an open preopercular canal and saccular otoliths; a lateral ridge; a posteroventral notch; and posterodorsal lamina on a square metapterygoid. Recognition at the generic level is based on several autapomorphic characters, including lack of teeth on basihyal and mesopterygoid; reduction of mandible breadth; extension of premaxilla and jaw length; and an unfused second ural centrum. Notably, at least three characters distinguish †*Speirsaenigma* from other osmerids but are shared with *Plecoglossus*: a laterally projecting dorsal maxillary flange; a distinctive lateral shelf on the ectopterygoid; and a straight dorsal margin on the quadrate. Hence, Wilson and Williams (1991) recognized *Plecoglossus* as an osmerid, and based on a tree derived from 34 osteological characters, †*Speirsaenigma* and *Plecoglossus* are sister taxa nested within the osmerid clade. The Paskapoo Formation fossils represent the oldest known osmerid specimens, surpassing the previous record by nearly 30 million years (genus †*Enoplophthalmus*, Oligocene deposit, 30 mya, Europe) (Wilson & Williams 1991).

At the Paskapoo Formation fish kill site, male and female specimens of †*S. lindoei* were found as evidenced by breeding tubercles on male specimens. The geologic attributes of the fluvial deposit indicate death occurred during a spring or early summer high-water event (Wilson & Williams 1991). In conjunction with geologic observations, the congregation of both sexes in breeding condition suggests that death occurred in close association with a spawning period. Further, the geographical position of the deposit was far removed from any putative marine environment; this fact, coupled with the migration patterns of extant osmerids, suggests that †*S. lindoei*, or at least the population examined, was exclusively fresh water, and their autecology was comparable to the Pond Smelt, *H. olidus*.

MORPHOLOGY

North American members of the family Osmeridae are small (<40 cm TL), silvery, laterally compressed, fusiform fishes with cycloid scales, a soft-rayed dorsal fin, an adipose fin, a forked caudal fin, and a bottom jaw typically protruding anteriorly to the upper jaw when compressed (Figs. 18.2–18.7). Teeth are present on several jawbones, including the mesopterygoid, basihyal, premaxillary, maxillary, vomer, and dentary (McAllister 1963). The teeth are

variable in size, and form characteristic canines in some species, such as *Osmerus mordax* and *Thaleichthys pacificus*. The lateral line is usually incomplete or reduced, sometimes extending only one-third of the body length, except in *Thaleichthys* where it is complete. Superficially similar to salmonids, osmerids are much smaller and differ in the absence of axillary processes at the pelvic-fin bases (McAllister 1963), presence of a characteristic cucumber odor caused by the chemical trans-2-cis-6-nonadienal (Moyle 2002), no or few pyloric caeca (McAllister 1963), and an open preopercular canal (Wilson & Williams 1991).

Intergeneric variation of morphology is not pronounced but includes variation in size, tooth-type, and mouth and fin shapes. *Hypomesus transpacificus* is the smallest osmerid, attaining a maximum of 120 mm SL (Moyle 2002; Fig. 18.4); comparatively, *O. mordax* can reach >330 mm TL (McAllister 1963). The genera *Osmerus*, *Spirinchus*, and *Thaleichthys* have large, robust, slightly oblique mouths with conical to canine-like teeth. In contrast, the mouth of *Hypomesus* is smaller, more facile, and moderately oblique, and the teeth are villiform. *Thaleichthys* has distinctive concentric striae on the opercle and subopercle areas (Fig. 18.7), markings which are weak or absent in all other Smelts in North America. Lastly, *Spirinchus* is distinctive in having unusually long pectoral fins, which nearly reach the pelvic-fin bases, hence, the common name, Longfin Smelt (Fig. 18.6). A detailed comparative osteological analysis is available on each genus, including narrative descriptions and illustrations of the cranium, hyoid apparatus, gill arches, pectoral girdle, caudal fin elements, and suspensorium (Chapman 1941). Beirão et al. (2015) described the spermatozoa ultrastructure of the Rainbow Smelt, which is typical of other osmerids (bullet-shape head, deep nuclear fossa with one deeply inserted, finned flagellum, and one mitochondrion).

Morphotype Complexes and Ecological Speciation

Except for *Osmerus*, intrageneric variation is limited. However, *O. mordax* is well known for a morphotype complex occurring in at least five lacustrine populations in northeastern North America: Lake Utopia, New Brunswick; Lac Saint-Jean, Quebec; Lake Heney, Quebec; Lochaber Lake, Nova Scotia, and Wilton Pond, Maine (Lanteigne & McAllister 1983; Saint-Laurent et al. 2003; Curry et al. 2004; P. Bentzen pers. comm.). Within these lakes, two freshwater eco-phenotypes are present, a dwarf phenotype, which rarely reaches 125 mm TL (range 76–143 mm TL), and a large phenotype, which averages 200–215 mm TL (range

181–226 mm TL) (Taylor & Bentzen 1993a; Lanteigne & McAllister 1983; Saint-Laurent et al. 2003; Curry et al. 2004; Shaw & Curry 2011; Fig. 18.5). Putatively, these morphotypes diverged in sympatry by virtue of ecological differentiation (trophic status) and subsequent temporal isolation of reproductive periods (Saint-Laurent et al. 2003; Curry et al. 2004; Shaw & Curry 2011). In a study of both forms in Lake Utopia, the large form spawned earliest (Fig. 18.14) had the largest eggs, and their larvae hatched earlier and grew faster during their first year; dwarf and normal forms had interannual variability in degree of overlap and divergence in growth in their first year or at age 1+ and 2+. The authors concluded earlier hatching, early growth trajectories, and later niche shifting were linked to maintaining the morphotypes (i.e., the process is controlled by the environment and sustained in part by spawning segregation) (Shaw & Curry 2011). Similarly, early life history constraints (different nursery habitats) and resource polymorphism support ecological speciation in estuarine-dependent *O. mordax* in the St. Lawrence River (Lecomte & Dodson 2004). In a broad geographic comparison, phenotypic and genetic differentiation in anadromous Rainbow Smelt supported the hypothesis that gene flow may be moderated by morphological divergence (Bradbury et al. 2006a; see genetics section).

GENETICS

Many Smelts are anadromous, thus much effort has been applied to determine if population structuring is predi-

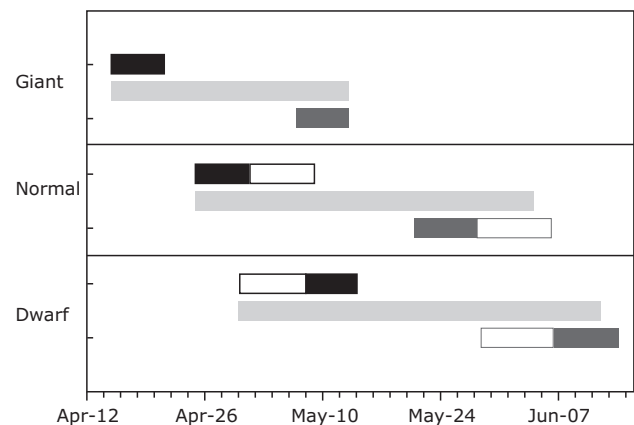


Figure 18.14. Periods of spawning (upper black bars), incubation (middle light gray bars), and hatching (lower dark gray bars) of the giant, normal, and dwarf forms of Rainbow Smelt, *Osmerus mordax*, in Lake Utopia, New Brunswick, in 2008. Hatched areas indicate approximation of dates (redrawn from Shaw & Curry 2011).

cated by freshwater spawning locations. Unlike salmonids, however, osmerids do not show precise fidelity to natal rivers and moderate mixing of populations occur during the marine phase of the life cycle. As a result, most genetic structuring of populations detected to date is at broad geographic scales and is probably driven by distance and barriers in the marine environments, but in some cases, genetic structuring occurs on relatively small scales (e.g., Newfoundland populations of Rainbow Smelt). Little or only moderate genetic differentiation among populations is shown even in those species in which multiple life histories are found (e.g., have anadromous and freshwater populations). An exception is the Rainbow Smelt, which presents an unusual case for genetic studies, having several apparently independently derived dwarf populations.

Karyology

Karyological analyses in the freshwater osmerids is limited; however, diploid chromosomal numbers are known for *Hypomesus olidus* and *H. transpacificus* ($2n = 54-56$) (Phillips & Rab 2001). In marine osmerids, chromosomal numbers range from $2n = 50$ in *Spirinchus starksi* (Night Smelt) to $2n = 52$ in *Hypomesus pretiosus* to $2n = 54-56$ in *Osmerus eperlanus* (European Smelt) (Ocallewicz et al. 2007). Among these species, chromosomal morphology is somewhat varied with the number of arms ranging from 60 to 78 and averaging 60–62, suggesting that multiple chromosomal rearrangements were involved in the transformation of the presumed ancestral teleost karyotype, containing 48 telocentric chromosomes, into the current karyotypes (Phillips & Rab 2001).

Species Identity and Phylogeography

Early genetic analyses using allozymes addressed conservation concerns for Smelts in the Sacramento-San Joaquin Estuary, California, an area severely degraded and modified over the last 70 years (see conservation section). Variability of 22 allozyme loci was examined among six species, including representatives of *Hypomesus* and *Spirinchus* from six different populations with special emphasis on *H. nipponensis*, *H. transpacificus*, and *S. thaleichthys* within the Sacramento-San Joaquin Estuary (Stanley et al. 1995). The status of genetic introgression between native *Hypomesus transpacificus*, and the introduced *H. nipponensis*, was of particular interest.

Separate taxonomic identities of the imperiled Delta Smelt and invasive Wakasagi (once considered polytypic)

were confirmed with the presence of species-specific alleles at 13 of 22 allozyme loci examined and a genetic distance (Nei's D-value) of 0.883, well above the expected 0.50 average for sister taxa. Despite overlapping ranges, no hybridization between the two species was detected (Stanley et al. 1995). A later study, however, discovered two F_1 hybrids (*H. transpacificus* × *H. nipponensis*) (Trenham et al. 1998); the frequency of hybridization events appeared low, and evidence of subsequent backcrossing and introgression between the two species was lacking. Likewise, in a hybridization study incorporating microsatellite loci, mitochondrial sequences, and 16 species-specific SNPs of Delta Smelt, Wakasagi, and Longfin Smelt, hybridization was detected at low frequencies, and no F_2 hybrids were recovered. Wakasagi was the maternal parent for all five Delta Smelt × Wakasagi hybrids and Longfin Smelt, the maternal parent for the single Delta Smelt × Longfin Smelt hybrid (Fisch et al. 2014). Thus, the genetic integrity of Delta Smelt (if not functionally extinct) is perhaps only marginally affected genetically by the introduction (see conservation section).

Allozyme variation was also assessed in *S. thaleichthys* populations within the Sacramento-San Joaquin watershed to determine if genetic divergence from the nearest population in Washington was sufficient to warrant recognition of a subspecies in California, which would confer legal protection (Stanley et al. 1995). Of the 22 allozyme loci, six were polymorphic, and significant differences existed in allele frequencies, but fixed differences were absent. The genetic distance between the Washington and California populations was low (Nei's D-value = 0.005), and the proportion of genetic variation attributable to among population differences was estimated at 6.3%, a number comparable to that calculated for marine species with high gene flow (Conover et al. 2006). Despite >600 km separation from the nearest conspecific population, the low level of genetic divergence did not support subspecific recognition of the California population.

Similarly, partitioning of populations of Eulachon among river systems throughout its range in the Eastern Pacific Ocean (Bering Sea to Columbia River) was examined using mtDNA restriction fragment length polymorphisms (RFLP) (McLean et al. 1999). Because Eulachon are anadromous, populations were expected to be highly structured as observed for example in salmonids. Thirty-seven haplotypes were identified from 14 populations spanning the studied range. Of those, three haplotypes composed 79% of the total variation and were present in every population examined with the most abundant haplotype accounting for 50%

of the total variation. Eleven of the 14 populations contained ≥ 1 unique haplotypes, but these were always at low frequencies. Haplotype divergence between populations was low (0.09–1.24%, mean = 0.39%), and variation within populations was high, accounting for 97.6% of the total variation. A parsimony mutational network revealed two haplotype clusters; however, this pattern was not supported in bootstrap and consensus tree analyses because only one restriction site change separated the clusters. Even when the data were assembled into larger spatial units, population partitioning was not detectable, indicating that the Eulachon probably consists of a single interbreeding metapopulation (see Gustafson et al. 2010, 2012).

Intraspecific variation among populations of Pond Smelt (mostly in the western Pacific) was analyzed using mtDNA cytochrome *b* and COI genes (Skurikhina et al. 2012). Genetic divergence was low (0.4%) despite considerable geographic distances among some populations. This value was not higher than the level of divergence between individuals within single populations. Even when individuals from Kamchatka and Alaska were included divergences were only 0.15%.

Taylor & Dodson (1994) examined populations of three species of *Osmerus*, then considered by some as conspecific or subspecies, including the Rainbow Smelt, Pacific Rainbow Smelt, and European Smelt, using mtDNA RFLP and cytochrome *b* sequence polymorphism. Sequence divergence from 300 base pairs of cytochrome *b* sequencing ranged from 6.1 to 8.5% between the species; divergence based on restriction fragments ranged from 5.6 to 8.9%. Divergence within species was $< 0.5\%$ for restriction fragments, and no differences were detected within species from sequence analysis. Although the strength of support was weak to moderate, various phylogenetic analyses suggested *O. mordax* and *O. dentex* were closer genetically to one another than to *O. eperlanus* (see next paragraph). Given the substantial genetic divergences among the three, the authors argued they were compatible with evolutionarily independent lineages (i.e., species), whether recognized taxonomically or not and despite general morphological and meristic similarity. Using provisional estimates of divergence times, the author's hypothesized the Rainbow Smelt and Pacific Rainbow Smelt diverged from a common ancestor during the early Pleistocene (Taylor & Dodson 1994).

Two other studies indicate genetic divergence among species of *Osmerus*. A broad study of Arctic fish species using DNA barcoding (cytochrome *c* oxidase 1 gene sequences) also supported separation of Rainbow Smelt and Pacific Rainbow Smelt (Mecklenberg et al. 2011). The mean genetic

distance between the two species was 8.5%, and *O. eperlanus* was genetically more similar to *O. dentex* than to *O. mordax*. A study incorporating restriction fragment length polymorphism of mtDNA and sequencing of cytochrome *b* and the COI genes (mtDNA) and a nuclear gene also revealed high levels of divergence (12.94%) between *O. eperlanus* and Russian populations of *O. dentex*. Interspecific divergence was $< 1\%$ in both species (Kovpak et al. 2011).

In an extensive mtDNA analysis of Rainbow Smelt across their native Atlantic Ocean range, Bernatchez (1997) concurred that the two *Osmerus* groups resolved earlier by Taylor & Bentzen (1993a) were phylogenetically distinct. The groups consist of two glacial refugia lineages, an Atlantic and Acadian clade, with a zone of secondary contact in the Gulf of St. Lawrence region (Bernatchez 1997). The contact zone is narrow in the St. Lawrence River estuary with different lineages predominating on each side of the river. In the southern Gulf of St. Lawrence, the contact forms a broad region of introgression between the two lineages. A second relatively narrow contact zone is present in southeastern Newfoundland (Bradbury et al. 2011). Patterns of postglacial dispersal suggest that the Atlantic clade recolonized northern regions about 5,000 years before the Acadian clade. In the contact zone, the groups are sympatric yet retain their genetic integrity. With no evidence of physical barriers to gene flow, the mechanism for reproductive isolation remains elusive. A study of population genetic structure based on the spatial distribution of larvae from the two groups did not support isolation at that life stage (Pigeon et al. 1998).

More local-scale population genetics of anadromous Rainbow Smelt were assessed using mtDNA analyses (Bernatchez & Martin 1996). Anadromous *O. mordax* from the Gulf of St. Lawrence region were resolved into four geographical groups based on genetic distance and genotype assemblages. Of the total mtDNA diversity, 22.38% was explained by variation among groups; a six-fold increase compared with the Eulachon (McLean et al. 1999). Latitudinal position and mtDNA haplotypes showed a slightly positive, but nonsignificant, correlation. Spatial patterns in mtDNA haplotype variation in Rainbow Smelt appear to support the member-vagrant hypothesis in which ecological processes determine population structure through the probability of encounter among sexually mature individuals and survival of early life-history stages (Bernatchez & Martin 1996).

In addition to allozyme, mtDNA, and nuclear genes, microsatellite loci and single nucleotide polymorphisms

(SNPs) were assessed in other species of Smelt (microsatellites: Eulachon, McLean & Taylor 2001; Flannery et al. 2013; Rainbow Smelt, Coulson et al. 2006b; Kovach et al. 2013; Longfin Smelt, Israel & May 2010; Delta Smelt, Fisch et al. 2009, 2013; Bradbury et al. 2011; SNPs, Delta Smelt, Lew et al. 2015; Eulachon, Candy et al. 2015). Cross amplification of microsatellite loci among different species in this group seems successful (Coulson et al. 2006b; Fisch et al. 2009). Studies using microsatellite data can normally better resolve population genetic structure than classic genetic markers (e.g., allozymes and mtDNA).

Using five microsatellite loci, McLean & Taylor (2001) evaluated Eulachon population structure across their entire range along the west coast of North America. The microsatellite F_{ST} (among population variation) was 0.045, somewhat higher than the value for mtDNA haplotype diversity for the same populations (McLean et al. 1999; $F_{ST} = 0.023$) but still indicative that among population variation accounts for only a small proportion (about 4%) of the total genetic variation. Thus, gene flow among Eulachon spawning in different rivers is much higher than expected (Ward et al. 1994). In a study examining 14 microsatellite loci for populations from southeast Alaska to Cook Inlet, a low degree of genetic divergence ($G_{ST} = 0.005$) was indicated, but that divergence was structured by broad-scale northern and southern geographic regions. The northern region included the Yakutat Forelands, Prince William Sound, and Cook Inlet, and the southern region encompassed upper Lynn Canal, Berners Bay, the Stikine Strait, and Behm Canal. Within the northern region genetic differentiation was essentially lacking, a likely result of the Alaska gyre facilitating larval dispersal and promoting gene flow in the region. Gene flow between the two regions is likely restricted by the Alexander Archipelago acting as a biogeographic barrier (Flannery et al. 2013). In a broader study also examining 14 microsatellite markers, significant genetic structure and a coast-wide gradient was revealed in Eulachon populations in the Northern Pacific Ocean (Beacham et al. 2004). Marine sampling in this study indicated that immature Eulachon from different rivers mix at a moderate (regional) spatial scale during the 2–3 years spent at sea before spawning. Thus, subdivision of populations is only detected with broad-scale, multiple marker assessments.

The broad regional-scale genetic structure of Eulachon populations was further supported in a study using restriction-site-associated DNA (RAD) sequencing to evaluate patterns of neutral and adaptive variation (Candy et al. 2015). The study included 12 populations from the

Columbia River, Washington, to Cook Inlet, Alaska.

Thousands of SNPs were discovered among which 193 putatively adaptive SNPs were identified. The putatively adaptive SNPs provided similar but greater resolution of stocks compared with the neutral panel or previous estimates with 14 microsatellite loci. A south-to-north cline of increasing genetic diversity was found in the adaptive panel but not the neutral markers (SNPs or microsatellites). Regional genetic structure indicated a southern Columbia-Fraser River group, a British Columbia-Southeast Alaska group, and a northern Gulf of Alaska group. Interestingly, meristic characters (i.e., number of vertebrae) also indicated at least a partial genetic boundary between the Fraser-Columbia Rivers and more northerly rivers in British Columbia (Hart & McHugh 1944; Hay & McCarter 2000).

Comparatively, species of *Osmerus* seem to have a moderate level of population structure with limited gene flow between populations; however, the partitioning may or may not be structured by river systems. Similar to Eulachon, populations can partition regionally. Rainbow Smelt were genotyped at 10 microsatellite loci from 18 river systems and 11 bays along the northeastern Atlantic Coast, covering the entire native U.S. range of the species (Kovach et al. 2013). Gene flow was rather high ($F_{ST} = 0.17$), and genetic variation followed an isolation by distance model (i.e., dispersal occurs most frequently among nearby rivers). Four to six genetically distinct population clusters were revealed; these varied in geographic extent according to coastal circulation patterns. Topographically structured bays with potential to retain larvae harbored genetically divergent populations. In contrast, long stretches of coast with indistinct topography showed high levels of gene flow; in those environments circulation patterns maximized larval dispersal (Kovach et al. 2013).

Using nine microsatellite loci, Bradbury et al. (2006a) revealed that Cabot Strait plays a major role in determining regional gene flow in Rainbow Smelt examined along the east coast of Canada between Newfoundland and the mainland. Further, significant isolation by distance and more restricted gene flow exists among the Newfoundland populations ($F_{ST} = 0.11$) than among the mainland populations ($F_{ST} = 0.017$).

Bradbury et al. (2008a) further analyzed metapopulation structure and gene flow in Rainbow Smelt in estuaries around Newfoundland and Labrador (see also Bradbury et al. 2009). Unexpectedly high genetic structure in estuarine populations suggested behavioral influences reduced dispersal, supporting the assumption and demonstration of active larval retention at or relatively near spawning sites

(Bradbury et al. 2006ab). Data from otolith elemental comparisons and adult tagging in populations from coastal Newfoundland corroborated the hypothesis of demographic isolation among estuaries (Bradbury et al. 2008b). Further, a multi-faceted assessment of dispersal during early life history from six spawning areas in Newfoundland indicated moderate genetic differentiation (F_{ST} about 0.05) occurred in adult spawning populations and juveniles isolated by >25 km but not in more proximate populations for either life history stage (Bradbury et al. 2008c). Also, otolith elemental analyses suggested limited movement between estuaries (<0.5%). The lack of evidence for straying and genetic admixtures of juveniles in proximate sites supports the hypothesis of selective mortality on dispersers in marine environments.

In an extended study of Newfoundland and Labrador populations of coastal Rainbow Smelt, Bradbury et al. (2011) examined mtDNA sequence variation (ND5) and 11 microsatellite loci in an area adjacent to a proposed glacial refuge (Pleistocene Grand Banks Refugium). Their mtDNA analysis confirmed the presence of two major mitochondrial clades previously identified, one in southeast Newfoundland and the other along the south shore of Newfoundland to the northern peninsula and Labrador (e.g., Taylor & Bentzen 1993a; Bernatchez 1997). Microsatellite results also supported the presence of two predominant groups for which the spatial distribution was largely consistent with the mtDNA clades. The study demonstrated the presence of repeated transitional zones in mtDNA and microsatellite clades in Newfoundland and Labrador despite the absence of any contemporary hydrographic or physical barriers to dispersal. Their results support the growing consensus that contemporary genetic structure in northern fishes is largely a reflection of the influence of Pleistocene glaciation and subsequent range expansions from Pleistocene refugia (Bradbury et al. 2011).

At a more local scale, analysis of nine Rainbow Smelt microsatellite loci revealed higher levels of genetic substructuring of a population with bimodal spawning runs compared with a population with a long continuous spawning run (Coulson et al. 2006a). The bimodal population, which spawns in Mosher Brook, Nova Scotia, has two distinct runs—an early run during late April and a non-overlapping late run in mid- to late-June. The other population, spawning in Smelt Brook, Newfoundland, has two peaks in spawning, but spawning is continuous over the month or so between the peaks. The F_{ST} values for the Mosher Brook early and late run individuals was low but significantly different; the early and late samples from

Smelt Brook showed no differences in F_{ST} values. A factorial correspondence analysis of multi-locus genotypes from the nine microsatellite loci revealed striking differences in the Mosher Brook samples relative to those from Smelt Brook. The early and late spawning groups in Mosher Brook were as genetically differentiated as Rainbow Smelt populations spawning at similar times hundreds of kilometers apart in Nova Scotia (Bradbury et al. 2006a). The results suggest that timing of reproduction in Rainbow Smelt is likely an important factor contributing to genetic differentiation in the species (Coulson et al. 2006).

Seventeen polymorphic microsatellite markers were analyzed from Longfin Smelt from 15 individuals each taken in Lake Washington, Washington, and the San Francisco Delta, California (Israel & May 2010). Populations from the two localities showed moderate levels of differentiation. They had a pairwise F_{ST} value of 0.091 and were completely separable by genetic distances visualized in principal components space (33% of genetic covariance). These results are concordant with an earlier allozyme analysis (Stanley et al. 1995) and support the distinctiveness and genetic isolation of the Longfin Smelt at least between these two geographically disparate populations (Israel & May 2010).

Microsatellite markers also are used in the captive breeding program for Delta Smelt for parentage analysis to reconstruct the pedigrees of brood-stock candidates (Fisch et al. 2013) (see conservation section). These 12 markers will likely be augmented by a low-density single nucleotide polymorphism panel consisting of 24 neutral, non-linked loci that is highly accurate in assigning parentage and yielded the first linkage map for the species (Lew et al. 2015).

In summary, development of population structure and diversification in Osmeridae seems contingent on local ecological conditions and selective pressures leading to limited regional or local (i.e., river system) population genetic structure. Environmental factors and phenotype-habitat associations may contribute to the development of population structure in *Osmerus*, but exact mechanisms remain unknown (Bernatchez & Martin 1996; Lecomte & Dodson 2004; Bradbury et al. 2008b). Moreover, evidence suggests the reduced population structure is probably the result of rapid post-glacial expansion (Bernatchez 1997). The period of time required to reach equilibrium of population division, given certain life-history traits (especially in the case of *Osmerus*), may take much longer than the current time of isolation since recent glaciation (Ilves 2007).

Life-history Variation

Life history may play a role in species divergence of several freshwater Smelt populations (see morphology section). A broad scale mtDNA RFLP study (Taylor & Bentzen 1993a), in which 16 populations of Rainbow Smelt encompassing anadromous, normal-sized lake forms and dwarfed lake forms were examined, revealed a moderate level of genetic heterogeneity. Ninety-three haplotypes were identified, and all RFLP patterns were based on single restriction site losses or gains; no differences in sequence length or heteroplasmy were detected. The three most abundant haplotypes represented 37.1% of the individuals with each representing 23.5, 7.7, and 5.9%, respectively. Sixty-four haplotypes had only a single representative. Additionally, sequence divergence ranged from 0.08 to 1.10% (mean = 0.32%), a range nearly identical to that estimated for *Thaleichthys* (McLean et al. 1999) and well above the 0.025% estimated for populations of *O. dentex* from the Asian Pacific (Skurkhina et al. 2004). For comparison, mtDNA sequence divergences >5.6% exist between the *O. mordax* and *O. dentex* (Taylor & Dodson 1994). Despite a modest level of mtDNA sequence divergence, genetic structuring of Rainbow Smelt by life-history traits is limited (Taylor & Bentzen 1993a). Two groups of haplotypes were resolved, but 93.5% of all individuals were clustered within one group; anadromous, normal-sized, and dwarf populations were not distinguished by mtDNA composition.

Conversely, direct comparisons of sympatric freshwater populations of large-sized and dwarf *O. mordax* using minisatellite DNA revealed noticeable differences in genotype frequencies between the forms, suggesting genetic dissimilarity of morphotypes (Taylor & Bentzen 1993b). Notably, at each site, Lake Utopia, Lochaber Lake, and Onawa Lake, the dwarf populations were more closely related to the local large-sized population than to dwarf populations in other lakes. Further, at least in Lochaber Lake, the two forms spawn simultaneously in the same streams but remain genetically differentiated even though some hybridization is occurring. Further, the morphs remain morphologically distinct and show evidence of reproductive isolation. Microsatellite analysis and cross-breeding experiments comparing allopatric and sympatric populations of the morphs indicate strong disruptive selection and reinforcement in sympatry plays a large role in the formation and maintenance of this diversity (Bradbury et al. 2010; Fig. 18.5). Given these results, *O. mordax* ecophenotypes are probably polyphyletic, and represent

multiple, independently diverged populations (Taylor & Bentzen 1993a). An earlier study in which anadromous and landlocked Rainbow Smelt populations were examined indicated significant haplotype heterogeneity in landlocked groups, warranting speculation of polyphyletic origins for dwarfism in this species (Baby et al. 1991). Subsequent studies of the *O. mordax* morphotype complex in Lac Saint-Jean (Saint-Laurent et al. 2003) and Lake Utopia (Curry et al. 2004) supported the hypothesis of polyphyly of dwarf forms.

Gene Expression

A microarray with 8,448 Expressed Sequence Tags was constructed to assess the effects of exposure of larval and juvenile Delta Smelt to several common environmental contaminants. To understand the sublethal effects of exposure of larvae to esfenvalerate—a synthetic pyrethroid insecticide widely used in agriculture (Connon et al. 2009)—the microarray was used to identify 94 unique genes (biomarkers) in Delta Smelt larvae that specifically responded to esfenvalerate, particularly those explaining swimming abnormalities at low concentrations ($LC_{50, 24 h} = 0.24 \mu\text{g/L}$). A high percentage of the responding genes (49%) were involved in various cellular processes, such as encoding for ribosomal proteins, t-RNA synthesis, telomerases, uncoupling genes, and genes involved in chromosome maintenance (Fig. 18.15). Interestingly, 19% of the genes were involved in neuromuscular responses and hence relatable to swimming abnormalities, but the insecticide was also linked to expression in genes controlling many other physiological processes (Connon et al. 2009). Another study using the same microarray investigated gene expression in Delta Smelt juveniles exposed to copper ($42.0 \mu\text{g/L Cu}^{2+}$ for 7 days) (Fig. 18.15). Genes most affected include those involved in digestion and metabolism, neuromuscular activity, immune response, and various cellular functions (Connon et al. 2011a). The microarray was also used to identify genes responding to 10 mg/L total ammonia (nominal concentration, four-day exposure) in 57-day-old Delta Smelt larvae (Connon et al. 2011b). The majority of responding genes were associated with membrane integrity and function (e.g., membrane bound proteins responsible for ion transport and ionic exchange). Other affected genes were involved in calcium signaling with strong implications for negative effects of ammonia exposure on muscle contraction and other neuromuscular impacts. The microarrays were also used to evaluate genetic responses in Delta Smelt larvae exposed

to ambient water collected from a Sacramento River site with poor water quality (e.g., sewage effluent, urban and agricultural contaminants) (Hasenbein et al. 2014). A total of 94 genes were assigned to a function-pathway. Metabolic pathways responsible for digestive processes, including pancreatic secretion, protein digestion and absorption, fatty acid metabolism, pentose phosphate pathways, glycolysis and gluconeogenesis, as well as the starch and sucrose pathway, were affected by exposure. Other gene responses were associated with the immune system, neuromuscular system, and bone structure and development (Hasenbein et al. 2014). Comparably, using an expansive oligonucleotide array consisting of >12,000 genes, Jeffries et al. (2015) showed permethrin (also a pyrethroid pesticide) down-regulated genes associated with immune response while up-regulating those associated with the degradation of proteins and apoptosis. In sum, the authors concluded that a complex mixture of contaminants in the Sacramento River, including ammonia, are likely adversely affecting Delta Smelt population dynamics through a variety of mo-

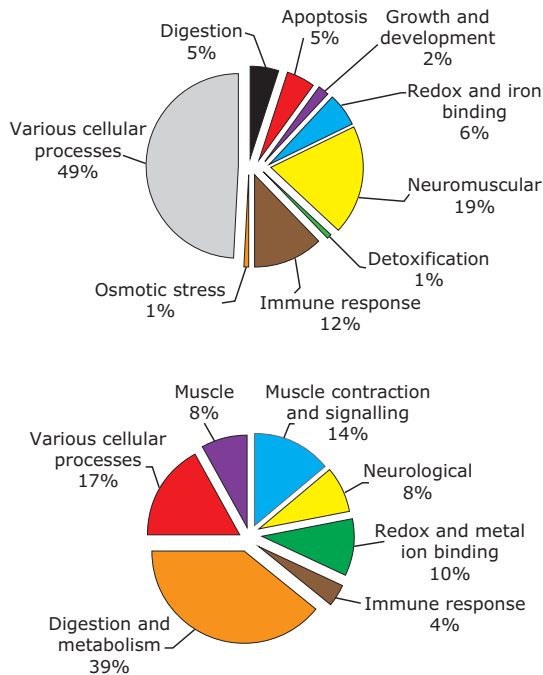


Figure 18.15. (upper) Functional classification of genes responding to esfenvalerate exposure (0.0625 and 0.125 $\mu\text{g/L}$, 24 h) in 52-day-old Delta Smelt, *Hypomesus transpacificus*. Percentages were calculated based on function and biological processes of 94 unique, differentially expressed genes (redrawn from Connon et al. 2009). (lower) Systematic analysis of Kyoto Encyclopedia for Genes and Genomes orthology and gene ontology-based functional classification of Delta Smelt genes significantly differing in juveniles exposed to copper (42.0 mg/L Cu^{2+}) for seven days (redrawn from Connon et al. 2011a).

lecular and metabolic pathways (Hasenbein et al. 2014; Jeffries et al. 2015).

PHYSIOLOGY

Environmental factors strongly control the distribution and abundance of Smelt populations throughout North America; however, systematic studies of Smelt physiology are limited. Water temperature, dissolved oxygen, pH, and salinity levels regulate behaviors as disparate as the distribution of larvae (e.g., Hobbs et al. 2010), to diel migration patterns, to timing of spawning. In perhaps the most comprehensive study to date, Swanson et al. (2000) compared environmental tolerances and kinematics of Delta Smelt with introduced Wakasagi in the Sacramento-San Joaquin Estuary. The study forms the basis of the following subsections and was a vital component in developing a more effectual conservation and management plan for the Delta Smelt. Understanding individual and population-level responses to environmental conditions, especially in terms of chronic bioenergetic costs (e.g., Brooks et al. 2012; Miller et al. 2012), likely will be at the forefront of future Smelt conservation efforts.

Temperature Tolerance

The Delta Smelt and invasive Wakasagi show relatively substantial differences in temperature tolerance. Delta Smelt can withstand temperatures ranging from 6 to 28°C (critical thermal minima 7.5°C, critical thermal maximum 25.4°C, acclimated at 17°C) (Swanson et al. 2000), and sometimes occupy water at temperatures close to their lethal limit of 29°C (Moyle 2002; summarized by Moyle et al. 2016). However, Delta Smelt found in the San Francisco Bay Estuary at such high temperatures often show oxidative damage and frequent single-cell necrosis in the liver associated with impairment of antioxidant enzyme activity (Bennett 2005). Analyses of trends in regional abundance with water quality within the Estuary indicated Delta Smelt became virtually absent from areas when water temperatures were near or >25°C, and the response to temperature appeared to be abrupt not gradual (Nobriga et al. 2008). In laboratory assessments, thermal tolerance decreased among successive ontogenetic stages with larvae exhibiting the high tolerance, perhaps an adaptation to larval habitat conditions, and post-spawning adults the lowest, likely associated with winter conditions after spawning (Fig. 18.16). The species

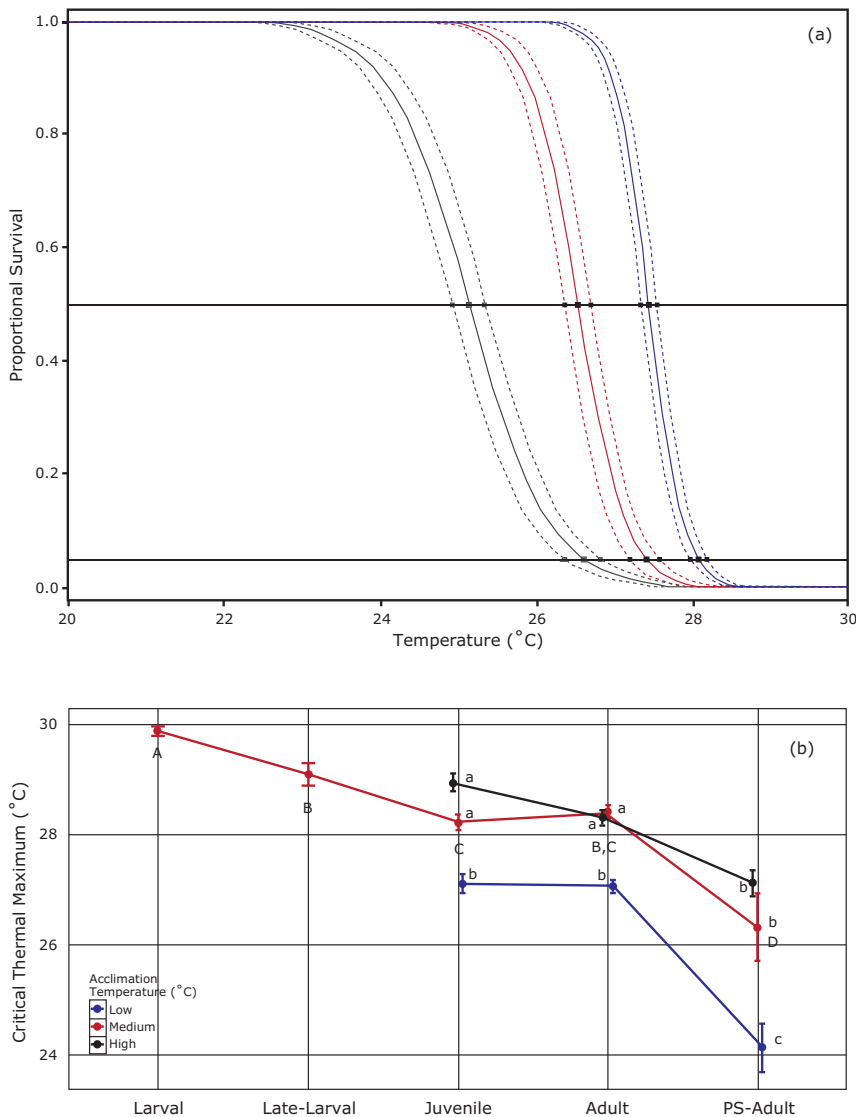


Figure 18.16. Thermal tolerance of Delta Smelt, *Hypomesus transpacificus*. (a) Estimates of chronic lethal thermal maximum (CLT_{max}; continuous lines) and 95% confidence intervals (dashed lines) for juvenile (blue), adult (red), and post-spawning Delta Smelt (black). Points denote the 50% morbidity (CLT_{max50}) and 95% morbidity (CLT_{max95}) estimated mean and 95% confidence interval for each ontogenetic stage on the respective curves. (b) Critical thermal maximum (CT_{max}) temperatures (means \pm SEM) (loss of escape ability) for ontogenetic stages of Delta Smelt at different acclimation temperatures with an offset (0.05) added to each point to avoid overlapping. Capital letters denote significantly different groups across all ontogenetic stages at the medium acclimation temperature only; lower case letters denote significantly different groups among stages of non-larval fish at low, medium, and high acclimation temperatures. Within each case, groups not sharing a common letter are significantly different at an adjusted α level of 0.05 as determined by a linear model and pairwise comparisons (details in Komoroske et al. 2014). Acclimation temperatures (for three weeks): low, 12.5°C; medium, 15.5–16.5°C; high, 18.5–19.5°C. PS-adult, post-spawning Delta Smelt (redrawn from Komoroske et al. 2014).

showed limited capacity to increase tolerance via thermal acclimation, which suggests vulnerability to increased temperatures from climate change (Komoroske et al. 2014). Comparatively, Wakasagi exhibit a broader range of thermal tolerance and can tolerate rapid temperature fluctuations. The critical thermal minima for Wakasagi was 2.3°C and critical thermal maximum was 29.1°C (acclimated at 17°C) (Swanson et al. 2000).

The microhabitat preferences of the Rainbow Smelt vary seasonally and are mediated by temperature and dissolved oxygen (Evans & Loftus 1987; Pientka & Parrish 2002). In freshwater habitats on Lake Champlain, Rainbow Smelt occurred in the spring at temperatures ranging from 7.4 to 9.5°C and dissolved oxygen concentrations ranging from 9.8 to 10.1 mg/L (Pientka & Parrish 2002). Interestingly, during the spring season Rainbow Smelt

forage in waters free of Atlantic Salmon (*Salmo salar*), their major predator, which seem excluded from these habitats by lower temperatures. Thus, predator avoidance may be a driving factor in seasonal thermal microhabitat preferences in Lake Champlain. More typically, Rainbow Smelt inhabit waters ranging from 6 to 18°C (Ferguson 1965). For instance, in Lake Michigan, larval Rainbow Smelt densities were highest in waters ranging from 9 to 14°C (Brandt et al. 1980; Tin & Jude 1983). Similarly, in Lake Superior and Lake Erie, waters ranging from 6 to 18°C were used by Rainbow Smelt. Peak densities in all three Great Lakes occurred at temperatures ranging from 9 to 16°C (Heist & Swenson 1983; Pientka & Parrish 2002). Similarly, Longfin Smelt can tolerate water temperatures $\geq 20^\circ\text{C}$, but prefer temperatures of 16–18°C (Moyle 2002). The temperature tolerances of other Smelts

have not been systematically evaluated in laboratory settings; however, maximum temperatures clearly play a major role in regulating species geographic distributions.

Swimming Performance

The introduced Wakasagi is an excellent swimmer, attaining maximum velocities of 56 cm/s with a stroke-and-glide movement and sometimes swimming at twice the rate of comparable-sized Delta Smelt (Swanson et al. 2000). The maximum swimming velocity for Delta Smelt was about 38 cm/s (detailed by Swanson et al. 1998). In relation, the mean critical swimming velocity, the maximum velocity Delta Smelt can sustain for a prolonged period of time, was 27.6 cm/s, and ranged from about 18 to 37.5 cm/s. The median endurance time significantly decreased between velocities of 10–15 cm/s, decreasing from 360 to 64 min. However, some fish could continually maintain position at water velocities approaching 30 cm/s. The interaction of maximum swimming velocity and endurance is decisive in controlling instances of impingement at water diversion points in the Sacramento-San Joaquin Estuary.

Kinematic analyses indicate Delta Smelt are subcarangiform swimmers and are well adapted for a variety of flow regimes. The species has three distinct swimming patterns, and the pattern displayed is contingent on water velocity (Swanson et al. 1998). At low water velocities (<10 cm/s), a stroke-and-glide action is used. Between velocities of 15–20 cm/s, a continuous stroking behavior was needed to maintain water position. Finally, at high water velocities (25–30 cm/s) and just before fatigue, a burst-and-glide behavior is exhibited, in which the fish displays continuous regular strokes with periodic high amplitude strokes followed by a transient glide period.

pH and Egg Development

The eggs of osmerids are often exposed to marked pH depressions for hours or days during incubation periods. These acid episodes are attributable to snow melt events during spring rains and ice melt at lake surfaces (Klauda & Palmer 1987). Generally, Rainbow Smelt egg survival is not related to pH: after 48 h of pH 4.5–5.5 the average survival is >80% (Geffen 1990). However, acid sensitivity does vary by developmental stage at initial exposure, and older eggs had better survival. The chorion of Rainbow Smelt eggs is structurally different from other species, perhaps contributing to their tolerance of low pH exposure (Johnson & Werner 1986).

Salinity Tolerance

Most Smelts show a wide salinity tolerance, as evidenced by the various life-histories. Wakasagi have a higher tolerance of salinity levels, 26.8 ppt maximum versus an upper limit of 19.1 ppt for Delta Smelt (Swanson et al. 2000; No-briga et al. 2008; reviewed by Moyle et al. 2016). This is one factor partially responsible for the successful establishment of Wakasagi. Likewise, salinity levels are a principal factor controlling the distribution and abundance of native Smelts in estuaries. Even though various life stages of Delta Smelt tolerated laboratory salinities spanning the range of expected habitat conditions for each ontogenetic stage, high salinity did impact survival of juvenile and adult stages (Fig. 18.17). Other studies also indicate negative physiological effects of high salinities and interactions with other factors. Laboratory trials subjecting Delta Smelt to a matrix of turbidities (5–250 NTUs) and salinities (0.2–15 ppt), both influenced by water flow through the San Francisco Bay Delta, revealed indicators of osmoregulatory stress (i.e., adenocorticotrophic hormone, whole body cortisol, transcription rates of various stress-indicating genes) were affected only by salinity, but increased turbidities resulted in reduced feeding rates, especially at 250 NTU (Hasenbein et al. 2013). Optimal performance was indicated at salinities >0–6 ppt; detrimental effects occurred at turbidities <120 NTUs and salinities >12 ppt. Larval and juvenile Delta Smelt survived 10 ppt salinity with incremental increases of 1, 2, and 4 ppt. Changes in salinity ≥ 2 ppt initiated physiological responses, including increased blood hematocrit, plasma osmolality values, and muscle water content. In addition, chloride cells showed increased apoptosis, Na⁺/K⁺ ATPase, and cell size over time in saline water indicating that turnover to new salinity tolerant chloride cells occurred (Kammerer 2014). Overall the data are congruent with habitat associations of greater Delta Smelt abundances in the low-salinity zone (0.5–6.0 ppt) of the Bay, a zone that also has optimal turbidities (>12 NTU) (e.g., Moyle et al. 1992; Kimmerer 2002; Hobbs et al. 2006; Feyrer et al. 2007; Sommer & Mejia 2013; Moyle et al. 2016). Comparably, in the San Francisco Bay Delta, a strong spatial correlation exists between seasonal flow, the distribution of the 2 ppt isohaline, and the abundance of juvenile and adult Longfin Smelt (Jassby et al. 1995; Moyle 2002; Hobbs et al. 2010). In this case, the seasonal freshwater outflows control the volume of brackish waters (salinities 2–18 ppt) required for rearing by larval Longfin Smelt (Hall 1991).

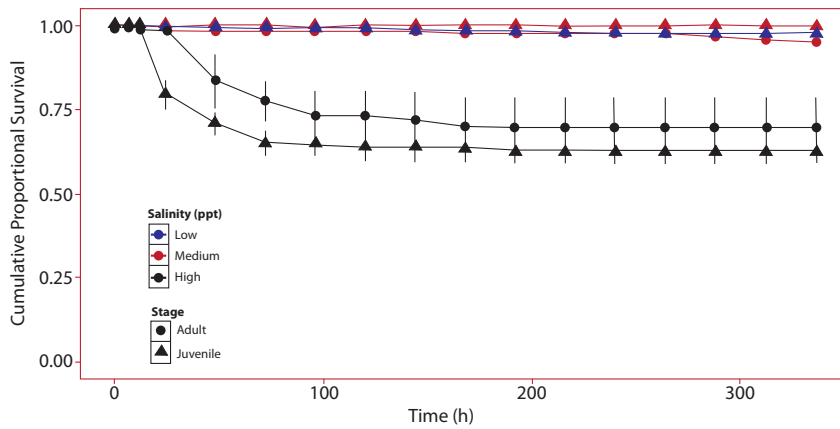


Figure 18.17. Cumulative proportional survival of juvenile and adult Delta Smelt, *Hyposmesus transpacificus*, in acute salinity maximum (AS_{max}) trials over two weeks of exposure (salinities: low, 2.3 ppt; medium, 18.5 ppt; high, 34.0 ppt). Late-larvae (not shown) exhibited no significant difference in survival across salinity treatments (redrawn from Komoroske et al. 2014).

Antifreeze Properties

Perhaps the most interesting aspect of Smelt physiology is the antifreeze properties of species residing in Arctic and polar areas, which are used to prevent ice formation in their blood. For instance, Rainbow Smelt live in the Atlantic Ocean of Canada where water temperatures can reach -1.8°C , 1°C below the -0.8°C freezing point of most teleost fishes (Driedzic et al. 1998). Not only is freezing resisted under these conditions, but activity of *Osmerus* remains high (Driedzic & Ewart 2004). Several components, colligative and non-colligative, are involved in the depression of the freezing point and prevention of cold denaturation in Rainbow Smelt tissues. Examples include the production of antifreeze proteins (AFPs) and accumulation of glycerol, trimethyl-amine N-oxide, and urea (Treiberg et al. 2002; Driedzic & Ewart 2004). The two most significant factors in freezing point depression are AFP and glycerol production. AFPs in the blood of Rainbow Smelt bind to ice crystals, inhibiting crystal growth and depressing the freezing point about 0.4°C (Driedzic & Ewart 2004; Yamashita et al. 2003). AFPs are useful but provide only limited protection from freezing (Raymond & DeVries 1977).

Glycerol, which functions colligatively, is produced primarily in the liver and is responsible for an additional $>1^{\circ}\text{C}$ depression of the freezing point (Driedzic & Ewart 2004; Driedzic & Short 2007; Robinson et al. 2011b; Ditlecadet & Driedzic 2013). Further, glycerol enhances the folding and consequent activity of Rainbow Smelt AFP (i.e., increases freeze resistance) so that protein chaperoning is apparently another role for glycerol in the species (Gong et al. 2011). Productions of both glycerol and AFP macromolecules show distinct seasonal profiles with elevated production in colder winter months; the upregulation of some genes in

winter is apparently associated with shifts in freeze resistant proteins (Richards et al. 2008). AFP production actually begins before significant cooling of the water occurs and is probably influenced by photoperiod (Fletcher et al. 2001). However, glycerol production appears controlled directly by temperature, and a sharp increase in production is observed when water temperatures approach 5°C (Raymond 1993, 1995; Driedzic & Ewart 2004; Lewis et al. 2004; Driedzic & Short 2007; Clow et al. 2008; Ditlecadet et al. 2011; Hall et al. 2012; Clow & Driedzic 2012). Glycerol levels in Rainbow Smelt seem to be only dictated by the rate of glycerol synthesis and not by other metabolic mechanisms. Synthesis is accelerated during the accumulation period with losses to the environment via apparent passive diffusion and deactivated during the decrease period (Ditlecadet et al. 2011). The direct dephosphorylation of glycerol-3-phosphate is the proposed pathway Rainbow Smelt use to produce glycerol (Driedzic et al. 1998, 2006). The natural production of glycerol and AFP require significantly higher energy and nutrient intake than under non-cold conditions (Driedzic & Short 2007). Glycerol is lost freely across the gills and other exposed surfaces of the fish and must be continuously replenished (Driedzic & Ewart 2004). Hence, during winter Rainbow Smelt must consistently consume considerable amounts of food to support the need for glycerol as well as AFP. Cytosolic glycerol-3-phosphate dehydrogenase plays a key role in glycerol accumulation and mitochondrial glycerol-3-phosphate dehydrogenase in the subsequent decrease of glycerol (Robinson et al. 2011b). As plasma glycerol levels increase so does glycerol in the red blood cells, heart, liver, kidney, muscle, brain, spleen, and ocular fluid (Driedzic & Short 2007; Gendron et al. 2011; Clow & Driedzic 2012). The antifreeze adaptations are accompanied by a cold acclimation response that also includes physiological shifts in the myotomal muscle

permitting a high level of muscle performance in extremely cold muscles (Woytanowski & Coughlin 2013). Loss of anti-freeze properties occurs in about three weeks with exposure to warmer water temperatures (14°C) and a long photoperiod (16 h light) (Duman & DeVries 1974; Driedzic & Short 2007; Clow et al. 2008).

Odorants

The cucumber odor found in Smelts is caused by trans-2-cis-6-nonadienal (McDowall et al. 1993). The same chemical is responsible for a similar odor in Australian Grayling (*Prototroctes maraena*), which is sometimes called the cucumber herring (Berra 1982). The origin of the smell is uncertain; it either results from bioaccumulation of the chemical from algal origins (Hart 1973) or as an endogenous metabolite originating in the fish (McDowall et al. 1993). The metabolic pathways involved in the production of trans-2-cis-6-nonadienal are unknown.

BEHAVIOR

The preponderance of literature on Smelt behavior deals with diel and seasonal movement patterns associated with foraging and various life-history stages. The movement of larval forms of anadromous Smelt during the transition from freshwater to marine stages is of particular interest for conservation. Other behavioral studies offer descriptions of spawning migrations and subsequent spawning events (see reproduction section).

Movement

Rainbow Smelt are negatively phototactic and primarily nocturnal, migrating vertically to shallower regions only at night to feed (Buckley 1989). This behavior seems to be an adaptation for avoidance of visual predators, particularly for larval and juvenile Smelt (Moyle 2002). An exception occurs in Rainbow Smelt in the St. Lawrence River Estuary, which, like Delta Smelt, appear to restrict feeding to daylight hours during flood tides (Sirois & Dodson 2000; Hobbs et al. 2006). However, others have noted nocturnal vertical behavior in nearly every other species of Smelt (Scott & Crossman 1973; Morrow 1980; Moyle 2002; Wydoski & Whitney 2003) and surmised that nocturnal vertical migrations coincide with the diel movements of preferred prey species of zooplankton (e.g., mysid shrimp), preferable hydraulic conditions, or both. For

illustration, Longfin Smelt in Lake Washington, Washington, reside at depths of 20–40 m during the day and spend most of the night in waters 12–20 m deep; a movement pattern analogous to that observed in the mysid shrimp *Neomysis arctica* (Wydoski & Whitney 2003). In sum, although in early life-history stages the vertical migration behavior may be conducive to predator avoidance, the primary driver is feeding strategy, and the diel vertical migrations continue throughout the life span.

Field and laboratory studies indicated larval Rainbow Smelt in the Salmonier River estuary, Newfoundland, use vertical migration to enhance estuarine retention (Bradbury et al. 2006b). A week after hatching, larvae were consistently negatively geotactic, but juveniles (90 days old) were deeper and displayed negative geotaxis in the light and positive geotaxis in the dark. The different light-mediated geotactic behaviors corresponded to ontogenetic increases in swimming ability and seasonal changes in estuarine circulation, resulting in limited transport and a tendency to limit recruitment to the estuary despite a long pelagic period.

Adult and larval Rainbow Smelt also actively seek out areas with more favorable microhabitat conditions, such as zones with optimal temperature regimes (Buckley 1989). A spatial analysis of larval Rainbow Smelt within the St. Lawrence River Estuary revealed active migrations to areas of high turbidity with warm temperatures (10–20°C) and low salinity (0–10 ppt) (Dodson et al. 1989). In contrast, Delta Smelt migrations appear less affected by temperature than in Rainbow Smelt and aggregations occur in waters of 6–28°C (Moyle 2002). Delta Smelt are attracted to favorable hydraulic regimes and position themselves near the interface of fresh and salt water (Moyle 2002). Flow conditions at the interface likely permit Delta Smelt to better maintain spatial position given their weak swimming capacity (Swanson et al. 1998; Moyle 2002; Moyle et al. 2016). Based on otolith microchemistry analyses, Delta Smelt, before 2002, typically spent the 30-day larval period in fresh water in the interior San Francisco Bay Delta, and juveniles migrated to the low salinity waters of Suisun Bay (Hobbs 2010). After 2002, larval distributions shifted upstream to the lower Sacramento River, and a higher proportion of freshwater populations delayed migration into low-salinity nursery areas. This shift was attributed to inter-annual variability of freshwater flows in this system (Nobriga et al. 2008; Hobbs 2010). Like Delta Smelt, Longfin Smelt in the Sacramento-San Joaquin Estuary also occupy turbid, low salinity zones with tidal influence (Bennett et al. 2002; Hobbs et al. 2010).

Shoaling

All species of Smelt, except Delta Smelt, form shoals as larvae and adults. The lack of schooling behavior in Delta Smelt emanates from the weak swimming capabilities and the pronounced stroke-and-glide kinematics, which impede coordination of large schools (Moyle 2002; Moyle et al. 2016; see physiology section). As a result, Delta Smelt form only loose aggregations when they are tracking optimal hydraulic conditions. Interestingly, Wakasagi display well-defined shoaling behavior despite similarities

to Delta Smelt in terms of kinematics, turning radius, and fast-start swimming behaviors.

REPRODUCTION

Most Smelts are semelparous, dying after they spawn, except *Osmerus*, which may spawn in multiple years (Table 18.1). In some typically semelparous osmerids, a small fraction of individuals may spawn a subsequent year or, in the case of Delta Smelt, delay their first spawn until the second year of

Table 18.1. Life-history attributes of four genera of North American Smelts (Osmeridae). The Pond Smelt (*Hypomesus olidus*) is used as the exemplar for *Hypomesus*, the Rainbow Smelt (*Osmerus mordax*) for *Osmerus*, the Longfin Smelt (*Spirinchus thaleichthys*) for *Spirinchus*, and the Eulachon (*Thaleichthys pacificus*) for *Thaleichthys*. Information compiled from McAllister (1963), Scott & Crossman (1973), Morrow (1980), Moyle (2002), Jelks et al. (2008), Gustafson et al. (2010), COSEWIC (2014), and USFWS (2014). AFS, American Fisheries Society; USFWS, U.S. Fish and Wildlife Service; COSEWIC, Committee on the Status of Endangered Wildlife in Canada.

	<i>Hypomesus</i>	<i>Osmerus</i>	<i>Spirinchus</i>	<i>Thaleichthys</i>
Number of extant species	6	2	3	1
Fresh water, anadromous, or catadromous	Fresh water	Fresh water and anadromous	Fresh water and anadromous	Anadromous
Maximum size (TL)	185 mm	324 mm	150 mm	300 mm
Maximum age	5 years	6 years	3 years	5 years
Age at reproductive maturity	2 years	2 years	2 years	3 years
Iteroparous versus semelparous	Semelparous	Iteroparous	Semelparous	Semelparous
Egg deposition; Substrate Preparation	Broadcast/no preparation	Broadcast/no preparation	Broadcast/no preparation	Broadcast/no preparation
Fecundity estimates (range and mean); egg size	1,200–4,000; 3,000; about 1 mm diameter	1,700–69,600; 30,000; 0.54–0.65 mm diameter	535–24,000; 18,000; about 1 mm diameter	7,000–60,000; 25,000; 0.8–1.0 mm diameter
Spawning season (dates and temperatures)	May–June 7–15°C	March–May 4–18°C	Nov–June 7–14.5°C	Feb–May 4.4–10°C
Habitat of spawning	Streams/rivers/littoral zones of lacustrine environment over coarse substrate	Streams/rivers/littoral zones of lacustrine environment over coarse substrate	Streams/rivers/littoral zones of lacustrine environment over coarse substrate	Streams/rivers over coarse substrate
Incubation period	18–24 days at 10°C	19–29 days at 6–10°C	10–12 days at 11–15°C	14–21 days at 10°C
Size at hatching	4–5 mm	5–6 mm	5–8 mm	3–7 mm
Parental care	None	None	None	None
Major diet items	Copepods, cladocerans, amphipods	Mysids, copepods	Mysids, copepods	Unknown; probably mysids
Year-round habitat	Pelagic lacustrine	Pelagic lacustrine/coastal marine	Pelagic Lacustrine/coastal marine	Coastal marine
Imperilment status	Stable; Delta Smelt, endangered (AFS, USFWS) and possibly functionally extinct	Stable; dwarf (AFS, COSEWIC) and large-bodied (COSEWIC) population of Rainbow Smelt in Lake Utopia, threatened	Longfin Smelt, threatened (AFS), candidate for listing (USFWS) (see text)	Eulachon populations from southern British Columbia to California, threatened (USFWS, COSEWIC) (see text)

life (Hay & McCarter 2000; Moyle 2002; Bennett 2005). Spawning behavior in Smelts usually involves a migration into shallow beaches of freshwater lakes or rivers with coarse substrates, such as sand or gravel where they often lay demersal eggs. In Smelt populations residing in reservoirs, rivers, or estuaries (e.g., species of *Hypomesus*, *Osmerus*, and *Spirinchus*), spawning can occur in littoral zones with organic debris, in tributaries with sandy or gravelly substrates, or in offshore sites (McAllister 1963; Morrow 1980; Moyle 2002; Lischka & Magnuson 2006). Spawning strategy shows some plasticity, and choice of spawning locality is related to external factors, especially discharge and water temperature.

Sexual Dimorphism

Smelts are sexually dimorphic, and differences are particularly noticeable during the spawning period (McAllister 1963). Generally, males are slightly smaller than females but have longer pectoral, pelvic, and anal fins (Figs. 18.5 and 18.18), which, during the breeding season, develop tubercles on the dorsal surfaces. The anal fin forms a shelf and is slightly enlarged in *Spirinchus*, *Osmerus*, and especially *Thaleichthys*. In anadromous Longfin Smelt, the longest anal-fin ray can reach >70% of the head length and the first ray of the paired fins is enlarged and rigid. Tubercles also form on the scales and head region of osmerid males but are absent or weakly developed in females (Fig. 18.5). Male individuals are often more darkly pigmented than females, with distinct stippling around the scale edges and, in some species, on the operculum and sub-operculum. Most spawning males have a distinctive mid-lateral ridge caused by the swelling of lateral musculature.

Spawning Runs, Conditions, and Habitats

The timing of spawning runs in river-spawning Smelts is largely cued by flow conditions. To optimize spawning success, Pond Smelt in the Chignik River system, Alaska, migrate upstream during the low-flow period just before late spring snowmelt. Presumably, this tactic conserves energy via avoidance of high discharges with low water temperatures, which accompany the annual snowmelt (Harvey et al. 1997). When high discharges prevent migration into river systems or when suitable stream habitat is unavailable, Pond Smelt typically spawn in littoral areas of lakes and ponds (Morrow 1980). Similarly, Great Lakes populations of Rainbow Smelt avoided migration into streams during periods of turbulent weather and high discharge, opting to spawn on offshore gravel shoals and flats



Figure 18.18. Ventral view illustrating the relative sizes of the pelvic fins of a breeding female (left) and breeding male (right) Eulachon, *Thaleichthys pacificus*. Note the enlarged fins of the male, which are also covered with tubercles on the dorsal surface (photograph taken along the Kemano River, British Columbia, by and used with permission of Dave Gordon).

(Scott & Crossman 1973). In the Delta Smelt, which is a weak swimmer, high outflows can literally flush adults out of the Sacramento-San Joaquin Estuary, significantly reducing the spawning stock (Moyle 2002). Analyses of abundance patterns of the Delta Smelt revealed a complex picture of distribution and dispersal before spawning. The fish show diffuse dispersal from several distributional loci in which they move from open waters of embayments and channels across the northern Delta to proximate freshwater sources delivered to the Delta via upland winter and spring storms (Murphy & Hamilton 2013). Notably, there is apparently no massive unidirectional upstream spawning migration from downstream rearing areas hypothesized by some (Sommer et al. 2011). During the spawning season when first flush events deliver high flows to the San Francisco Estuary, occurrence patterns of Delta Smelt at the shoal-channel interface and near shorelines is synchronized with tidal flows and associated turbidity gradients. Probability of occurrence is highest at the shoal-channel interface during flood tides and along shallow shorelines during ebb tides. The highest occurrence in each habitat is coincidental with higher turbidities. The apparent selective tidal movements likely facilitate maintaining position or moving upriver on flood tides and minimizing advection down-estuary on ebb tides. The movements may also indicate responses to lateral gradients in water turbidity in these habitats. The movements appar-

ently minimize energy expenditures against strong river and tidal currents and decrease predation risk in turbid water (Ferrari et al. 2014; Bennett & Burau 2015).

Extremely low outflow conditions also can impede spawning success by preventing upstream migration and forcing Smelts to spawn in sub-marginal habitats, often in conditions of higher temperatures, higher salinities, or both. Thus, the reproductive success of all Smelts is generally greatest in years of moderate outflow (Moyle 2002), suggesting alternative sites, although suitable, are inferior compared with preferred spawning grounds. However, alternative spawning strategies most definitely confer an adaptive advantage and improve spawning success during adverse conditions.

Anadromous populations of Smelts (e.g., genera *Osmerus*, *Spirinchus*, and *Thaleichthys*) congregate, often in enormous numbers, near stream mouths before ascension up coastal rivers to spawn (Figs. 18.19–18.22). These Smelts normally return to natal regions for spawning; however, the homing instinct is not as strong as that observed in salmonids, and site selection for spawning is much more general. Some evidence of population partitioning is known in *Osmerus* based on biochemical data; however, the structuring was not associated with spawning locations within rivers (Bernatchez & Martin 1996; see genetics section). In the Parker River Estuary, Massachusetts, spawning male Rainbow Smelt migrated between stream systems and used multiple spatially dispersed spawning sites, traveling ≤ 16 km in 48 h (Murawski et al. 1980). Similarly, Eulachon disappear from regular spawning sites, only to return years later to the same river sections (McLean et al. 1999; see conservation section). Such behavior implies a limited role of homing in spawning site selection and the lack of consistent homing can contribute to low genetic population structure in many Smelt species. As with inland populations, flow discharges affect migration distances and spawning site choice.

The distance traveled upstream during spawning is relatively short, usually only a few kilometers, and in some cases spawning takes place near the interface of brackish and fresh water (e.g., Rainbow Smelt can spawn in low salinity tidal zones of estuaries) (McKenzie 1964). Obstructions, such as dams, weirs, and water diversions, act as barriers and are likely the causative agents for most spawning within brackish water (Scott & Scott 1988). However, there are a few cases of longer migrations. Eulachon sometimes travel 160 km up the Columbia River (Moyle 2002; Fig. 18.19), and some populations of the Rainbow Smelt migrate distances $>1,000$ km (McPhail & Lindsey 1970).

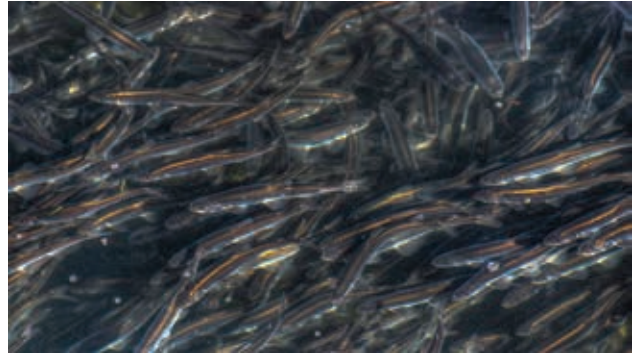


Figure 18.19. After spending 2–3 years at sea, Eulachon, *Thaleichthys pacificus*, make their annual spring spawning runs in freshwater rivers where they can congregate in enormous numbers as exemplified in (upper) Alaganik Slough, Copper River Delta, Chugach National Forest, in May 2010, and (middle and lower) the Chilkoot River, Haines, Alaska, in April 2011 (courtesy of © Tom Kline/Alaska Stock Image, upper, and Scott Wickard, middle and lower).

Normally, males precede females in upstream migrations and outnumber females at spawning grounds. Eulachon fishers of the Cowlitz Indian Tribe, Washington, refer to the initial male migration as the pilot or scout run, which is followed by the main run (Reynolds & Romano



Figure 18.20. Many populations of Rainbow smelt, *Osmerus mordax*, are anadromous, spawning in freshwater but spending the rest of their lives in salt water. The inland migrations occur mainly in the spring, and the journey upstream is not always easy. Many blockages along the way can be bypassed by other species (e.g., salmon), but because of their small size, Rainbow Smelt find it more difficult to overcome barriers. Most individuals look for the path of least resistance, but as shown here, some attempt to jump over small falls (photograph in a Prince Edward Island river by and used with permission of Sean Landsman Photography).

2013). A notable exception to the males preceding the females is the Pond Smelt, in which females tend to outnumber males 3:1 (Harvey et al. 1997). However, estimation of sex ratios may be slightly biased because the sexes occupy spawning grounds for different lengths of times with males remaining at spawning grounds longer than females. For example, the average spawning period for *O. mordax* males in a Massachusetts river was 11–22 days (Murawski et al. 1980), but the average spawning period for females was only 8–14 days. The male to female ratio during this period was estimated at 5–7:1. Other Smelt species show lower ratios; however, in each case (except Pond Smelt) males tend to outnumber females at least 2:1 (Scott & Crossman 1973; Morrow 1980; Moyle 2002).

Spawning

Once the spawning destination is reached, actual reproductive behavior occurs en masse and only at night (Hay & McCarter 2000; Curry et al. 2004; Fig. 18.23). During the day, Smelts retreat to deeper channels of the river or downstream into areas with slower, deeper waters (Moyle 2002). Sensitivity to sunlight and predator avoidance apparently contributes to the diel migrations during the spawning season (Rupp 1959; Loftus & Hulsman 1986). Spawning takes place over coarse substrates, such as sand, pebbles, organic debris, and aquatic plants (Figs. 18.23 and 18.24). Because Smelt eggs are adhesive and demersal (Morrow 1980; Moyle 2002), the substrate type and water velocity are important to egg development and subsequent dispersal. Smelts are broadcast spawners, and eggs are deposited in areas with low to moderate velocities (Table 18.1). Once released, eggs adhere to coarse sub-

strate by virtue of a tiny pedicle formed from the breaking up and inversion of the outer coating of the egg (Morrow 1980; Fig. 18.24). Smelts are not known to build a nest or provide parental care to young.

Delta Smelt spawn from early April through mid-May at water temperatures of 7–22°C with the majority of activity occurring between 7–15°C (Moyle 2002; Bennett 2005). Spawning is nocturnal, coincidental with new or full moons, and occurs over coarse substrate in shallow flats and edge areas in freshwater zones, and usually takes place during low tide. Laboratory observations of reproductive behavior in the Delta Smelt indicate that actual spawning begins when a female breaks from the school and positions herself near the bottom facing into the current (Moyle 2002). A male follows the female into the current and aligns himself parallel. The pair move forward with flanks touching and in concert, expel eggs and milt. In a hatchery tank with mature, sexed adults (37 females, 67 males), genetic parentage analysis indicated females spawned 0–4 times (mostly 0–3 times) and males 0–10 times (mostly 0–3 times) over the course of 12 samples from mid-March to mid-May. The number of sires assigned at each sample date greatly outnumbered the number of dams indicating a polyandrous mating system (LaCava et al. 2015). In the wild, females produce between 1,200–2,600 eggs, which are about 1 mm in diameter, and fecundity increases with size. The fecundity (F , number of mature eggs / female) at length relationship is estimated as $F = 0.266TL^{2.089}$ (Moyle 2002).

Pond Smelt spawn throughout June in Alaska (McAllister 1963; Scott & Crossman 1973; Morrow 1980) with migrations to spawning areas occurring throughout May (Scott & Crossman 1973; Harvey et al. 1997). Similar to the Delta



Smelt, spawning occurs in water temperatures of 7–15°C, (Morrow 1980), and adult females can produce 1,200–4,000 eggs, which are about 1 mm in diameter. Pond Smelt favor shallow areas over organic material and lay adhesive eggs, which attach to roots and other objects (Scott & Crossman 1973; Coad et al. 1995; Coker et al. 2001).

In contrast, Longfin Smelt have a protracted spawning period, ranging from early October to late June for anadromous populations (Morrow 1980; Moyle 2002). In Lake

Figure 18.21. (upper) Thousands of anadromous Rainbow Smelt, *Osmerus mordax*, ascend Gulliver Creek, a small tributary to the Neponset River estuary near Milton, Massachusetts, March 2012 (courtesy of Tom Palmer, Neponset River Watershed Association). (upper middle) Anadromous Rainbow Smelt moving upstream at night during a spawning run in Mosher Brook, a small Atlantic Ocean tributary, Nova Scotia, April 2005. Because males enter the spawning streams on many more nights in a season than females, on any given night males outnumber females (P. Bentzen pers. comm.). (lower middle and lower) Close-ups of tuberculate male Rainbow Smelt during spawning runs in Mosher Brook (lower middle), and the Pisquid River, Prince Edward Island (lower). The whitish, raised structures on the head and adorning the body in parallel rows are tubercles, which are hardened, sharp, raised structures developed by males during the breeding season. The fish use the tubercles during spawning to distinguish body contact with smooth, non-tuberculate females from body contact with roughened, tuberculate males. Body contact with the opposite sex initiates release of milt and eggs (upper middle and lower middle courtesy of Paul Bentzen; lower courtesy of © Sean Landsman / Engbretson Underwater Photography).

Washington, Washington, the spawning season extends from January through April, often peaking around mid-March (Chigbu & Sibley 1994; Wydoski & Whitney 2003). Spawning generally occurs at temperatures of 7–14.5°C and eggs average 1 mm in diameter, similar to other Smelt species. Fecundity is positively correlated with fish size but is extremely variable, ranging from 535–24,000 eggs/female with a mean of 18,000 (Morrow 1980; Chigbu & Sibley 1994; Moyle 2002). In Lake Washington, fecundity of the Longfin Smelt has declined significantly since the 1960s; mean fecundity has decreased from 18,000 to 10,000 eggs/female (Chigbu & Sibley 1994). The decline in fecundity is attributed to local environmental changes, such as relative food availability, pollution, and density-dependent



Figure 18.22. (upper) Freshwater, dwarf-morph Rainbow Smelt, *Osmerus mordax*, ascend McNab Brook, a tributary of Lochaber Lake, Nova Scotia, at night during a spawning run, April 2005. (middle and lower) Close-ups of tuberculate, dwarf-morph males during a spawning migration into tributaries of Lochaber Lake, April 2010. Note the Smelt eggs on the stream bottom (courtesy of Paul Bentzen). Freshwater, dwarf- and large-morph Rainbow Smelt in this system spawn simultaneously in the same tributary streams but maintain their morphological distinctiveness (Paul Bentzen pers. comm.).

competition (Chigbu & Sibley 1994). Likewise, Longfin Smelt in the San Francisco Bay Estuary also have relatively low fecundity, averaging 9,752 eggs/female in the 1970s (Moyle 2002).

Eulachon spawning periods extend from mid-March through mid-May with migrations into fresh water beginning as early as December (Morrow 1980; Moyle 2002; Gustafson et al. 2010, 2012; Fig. 18.19). Eulachon spend most of their life in marine waters (>95%) and generally migrate only a short distance from saltwater (<10 km) to spawn, but in large rivers, like the Columbia and Fraser

Rivers, they migrate greater distances (Hay & McCarter 2000). Eulachon appear to prefer to spawn in glacial-fed rivers (McLean et al. 1999) with water temperatures ranging 4.4–7.8°C (Scott & Crossman 1973), a much cooler and narrower range compared with other Smelts. Migration is cued between 2–4°C and movement to spawning locations halts completely at temperatures >8°C, but spawning may continue at temperatures of 10°C (Moffitt et al. 2002; Moyle 2002; Gustafson et al. 2010).

The duration of Eulachon spawning events is variable, lasting hours or days (Hay & McCarter 2000). Fecundity estimates range from 7,000–60,000 eggs/female with a mean of about 25,000; however, fecundities as low as 3,000 are known in some populations (Scott & Crossman 1973; Morrow 1980; Moyle 2002; Gustafson et al. 2010). In a 4-year study of Eulachon in the Copper River, Alaska, fecundity ranged from 12,202–52,722 and averaged 35,519 (Moffitt et al. 2002). As with other Smelts, fecundity is correlated positively with female size and averages 790 eggs/g body weight (Moffitt et al. 2002). But this relationship can be quite variable with some small Eulachon exhibiting high fecundity and vice versa (Hay & McCarter 2000). Eggs usually range from 0.8–1.0 mm in diameter and are irregular in shape.



Figure 18.23. (upper) In a virtual shower of eggs, anadromous male Rainbow Smelt, *Osmerus mordax*, crowd together and jockey for a spawning position with a female during a June spawning run in Mosher Brook, a direct Atlantic Ocean tributary, Nova Scotia. (lower) An anadromous male Rainbow Smelt (top) attempts to spawn with a female (bottom) amidst a pile of previously spawned and mostly dead eggs during the June spawning run in Mosher Brook. Upon close inspection, a Rainbow Smelt larva is visible under the jaw of the female. The bimodal spawning runs (April-early May and mid-late June) in this and other populations have received relatively little study (Coulson et al. 2006a), but local residents are quite familiar with them, dubbing the second run as the strawberry run because it coincides with the local strawberry season (Paul Bentzen pers. comm.) (courtesy of Paul Bentzen).

Like Eulachon, Rainbow Smelt characteristically begin spawning migrations in March or early April when water temperatures reach 2–4°C (Morrow 1980; Lischka & Magnuson 2006; Figs. 18.21–18.23). Spawning usually does not commence until water temperature is >4°C (Buckley 1989; Lischka & Magnuson 2006); however, Rainbow Smelt in the Monaquot River, Massachusetts, initiated spawning at 1°C (Chase & Childs 2001). Anadromous populations usually begin spawning at lower temperatures than lacustrine populations, which delay migration until water temperatures reach 10°C (Buckley 1989). Most spawning, however, begins by about 6°C for both forms (Buckley 1989; Chase & Childs 2001) with upper limits of spawning temperature estimated at 18.3°C (Scott & Crossman 1973; Bradbury et al. 2006). In a 3-year spawning study in the Salmonier River, Newfoundland, spawning initiation and peak were remarkably consistent (Fig. 18.25). Larval flux began on about day 160 (9 June) and peaked between days 170 (19 June) and 180 (29 June) in each year. Hatch was completed by day 190. During the hatch period, water temperatures increased about 10–20°C. The majority of larval production occurred over a four- to five-night period; hatching peaked at 16°C (Bradbury et al. 2006; see also Simonin et al. 2016).

Spawning Rainbow Smelt display no distinguishing courtship behavior. The fish assemble into a tight group and align themselves parallel, facing into the current (Figs. 18.23 and 18.24). The sex ratio in these small spawning schools does not exceed a ratio of 4:1 males to females (Morrow 1980). The fish then synchronously writhe back and forth in an exaggerated swimming movement (Morrow 1980) with flanks in contact. Male-to-male contact does not initiate any gamete release; however, when male-to-female contact occurs, milt and eggs are released immediately. The tubercles on the males may serve as a tactile stimulus for sex identification such that gamete release occurs only when there is alternate-sex contact with a rough surface (tuberculated males) and a smooth surface (untuberculated females) (Morrow 1980; Figs. 18.21–18.23).

Rainbow Smelt fecundity varies considerably and increases with fish size; estimates range from 1,700–69,600 eggs/female (Bailey 1964; Scott & Crossman 1973; Morrow 1980; Scott & Scott 1988; Buckley 1989). For example, a 12.7 cm TL fish contained 8,500 eggs, and a 20.9 cm TL female yielded 69,600 mature eggs (Buckley 1989). Populations of Dwarf Rainbow Smelt produce eggs ranging from 0.54–0.65 mm in diameter (Lanteigne & McAllister 1983), and some anadromous populations produce 0.9–1.2 mm diameter eggs (Bailey 1964; Buckley 1989).



Figure 18.24. (upper) Egg crowding can be a problem for Rainbow Smelt, *Osmerus mordax*, and other Smelt species as shown here in a spawning aggregation in a river on Prince Edward Island. Crowding can occur below dams, waterfalls, culverts, beaver dams, and other obstructions. Large groups of fish all spawning together causes eggs to clump on top of each other. The eggs form a thick layer (the yellowish masses in between the rocks) and only the top layers of eggs will survive if oxygen exchange is inadequate in deeper layers. (lower) Close-up of Rainbow Smelt eggs adhering to vegetation in Gulliver Creek, a small tributary to the Neponset River estuary near Milton, Massachusetts, in March 2012. Note the tiny pedicle anchoring each egg to the vegetation. The pedicle is formed from the breaking up and inversion of the outer coating of the egg (chorion) (courtesy of Sean Landsman Photography, upper, and Tom Palmer, lower, Neponset River Watershed Association).

Egg, Embryo, and Larval Development

Mature eggs and larval stages are similar in all Smelt species (Figs. 18.26 and 18.27). Ova are about 0.5–1.0 mm in diameter at the time of deposition and have a double membrane. When the ovum comes into contact with the water, the outer membrane ruptures and peels off except for a single attachment on the egg's surface. The membrane inverts and forms an adhesive stalk, which is used to anchor the egg to coarse substrate material along the bottom surface of the stream or lake, such as rocks or submerged vegetation (Rupp 1965; Scott &

Crossman 1973; Morrow 1980; Moyle 2002; Gustafson et al. 2010; Fig. 18.24), where they remain until hatching into larvae.

Incubation periods depend greatly on water temperature and larval size at hatching varies between species. Delta Smelt have a 9–13 day incubation period at 14.8–16.5°C (Moyle 2002), and at 16–18 mm SL, the larvae have fully developed fins and swim bladder and begin a

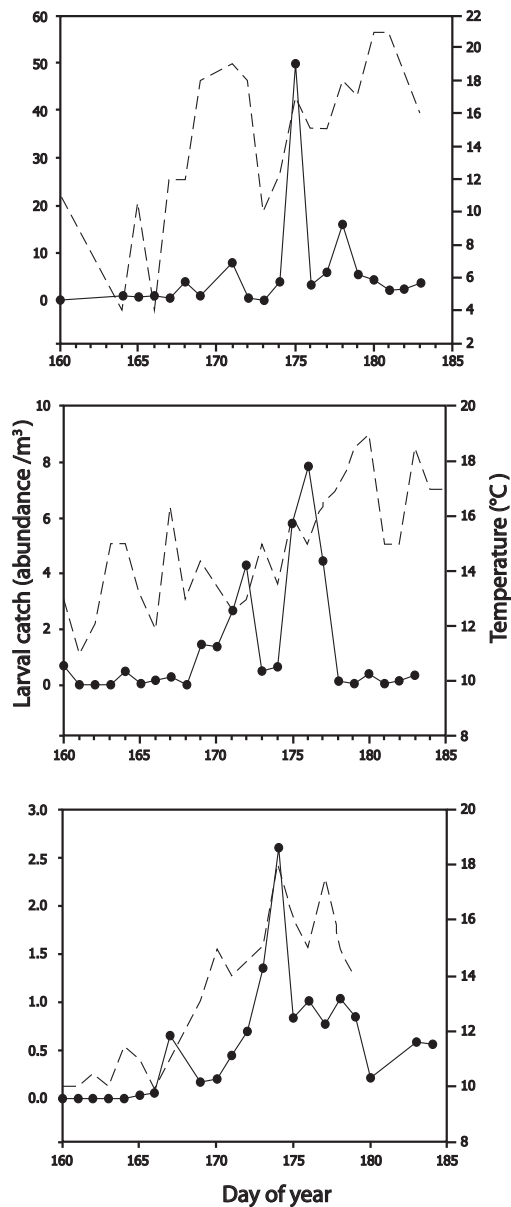


Figure 18.25. Rainbow Smelt, *Osmerus mordax*, larval abundance (solid circles and lines) and water temperature (broken lines) in the Salmonier River, Newfoundland, nightly at 2200 h during spawning in June of 2003 (upper), 2004 (middle), and 2005 (lower) (redrawn from Bradbury et al. 2006b).

downstream migration. Hatching of Pond Smelt usually occurs in about 11 days at 11–15°C and 18–24 days at 10°C (Scott & Crossman 1973; Morrow 1980). Larvae are 4–5 mm SL at hatching and grow to 30–40 mm SL by the end of the first summer (Morrow 1980). The incubation period for Longfin Smelt is about 40 days at 6.9°C (Scott & Crossman 1973). At hatching, the larvae are 5–8 mm

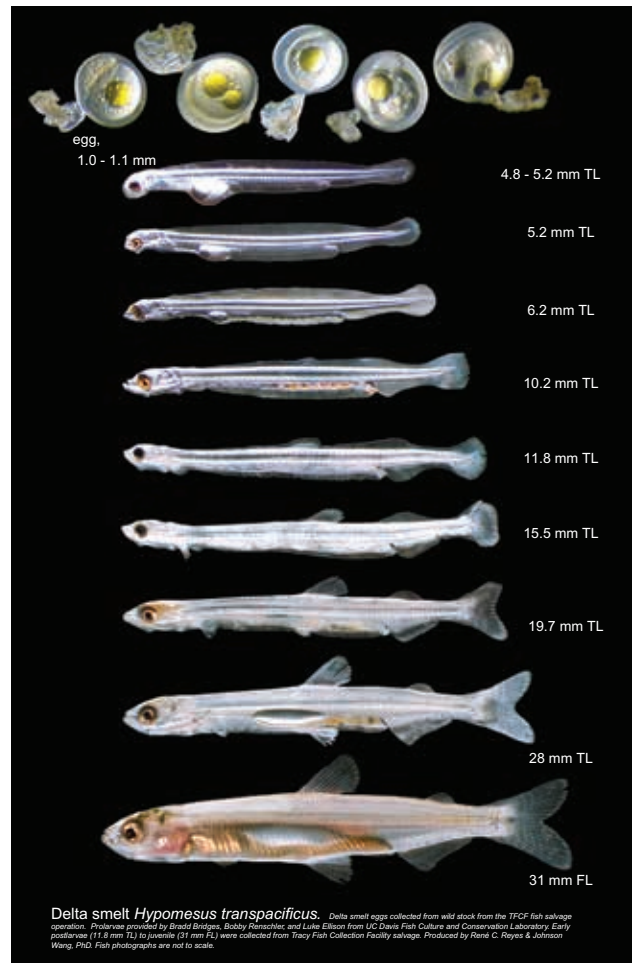


Figure 18.26. Developmental stages of the Delta Smelt, *Hypomesus transpacificus* (redrawn from a photograph that is in the public domain and by and used with permission of René Reyes, Tracy Fish Facility, U.S. Department of the Interior, Bureau of Reclamation, Stockton, California).

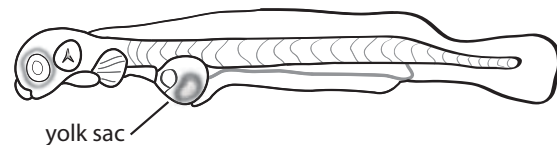


Figure 18.27. Early developmental stage (about 10 days) of Wakasagi, *Hypomesus nipponensis*, showing yolk sac (redrawn from Torao 2000).

SL in length and fastest growth occurs within the first nine months, in which individuals reach 60–75 mm SL (Moyle 2002).

Similarly, Eulachon hatch in 14–21 days at 8.5–12.8°C and 30–40 days at 4.4–7.2°C (Morrow 1980; Moyle 2002; Gustafson et al. 2010). Newly hatched larvae are 3–7 mm TL (Moffitt et al. 2002) and typically grow to 50–80 mm TL before entering into the marine environment (Moyle

2002). However, Moffitt et al. (2002) observed some larvae entering marine environments within 24 h of hatching. Scott & Crossman (1973) also mentioned larvae of 23 mm TL being captured in coastal areas.

Incubation takes 10–20 days for Rainbow Smelt, depending on temperature, which usually ranges from 14–16°C (Rothschild 1961; McKenzie 1964). Estimates of Rainbow Smelt and incubation periods are available for multiple water temperatures (e.g., 19–29 days at 6–10°C; 8–18 days at 11–16.5°C) (Scott & Crossman 1973; Morrow 1980; Buckley 1989). Scott & Scott (1988) gave slightly longer estimates for incubation periods at comparable temperatures: 8–11 days at 12.2–20.0°C; 16–21 days at 9–11.7°C; 25–29 days at 6–8°C; and 51–63 days at 3.9°C. Larvae are about 5 mm SL at hatching. Interestingly, Rainbow Smelt in St. Mary's Bay, Newfoundland, showed a synchronized hatch time at about 2200 h (Bradbury et al. 2004). Yolk-sac absorption occurs at about seven days post-hatching, and flexion at about 31 days post-hatch or at 10–15 mm SL. Upon hatching, larvae are transported to the estuary where they develop (Bradbury et al. 2006b).

All Smelt larvae have at least one oil globule in the yolk sac (Fig. 18.27) that confers buoyancy and allows newly hatched Smelt to remain in the lower portion of the water column just off the bottom (Scott & Crossman 1973; Moyle 2002; Bennett 2005; Torao 2000). For *Hypomesus* and *Osmerus*, this feature is crucial for retaining larvae in optimal areas before moving downstream into juvenile rearing and adult habitats, a migration that occurs only after the yolk sac is completely absorbed and jaw and mouth parts are developed (Buckley 1989; Morrow 1980; Moyle 2002; Bennett 2005). Other Smelts, such as the Eulachon and Longfin Smelt, are quickly transported by surface currents to estuarine and coastal marine environments shortly after hatching (Hart 1973).

In terms of larval development, Wakasagi are perhaps the most well studied and documented species. Torao (2000) divided Wakasagi development into seven stages (Phases A→G) and presented helpful diagrams of larval conditions during each phase. By the end of Phase B (day 4), individuals are about 9 mm TL, melanophores are distributed along the body, the snout begins to protrude, and the jaws begin development. During Phase C→D (day 5–35) the larvae grow to 14.5 mm, fin-ray elements begin to form and the adipose fin becomes visible. Transformation into the juvenile stage occurs in Phases E→G (day 35–115). Fins are fully developed by day 60 and the lateral line becomes conspicuous after day 90. Individuals average 55 mm TL at the termination of Phase G.

ECOLOGY

Smelts exhibit a wide variety of life-history patterns, ranging from exclusively fresh water, to estuarine, to anadromous. Diets and feeding behavior are similar with most species undergoing a diel vertical migration and swimming to shallow areas at night to feed on insects and zooplankton. The Pacific Rainbow Smelt is the longest lived species, regularly surviving 8–15 years; Rainbow Smelt survive 5–7 years (reviewed by Haldorson & Craig 1984). Most other species live only 2–3 years. Further, Smelts are important components of aquatic and terrestrial food webs, and are target prey items, especially during spawning runs.

Habitat

Delta Smelt are endemic to the Sacramento-San Joaquin Estuary and occur mostly within shallow, open areas, usually <3 m in depth, near deeper channels. In low-flow years Delta Smelt are restricted to main river channels, and under extremely high flows this weak swimming species can be washed out of the estuary. Abundance is highest at the mixing zone of saline and fresh water or the areas just upstream (Moyle et al. 1992, 2016), where salinities are <6 PSU, turbidity >12 NTU, and temperatures are ≤25°C (reviewed by Sommer & Mejia 2013; Moyle et al. 2016 and references therein). Delta Smelt are only rarely observed outside tidal areas and avoid areas with dense submerged aquatic vegetation or the blooms of the toxic algae, *Microcystis* (Sommer & Mejia 2013). As such, Delta Smelt are highly dependent on freshwater outflows into the estuary (Meng & Matern 2001), but population dynamics do not appear to be driven solely by river flows (Stevens & Miller 1983; see conservation section). Their survival is linked to high densities of calanoid copepods in the low salinity zone (e.g., Nobriga 2002; Moyle 2002; see diet subsection in this section). In general, freshwater outflows and associated hydrodynamics largely govern the spatial distribution of Delta Smelt within the estuary (Moyle 2002).

In contrast, Pond Smelt are strictly freshwater inhabitants and occupy lakes and streams in northwestern Alaska and Canada. In both habitats, the fish is pelagic and undergoes diel vertical migrations similar to other Smelts (Scott & Crossman 1973; Morrow 1980). Preference of temperature and effects on distribution within the water column are known only insofar as they pertain to spawning behavior (see reproduction section).

The Longfin Smelt is also an open-water, shoaling species whether in a marine, estuarine, or lacustrine environment (Chigbu & Sibley 1998; Moyle 2002) and regularly exhibits a diel vertical migration, moving up into shallow water at night to feed and retreating to deeper water during the day (Moyle 2002). Relatively little is known about activity of this species in the marine environment. Abundance of the species in the San Francisco Estuary, which can fluctuate greatly, was positively correlated with river flow during the spawning (about December–April) and nursery (spring–autumn) months (Stevens & Miller 1983). Adults of anadromous populations were captured by shrimp trawls off the coast of Alaska at depths ≤ 41 m (Morrow 1980) with most individuals captured in the lower half of the water column (Moyle 2002).

Comparable to Longfin Smelt, Eulachon probably remain in coastal areas above the continental shelf not far from spawning regions throughout their life span (Morrow 1980). Most commercial catches of Eulachon occur in shoals in near-shore waters (<100 m deep) in the food-rich echo-scattering layer (Scott & Crossman 1973; Hay & McCarter 2000). Bycatch from shrimp trawls indicate that Eulachon can be captured at depths ≤ 500 m, but this may be a result of entrainment into nets at shallower depths (Hay & McCarter 2000). Marine catch of Eulachon follows a seasonal trend with the highest levels of incidental capture taken in summer and in shallow water (<50 m).

North American species of *Osmerus* inhabit coastal marine waters and lakes (Morrow 1980; Haldorson & Craig 1984; Scott & Scott 1988; Page & Burr 1991, 2011). The Rainbow Smelt is pelagic and shoals usually congregate in middle portions of the water column. Rainbow Smelt are negatively phototactic and like other Smelt species have a diel vertical migration. Adults in large lakes (e.g., Lake Erie, Lake Cham-

plain) descend to depths >25 m during the day (Fig. 18.28) (Scott & Crossman 1973; Simonin et al. 2012). Cannibalism in deep lakes that stratify in the summer is reduced because adults remain during the day below the thermocline and age-0 Rainbow Smelt are in the warmer epilimnion (Parker Stetter et al. 2007; Stritzel Thomson et al. 2011; Fig. 18.29). Anadromous populations residing in coastal waters behave similarly to the Eulachon, staying ≤ 10 km of the shore (Morrow 1980) and usually at depths <40 m (Buckley 1989).

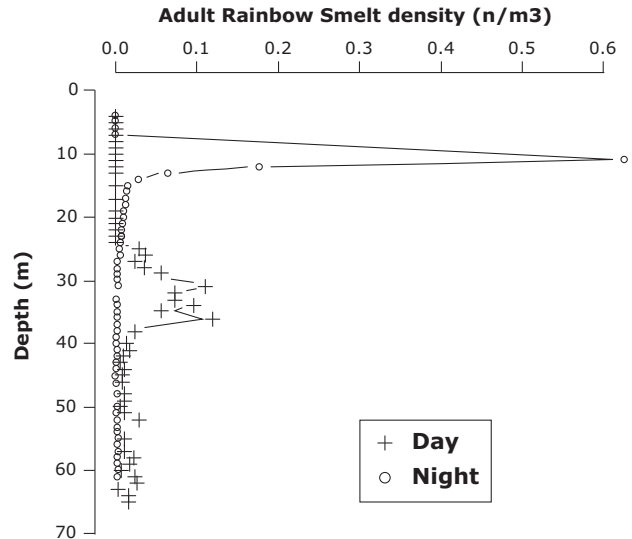


Figure 18.28. Example of adult Rainbow Smelt, *Osmerus mordax*, vertical distribution in the Main Lake of Lake Champlain during the day and night (data from July 2007). During summer stratification of the lake, adult Rainbow Smelt occupied hypolimnetic water ($4\text{--}6^\circ\text{C}$) during the day, but during the night, they migrated to thermocline depths ($4\text{--}20^\circ\text{C}$), presumably following the vertical migration of mysid shrimps, a major prey item (n/m^3 , numbers of individuals/ m^3) (redrawn from Simonin et al. 2012).

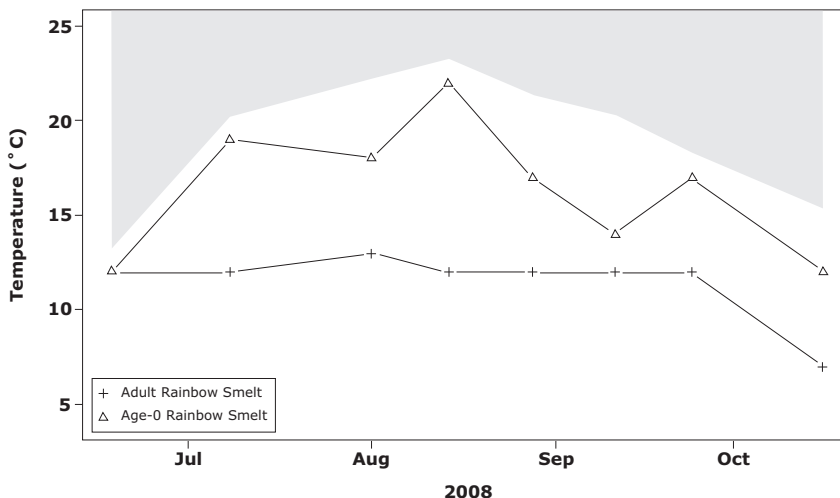


Figure 18.29. Temperatures at which adult and age-0 Rainbow Smelt, *Osmerus mordax*, were most dense in the Main Lake of Lake Champlain from June to October 2008. The unshaded region represents available temperatures within the lake. The temperature segregation presumably functions in reducing predation (redrawn from Simonin et al. 2012).

Within the Laurentian Great Lakes and other northern inland lakes, non-native Rainbow Smelt can compose a major part of the fish biomass and are implicated as important predators and competitors with most other pelagic fishes (e.g., Evans & Loftus 1987; Lantry & Stewart 1993; Hrabik et al. 1998, 2001; Gamble et al. 2011ab).

The Pacific Rainbow Smelt apparently spends winters in Arctic waters congregated near the mouths of rivers (Hal-dorson & Craig 1984). In a study in the Alaskan Beaufort Sea, most Pacific Rainbow Smelt were caught in winter in a bay just downstream of the sill of the Colville River Delta. The species accounted for <1% of the fish captured over two summers, and those caught were usually small and immature. In contrast the Pacific Rainbow Smelt was the dominant species in nearshore waters in the winter accounting for 56% of the catch. The winter catch was dominated by large, mature individuals in pre-spawning condition.

Diet

Smelts play an important role in both marine and freshwater food webs, and the diets of Smelts are moderately well studied. Although many similarities in diet exist among species, notable region-specific idiosyncrasies occur. Chigbu & Sibley (1998) completed an excellent cross-seasonal study of the diet of Longfin Smelt in Lake Washington, documenting stomach contents, in terms of percentage dry weight, from 683 individuals. Young-of-the-year feed on chironomids, copepods, and cladocerans with copepods constituting 85.7% of the consumption during the first six months of life. However, some researchers have suggested that larval and juvenile Longfin Smelt also may consume phytoplankton during the first summer (McPhail & Lindsey 1970). In Lake Washington, juveniles showed a distinct seasonal shift to a more diverse diet in the summer, accompanied by a change in diet composition. Cladocerans became the most frequent prey items, making up 50% of the diet, with chironomids accounting for 25% and copepods decreasing to 22% (Chigbu & Sibley 1998). By autumn, young Longfin Smelt exhibited a feeding pattern similar to adults and began to consume mysids, which generally composed 50–70% of the diet in all seasons, a result consistent with observations farther south in the San Francisco Estuary (Feyrer et al. 2003). However, during autumn and winter months, amphipods and cladocerans remained important prey items and collectively accounted ≤50% of the diet. An increase in copepod consumption occurred during spring, effectively replacing the amphipod portion of the autumn–winter diet. Like

young-of-the-year, the summer diet of adult Longfin Smelt is the most diverse with mysids and cladocerans comprising 70% and 15%, respectively, of the total diet and five other food types accounting for about 15%. Piscivory was insignificant in all seasons and life-stages and accounted for <1% of the diet (Chigbu & Sibley 1998).

The diets of *Hypomesus* are similar to that of the Longfin Smelt and largely comprise of copepods, cladocerans, amphipods, and mysid shrimp (Table 18.1). Similar ontogenetic and seasonal shifts in diet composition also occur (Morrow 1980; Moyle 2002; reviewed by Moyle et al. 2016). Copepods are the most important prey items for all age and size classes of Delta Smelt (Moyle 2002), but mysid shrimp, cladocerans, and larval chironomids, if available, can be seasonally important (Feyrer et al. 2003; Whitley & Bollens 2014). Summer to fall survival is positively linked to copepod biomass (Kimmerer 2008). First feeding larvae (5–8 mm SL) consume subadult cyclopoid and calanoid copepods (Bennett 2005; Slater & Baxter 2014). Early life stages may preferentially select *Eurytemora affinis*, a once cosmopolitan calanoid copepod in the San Francisco Bay Estuary (Bennett 2005), or its invasive replacement *Pseudodiaptomus forbesi* (Slater & Baxter 2014). During periods of scarcity of preferred prey, Delta Smelt will consume smaller and more predator-evasive species (Slater & Baxter 2014). In more northern Pond Smelt populations, rotifers may be an important food item for larvae and juveniles (Scott & Crossman 1973; Morrow 1980). Pond Smelt also differ by feeding on larval insects and, to a lesser extent, algae (Morrow 1980).

The diet of the Rainbow Smelt varies only slightly from other Smelts with the majority of juvenile and adult diets being planktonic crustaceans (Table 18.1), such as copepods and cladocerans (e.g., *Daphnia* spp.) as well as amphipods, mysids, and insect larvae (Beckman 1942; Morrow 1980; Lanteigne & McAllister 1983; Scott & Scott 1988; Buckley 1989; Pothoven et al. 2009; Gamble et al. 2011ab; Sheppard et al. 2012). Rainbow Smelt (29–178 mm TL) diets, which were assessed from 1,615 individuals captured by day and night trawling at multiple nearshore sites in Lake Superior, were dominated in biomass by *Mysis* (about 70% of diet in spring, 94% in summer, 80% in autumn). The amphipod *Diporeia* contributed to the remainder of the spring diet, and the balance of the autumn diet was the cladoceran *Daphnia* (Gamble et al. 2011b). In a similar offshore study in Lake Superior, diets of the species (28–171 mm TL, 163 individuals) were also dominated by *Mysis* (≥80% of biomass), irrespective of season. Individuals ate large numbers of calanoid copepods in spring; *Mysis* and *Daphnia* domi-

nated counts in summer, but calanoid copepods, fish eggs, and the cladoceran *Bythotrephes* were also present (Gamble et al. 2011a). In autumn, frequencies were highest for calanoid copepods and *Mysis*. In a related Lake Superior diet study incorporating prey availability, Rainbow Smelt (66–207 mm TL, >2,100 individuals) exhibited a strong positive selection for *Mysis* across all seasons, depths, and almost all sample stations, often with *Mysis* being the only prey item consumed (Isaac et al. 2012; Fig. 18.30). Notably, Rainbow Smelt differ in respect to the relative importance of piscivory; adult Rainbow Smelt feed on Sculpins (*Cottus* spp.), Mummichogs (*Fundulus heteroclitus*), Anchovies (*Anchoa* spp.), Alewives (*Alosa pseudoharengus*), age-0 Emerald Shiners (*Notropis atherinoides*), Walleye (*Sander vitreus*), and other small fishes (Scott & Scott 1988; Buckley 1989; Pothoven et al. 2009; Stritzel Thomson et al. 2011). Cannibalism on age-0 individuals by age-1+ fish also is evident and often quite prevalent, particularly in years with high densities of age-0 individuals (Parker Stetter et al. 2007; Pothoven et al. 2009; Stritzel Thomson et al. 2011). In Lake Champlain, presumed cannibalistic age-1+ Rainbow Smelt occurred in 15 of 25 trawl hauls, making up 0.04 to 0.70 of the trawl catch. Age-0 fish occurred in 88% of age-1+ fish with fish in their guts. The degree of cannibalism was inversely associated with the strength of the thermocline; stronger thermoclines increased spatial separation of age-0 and age-1+ fish (Parker Stetter et al. 2007). Even so, fish commonly account for only 5–10% of the total diet, and consumption peaks ($\leq 83\%$ of dry mass consumed) during late fall and winter months when zooplankton is less abundant (Scott & Crossman 1973; Pothoven et al. 2009).

Based on 39 Pacific Rainbow Smelt sampled in November from the Beaufort Sea, the diet by wet weight was primarily composed of mysid shrimp and fish, especially Arctic Cod (*Arctogadus glacialis*), followed by a variety of amphipods, although fish only occurred in the gut of 18% of the individuals examined. As winter progressed, feeding declined from 30% empty stomachs in November to 100% empty stomachs by winter's end in May (Haldorson & Craig 1984).

The diet of the Eulachon is not well known, but available evidence suggests strong similarities to other Smelt species. Eulachon appear to feed mainly on euphausiid shrimp (krill, *Thysanoessa spinifera*), various copepods, and other crustaceans (Hart & McHugh 1944; Morrow 1980; Hay & McCarter 2000). Scott & Crossman (1973) suggested that Eulachon are not piscivorous at any time in their life span. Moreover, the low number of gill rakers found in the Eulachon indicate that filter feeding, as seen in the Pacific Herring (*Clupea pallasii*) and some other os-

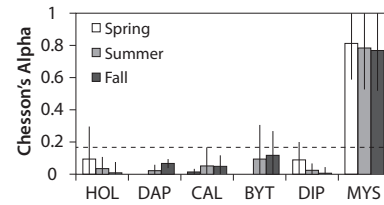


Figure 18.30. Seasonal prey selection of Rainbow Smelt, *Osmerus mordax*, in Lake Superior in 2005 averaged across multiple trawling stations ($n = 18$) and seasons (spring, summer, autumn). Prey items are arranged by size from left to right: HOL = the cladoceran *Holopedium gibberum*; CYC = adult cyclopoid copepods; DAP = *Daphnia*; CAL = adult calanoid copepods; CLM = sphaeriid clams; BYT = the invasive cladoceran *Bythotrephes*; CHR = chironomids; DIP = the amphipod *Diporeia*; MYS = Opossum Shrimp, *Mysis diluviana*. Dashed lines indicate neutral selection and vertical lines, 95% confidence intervals (redrawn from Isaac et al. 2012).

merids, is probably not part of their forage strategy (Hart 1973). However, similar to many *Osmerus*, other sources suggest that Eulachon exhibit some level of cannibalism with adults sometimes feeding on larval and juvenile stages of their own species (Beckman 1942; Morrow 1980; Lanteigne & McAllister 1983).

Age and Growth

In most cases, Smelts are aged according to scale annuli; however, efforts to validate this method have produced discordant results within and among species. Thus, the ages provided are based on averages of scale annuli and otolith evaluations, where available. Delta Smelt are for the most part an annual fish, with only a few individuals surviving a second year. Juveniles typically grow to about 45 mm SL within about five months. Growth rates significantly increase after the fish reaches 30 mm SL coinciding with a seasonal peak in food availability. By the sixth month the fish is near maximum length (55–50 mm SL), growing <9 mm after month seven (Moyle 2002). However, fish that live to two years of age can reach 90–120 mm SL (Table 18.1). Comparatively, Wakasagi, the introduced *Hypomesus* species most similar to the Delta Smelt, commonly live about two years and attain adult lengths between 73–120 mm SL (Moyle 2002; Table 18.1).

Pond Smelt live two years, at which time sexual maturity is reached and most individuals spawn and die (Moyle 2002). Some fish survive to age 4 and possibly spawn multiple times, but such survival and iteroparity are extremely rare. Interestingly, in a unique population of Pond

Smelt in the Yukon Territory, Canada, estimates of age based on scale annuli suggest individuals live 8–9 years (Morrow 1980). However, individuals of this population show extraordinarily slow growth rates; individuals estimated to be 5 years old are similar in size to 1-year-old fish in other lakes. Also, some studies suggest lake populations of Longfin Smelt are smaller in size than anadromous populations (Morrow 1980), but no recent findings support this hypothesis (Chigbu & Sibley 1994). For regular populations of Pond Smelt, lengths of 50–70 TL mm are attained within one year, 80–100 mm TL at year two, and ≤185 mm TL at the fourth year (McAllister 1963; Scott & Crossman 1973; Morrow 1980).

Eulachon mature in 2–3 years with some fish surviving to five years (Hart & McHugh 1994; Moffitt et al. 2002; Moyle 2002). In some Alaskan streams, age-4 and age-5 fish can constitute ≤90% of the spawning population in select years (Moffitt et al. 2002), but this is probably not a common occurrence. Growth rates average 40–50 mm/year (Morrow 1980), and mature Eulachon are 140–200 mm TL (Moffitt et al. 2002) and reach a maximum of about 300 mm TL (McAllister 1963).

The longest-lived Smelt species, barring a questionable population of the Pond Smelt, are the Pacific Rainbow Smelt and Rainbow Smelt. The Pacific Rainbow Smelt lives longer, matures later, and grows more slowly than Rainbow Smelt, all likely adaptations to Arctic conditions (Haldorson & Craig 1984). In a Beaufort Sea population of Pacific Rainbow Smelt aged by otolith rings, longevity was 8–15 years and 33% of individuals examined were ≥9 years. Most fish were mature at 6–7 years (200–220 mm FL); no differences occurred between the sexes in size or age at sexual maturity. Growth is slow relative to Rainbow Smelt with individuals only averaging 143 mm FL at 3 years old. Adults ranged from about 197–256 mm FL (maximum about 310 mm FL).

The Rainbow Smelt regularly survives to six years (maturing at two years) spawning multiple times (Bailey 1964; Murawski & Cole 1978; Scott & Crossman 1973; Lanteigne & McAllister 1983; Haldorson & Craig 1984; Scott & Scott 1988). In Rainbow Smelt 4–6-year-old fish rarely constitute >10% of the spawning population (Scott & Crossman 1973; Murawski & Cole 1978). Generally, adult Rainbow Smelt average 150–250 mm TL; however, the dwarf morphotype is seldom >125 mm TL (but can reach 140 mm TL in Lochaber Lake populations, Newfoundland) (Murawski & Cole 1978; Morrow 1980; Lanteigne & McAllister 1983; Buckley 1989; Taylor & Bentzen 1993b). The largest recorded size is 324 mm TL (McAllister 1963). Growth is most rapid within the first year with young-of-the-year

reaching 20–40+ mm TL in ≤3 months (Scott & Crossman 1973; Simonin et al. 2016), 50–65 mm TL at six months (Scott & Scott 1988), and averaging 110–172 mm TL at one year (Murawski & Cole 1978; Morrow 1980). During the next four years growth decreases with age and averages 50, 30, 20, and 10 mm/year (Morrow 1980; Buckley 1989).

The growth rates of Rainbow Smelt seem to be strongly linked to population densities in the Great Lakes, where the species was introduced and is well established, and other landlocked populations. In a study of Rainbow Smelt in Lake Champlain, population densities affected growth rates of all age classes; however, the patterns were inconsistent between age classes (Stritzel Thompson et al. 2011). For example, growth rates of age-0 Rainbow Smelt were negatively correlated with age-0 density, suggesting some level of intraspecific competition for zooplankton. In contrast, the growth rates of other age classes (≥1) were positively correlated with age-0 densities, alluding to a possible role of cannibalism. In fact, a study to document cannibalism in Lake Champlain indicated age-1+ Rainbow Smelt are probably the primary predators on age-0 Rainbow Smelt in summer and early fall in the lake (Parker Stetter et al. 2007). In Lake Huron, recruitment of Rainbow Smelt was regulated by intraspecific competition with (or cannibalism by) older conspecifics (i.e., compensatory, density dependent mortality), spring precipitation, which likely influenced spawning habitats, and predation by Lake Trout (*Salvelinus namaycush*) on age-2+ Rainbow Smelt (O'Brien et al. 2014).

Predation and Parasitism

Delta Smelt and Wakasagi seem to experience little predation as adults occur infrequently in the stomachs of local predatory fishes (Moyle 2002; reviewed by Moyle et al. 2016); however, detailed studies of predation and parasitism for these species are lacking. Predation on eggs and larvae is undoubtedly higher, and egg and larval predation by introduced Silversides (Atherinopsidae; referred to by various authors as Mississippi Silversides, *Menidia audens* or Inland Silversides, *M. beryllina*) may be particularly significant (Moyle 2002; Bennett 2005; Schreier et al. 2016; reviewed by Moyle et al. 2016). Compounding the issue, the Delta Smelt and non-native silverside are also similar in morphology, diet, and life span, thus making the silversides highly competitive with native Delta Smelt (Bennett 2005). Moyle (2002) mentioned anecdotally that parasitism by a tapeworm has become more common in Delta Smelt populations in recent years, but no description of

the organism was given. Similarly, no comprehensive studies of predation and parasitism in the Pond Smelt are available. However, McPhail & Lindsey (1970) stated that the Pond Smelt has no predators in Black Lake, Alaska.

In contrast, Longfin Smelt are prey of Northern Pike-minnows (*Ptychocheilus oregonensis*), Cutthroat Trout (*Oncorhynchus clarkii*), and Rainbow Trout (*Oncorhynchus mykiss*) in Lake Washington, Washington (Beauchamp 1994; Hansen & Beauchamp 2014). The introduced Striped Bass (*Morone saxatilis*) and native piscivores, such as the Sacramento Perch (*Archoplites interruptus*), Thick-tail Chub (*Gila crassicauda*), and steelhead (*Oncorhynchus mykiss*), also likely prey on Longfin Smelt in California rivers and estuaries (Moyle 2002). Like *Hypomesus* spp., eggs and larvae of Longfin Smelt are likely heavily preyed on by introduced Inland Silversides (Moyle 2002).

Most observations of predation on Eulachon are when adult fish congregate at river mouths before spawning. At this time, Eulachon are prey of numerous fishes, mammals, and bird species, including Spiny Dogfish (*Squalus acanthias*), Sturgeon (*Acipenser* spp., mainly Eulachon eggs), Pacific Halibut (*Hippoglossus stenolepis*), Sablefish (*Anoplopoma fimbria*), Pollock (*Pollachius virens*), Pacific Cod (*Gadus macrocephalus*), Pacific Hake (*Merluccius productus*), various salmonids (*Oncorhynchus* spp. and *Salvelinus* spp.), Arrowtooth Flounder (*Atheresthes stomias*), Humpback Whales (*Megaptera novaengliae*), Beluga Whales (*Delphinapterus leucas*), Harbor Seals (*Phoca vitulina*), Northern Fur Seals (*Callorhinus ursinus*), Steller Sea Lions (*Eumetopias jubatus*), California Sea Lions (*Zalophus californianus*), bears (*Ursus* spp.), Gray Wolves (*Canis lupus*), River Otters (*Lontra canadensis*), and many waterfowl, such as grebes (*Podiceps* spp.), gulls (*Larus* spp.), scoters (*Melanitta* spp.), kittiwakes (*Rissa* spp.), mergansers (*Mergus* spp.), loons (*Gavia* spp.), and Marbled Murrelets (*Brachyrhampus marmoratus*) (Scott & Crossman 1973; Morrow 1980; Speckman & Piatt 2000; Marston et al. 2002; Willson & Marston 2002; Gustafson et al. 2010; Paquin et al. 2014; Coutré et al. 2015). Numerous fishes also consume the larvae of Eulachon (e.g., Pacific Herring; Surf Smelt, *Hypomesus pretiosus*; Pacific Sand Lance, *Ammodytes hexapterus*; Kelp Greenling, *Hexagrammos decagrammus*; various salmonids; reviewed by Gustafson et al. 2010). In the Columbia River, 1,000–1,500 Harbor Seals were observed using haul out sites ≥ 72 km upriver apparently exploiting Eulachon runs in the winter. Based on the presence of otoliths in Harbor Seal scat collected from the Columbia River during 1981–1982, Eulachon were eaten by 12–87% of the Harbor Seals present from

January–April. During the winters of 1986–1988, 98% of the prey eaten by Harbor Seals in the Columbia River were Eulachon, and 100% of Harbor Seal stomachs examined contained eulachon (Gustafson et al. 2010 and references therein). In one study alone (Berners Bay, Alaska; Marston et al. 2002), 34 species of birds foraged on Eulachon as they entered the river to spawn, amounting to 36,500–46,000 avian predators in one bay.

Rainbow Smelt are frequently preyed on by Trouts and Salmonids (*Oncorhynchus* spp., *Salmo* spp., *Salvelinus* spp.), whitefishes (*Coregonus* spp.), Herrings (Clupeidae), American Eels (*Anguilla rostrata*), Yellow Perch (*Perca flavescens*), Gars (*Lepisosteus* spp.), Burbot (*Lota lota*), Walleyes (*Sander vitreus*), Temperate Basses (*Morone* spp.), Bluefish (*Pomatomus saltatrix*), gulls (*Larus* spp.), and crows (*Corvus* spp.) (Scott & Crossman 1973; Becker 1983; Buckley 1989; Roseman et al. 2014). Like Eulachon, Rainbow Smelt are often seasonal prey for many species (Sayers et al. 1989; Pientka & Parrish 2002), and predation is most certainly highest during spawning runs. Of particular interest is the purported level of cannibalism in Rainbow Smelt. Once Rainbow Smelt reach about 150 mm TL they can shift to a largely piscivorous diet, and smaller Rainbow Smelt are often the most numerous fish found in stomach contents (Becker 1983; Parker Stetter et al. 2007).

Common parasites recorded for Rainbow Smelt are numerous and include a microsporidian (*Glugea hertwigi*), tape worms (*Diphyllobothrium sebago* and *Protocephalus tetraostomus*), and a myriad of protozoans, flukes, cestodes, acanthocephalans, crustaceans, trematodes, nematodes, and leeches (Scott & Crossman 1973; Buckley 1989; Hoffman 1999; Scholz et al. 2004). A viral disease affecting the red blood cells and causing severe anemia, piscine erythrocytic necrosis (PEN), also was detected in Rainbow Smelt populations (Buckley 1989). Other Smelt species likely have similar, but as yet undiscovered, parasites. Although no North American osmerids are confirmed as hosts to freshwater mussels, a European species, *Osmerus eperlanus* (European Smelt), was infested with glochidia of a species of *Anodonta* but metamorphosis was not observed (Anders & Wiese 1993).

CONSERVATION

Delta Smelt

The Delta Smelt is considered Threatened (Table 18.1) but may be functionally extinct. The Delta Smelt is endemic to the Sacramento-San Joaquin River drainage, California, a

highly altered watershed (reviewed by Sommer et al. 2007; Moyle et al. 2016 and references therein), and is currently protected under the Federal Endangered Species Acts as a Threatened species (Federal Register 1993 Appendix A-1) and under the California Endangered Species Act as Endangered (Sweetnam & Stevens 1993; CFGC 2009). The American Fisheries Society considers the Delta Smelt as Threatened (Jelks et al. 2008). Significant population declines began in the early 1980s, increased sharply in the early 2000s, and numbers continue to remain alarmingly low (Feyrer et al. 2007; Sommer et al. 2007; MacNally et al. 2010; Thomson et al. 2010; Miller et al. 2012; Sommer & Mejia 2013; Moyle et al. 2016). An annual trawl survey in the estuary where the species usually aggregates recovered only four females and two males during an extended and severe California drought (beginning about 2012). The survey ordinarily captures hundreds of individuals of the species. Based on these results and those of previous years, Peter Moyle, an expert and long-time researcher on the species, expressed to scientists of the Delta Stewardship Council that the species is likely functionally extinct and beyond the point of recovery (Quinton 2015; reviewed by Moyle et al. 2016).

The decline of the Delta Smelt is coincident with the human-driven transformation of its native habitat, the San Francisco Bay Estuary (reviewed by Moyle et al. 2016). Major physicochemical changes include shifts in salinity (Feyrer et al. 2007; Enright & Culbertson 2010; Hobbs et al. 2010) and turbidity (Feyrer et al. 2007; Nobriga et al. 2008; Hasenbein et al. 2013), increasing water temperature (Wagner et al. 2011; Cloern & Jassby 2012; Komoroske et al. 2014), flow changes (Feyrer et al. 2010), shifts in nutrient loading (Glibert 2010), and contamination by chemicals (Connon et al. 2009; Hasenbein et al. 2014; Weston et al. 2014). The Estuary has also undergone relatively dramatic food web alterations (Moyle et al. 1992; Moyle 2002; Winder & Jassby 2010; Winder et al. 2011; Hasenbein et al. 2013). Climate change is expected to further compound these environmental alterations (Wagner et al. 2011) by increasing pollutant loading through more frequent and intense storms, increasing thermal stress, and elevating the rate at which pollutants are metabolized (Wagner et al. 2011; Brooks et al. 2012).

Analysis of long-term changes in the abundance of Delta Smelt (and other fishes) in relation to other factors in the Sacramento-San Joaquin Delta, such as water quality, prey density, and nutrient loading, implicated changes in the habitat and food web as a major cause for the decline of Delta Smelt (reviewed by Moyle et al. 2016). Regionally fo-

cused water-quality analyses across the San Francisco Bay Estuary linked Delta Smelt abundance most strongly and negatively to increases in water clarity in San Joaquin River region (Miller et al. 2012). High clarity likely increases predation risk for Delta Smelt (Schreier et al. 2016) or affects their ability to capture prey. High conductivity, a surrogate for salinity, and high temperature were also linked to abundance. Delta Smelt abundance was low or near zero at conductivities >25,000 $\mu\text{S}/\text{cm}$ (about 20 psu) and temperatures >25°C (see also temperature subsection, physiology section). Regression models derived from long-term trawling data and a consideration of an array of environmental factors showed strong evidence of density-dependent population regulation (see also Feyrer et al. 2007); the best regression models indicated the density of prey was the most important factor explaining variations in Delta Smelt abundance from 1972 to 2006 and more recently. Predation and water temperature also showed effects on abundance (Miller et al. 2012). In a Bayesian analysis of an expert-derived model considering an array of biological and physical factors, abundance of Delta Smelt was related to biomass of the calanoid copepod prey base in summer. In turn, calanoid copepod biomass was related to the extent that freshwater inflows (2 ppt isohaline boundary) reached into the Delta in spring. In addition, high mean summer water temperatures, water diversions in spring and winter, and Largemouth Bass (*Micropterus salmoides*) abundance were negatively, albeit more weakly, related to Delta Smelt abundance (MacNally et al. 2010). The authors concluded that the multiple effects of temperature, feeding, water diversions, and introduced predators are more consistent with the known biology of the species (Moyle 2002; Bennett 2005) than are effects of any individual covariate in the model (MacNally et al. 2010). In another Bayesian analysis focused on identifying change points (abrupt shifts) in population abundance, winter water diversions and water clarity were implicated as covariates of abundance. Dramatic long-term changes in nutrient loading (i.e., nitrogen; nitrogen:phosphorous; changes in nitrogen form) showed a strong relationship in the Delta to changes in the aquatic food web, notably affecting the abundance and kinds of zooplankton on which Delta Smelt depend. The changes in nutrient loading cascaded through the food web and were strongly correlated with the population decline of the Delta Smelt as well as to changes in abundance of other fishes, including predators (Glibert 2010).

Water diversions, droughts, and river flows affect the species (Moyle 1994), but demonstrating strong direct links of these factors to observed population declines is

not a straightforward exercise (Stevens & Miller 1983; Bennett 2005; Sommer et al. 2007; Kimmerer 2008; Grimaldo et al. 2009; MacNally et al. 2010; Thomson et al. 2010; Miller et al. 2012; reviewed by Moyle et al. 2016; see Nobriga et al. 2008). Low water levels alter the location and size of the freshwater-saltwater mixing zone, forcing the Delta Smelt into suboptimal river channel habitats during low flow years (Moyle 1994; Swanson et al. 2000; Moyle 2002). Delta Smelt in the channel habitats are more vulnerable to entrainment or impingement (Kimmerer 2008), starvation, and increased predation (Moyle 2002). Even in regular flow conditions, the weak swimming capacity of Delta Smelt leads to high rates of entrainment and impingement at large diversions and >2,500 smaller diversion points in the upper estuary (Swanson et al. 2000; Nobriga et al. 2004; Sommer et al. 2007; Kimmerer 2008; MacNally et al. 2010; Moyle et al. 2016). Age-0 and adults are susceptible to entrainment at least seasonally when their particular life stage brings them close to diversion points (Nobriga et al. 2004; Grimaldo et al. 2009). Most diversion points are adjacent to known spawning grounds, making both age-0 and adult Delta Smelt vulnerable thus decreasing both spawning and rearing success (Moyle 2002).

Multiple sublethal stressors (e.g., water pollution) can affect Delta Smelt populations in the San Francisco Bay Delta, but again, direct strong linkage of these stressors to changes in population viability has proven challenging (Bennett 2005; Sommer et al. 2007; reviewed by Moyle et al. 2016; see Glibert 2010; see gene expression subsection, genetics section). The Sacramento-San Joaquin Estuary receives a variety of toxic and damaging effluents from adjacent urban and agricultural areas, including wastewater, heavy metals, pesticides, fertilizers, and urban runoff (Bennett 2005; Cannon et al. 2009; Glibert 2010; Brooks et al. 2012; Hasenbein et al. 2014; Weston et al. 2014; Moyle et al. 2016). For example, after rain events, waters in parts of the Delta become toxic to copepods, a primary food of Delta Smelt, because of an influx of pyrethroid insecticides from upstream urban and agricultural sources (Weston et al. 2014). When Delta Smelt are exposed to these pesticides, increases in protein degradation and cell apoptosis and a concurrent decrease in immune system function are observed (Jeffries et al. 2015). In sum, contaminant stress (histopathological lesions), poor short-term nutritional and growth indices, and morphometric condition of juvenile Delta Smelt support the hypothesis that multiple stressors are contributing to the decline of the species (Hammock et al. 2015).

Because Delta Smelt are found nowhere but the San Francisco Estuary (Moyle 2002), no alternate source population is available to replenish locally depleted populations. The main issues of restoration for the Delta Smelt involve managing water flows and water quality to benefit the fish population with minimal impact on human water use (Sommer et al. 2007). Restoration of tidal wetlands is a population restoration strategy for fishes in the San Francisco Estuary (Brown 2003; Bennett 2005; Sommer et al. 2007). The potential effect of tidal wetland restoration or any other project, however, is unclear due to limited information on life history (especially reproductive strategies and spawning habitats), effective population size and genetic diversity, fundamental information on growth and mortality, carrying capacity in the Delta and river systems, interaction with exotic species, impacts of toxic chemicals, and ability to manage wastewater discharges (e.g., nutrients) (Bennett 2005; Sommer et al. 2007; Glibert 2010).

In addition to hydrological modifications and water pollution, the increase in exotic copepods and clams coupled with the decrease in preferred food organisms has drastically changed the energetics and trophic ecology of the Delta Smelt. Some of the invasive copepods (e.g., *Sinocalanus*, *Limnoithona*, and perhaps others) are more difficult for Delta Smelt to capture and consume than the once dominant native species (*Eurytemora affinis*), and further, the introduced Overbite Clam (*Potamocorbula amurensis*) is decreasing the food availability of larval Delta Smelt by significantly reducing the phytoplankton and zooplankton populations (Moyle 2002; Bennett 2005 and references therein; Bouley & Kimmerer 2006). Further, a threat of competition and potential hybridization exists with the introduced and ecologically similar Wakasagi (Trenham et al. 1998; Swanson et al. 2000; Moyle 2002; Fisch et al. 2014). Comparisons of environmental tolerances and examination of genetic data confirm that Wakasagi are more ecologically labile than Delta Smelt and can produce hybrid offspring with that species (see genetics section), possibly compromising the genetic integrity of the Delta Smelt population. In sum, Delta Smelt face a myriad of conservation challenges, and a whole-system approach may be necessary to ensure the persistence of this species. Unfortunately, and as previously noted, monitoring data in the estuary in 2013 appeared to indicate the Delta Smelt is functionally extinct in the wild (Quinton 2015 citing Peter Moyle).

In response to the decline of the species and concern over its long-term viability, a captive breeding program was initiated in 2008 by the Fish Conservation and Culture

Laboratory in collaboration with the Genomic Variation Laboratory, University of California, Davis, and the U.S. Fish and Wildlife Service. The program serves two purposes: provide a self-sustaining supply of cultured fish for research and serve as a genetic bank in the event of extinction in the wild (Fisch et al. 2013; Lindberg et al. 2013; reviewed by Moyle et al. 2016). As of this writing, no cultured fish have been released in the wild, but the cultured ark population may ultimately provide supplementation to the existing population or reintroduction of the species (Lew et al. 2015).

Other Imperiled Smelt

Other species of Smelt considered of conservation concern are the Lake Utopia (New Brunswick) population of Rainbow Smelt, which includes a dwarf morphotype, and some populations of the Eulachon and Longfin Smelt. The American Fisheries Society (Jelks et al. 2008) considered the dwarf form of the Lake Utopia population of Rainbow Smelt Threatened. In Canada, the small and large-bodied morphs in Lake Utopia are considered Threatened (COSEWIC 2014). The large-bodied and small-bodied form spawns in only three small streams, which could be subject to degradation from development, and both are subject to a dip-net fishery, which is illegal for the small-bodied form (COSEWIC 2011).

The American Fisheries Society (Musick et al. 2000) considered the estuarine California population of Longfin Smelt as Threatened because this once abundant (Rosenfield & Baxter 2007; Moyle et al. 2011) and widespread (Merz et al. 2013) species is now rare in the state. Although petitions in the 1990s to list the species were denied by the U.S. Fish and Wildlife Service, if it were a salmonid, the California populations would likely be protected under the U.S. Endangered Species Act as ESUs (Moyle 2002). As of 2014, the U.S. Fish and Wildlife Service considered the San Francisco Bay-Delta population as a Candidate for Listing (USFWS 2014). The species is considered Threatened under the California Endangered Species Act (CDFW 2009). Multiple, synergistic factors, similar to those implicated in the decline of the Delta Smelt, are likely the cause of the decline (e.g., water quality changes, reduction in estuarine outflows, entrainment losses to water diversion, toxic substances, non-native predators and competitors) (Stevens & Miller 1983; Moyle 1994, 2002; Rosenfield & Baxter 2007; Sommer et al. 2007; Glibert 2010; Moyle et al. 2011). Population dynamic models of Longfin Smelt in California suggest the

production of age-0 individuals is mediated primarily by estuarine flow regimes; however, survival of subsequent stages show a density-dependent pattern of decline which indicates trophic-related processes (i.e., food web modifications) are controlling abundances of those stages (Nobriga & Rosenfield 2016).

Populations of Eulachon in Canada and the United States are also given protected status primarily because of abrupt and often dramatic declines in spawning runs that began in the 1990s. An expert knowledge assessment of Eulachon in the lower Klamath River system, California, considered the species Highly Vulnerable, an indication the species is on the path toward extinction as the result of climate change (Moyle et al. 2013); the population in northern California has been virtually absent for nearly two decades (Gustafson et al. 2010, 2012). The population in the Columbia River was considered Threatened by the American Fisheries Society (Musick et al. 2000) based on a 99% decline in commercial landings between 1939–1989 (average 952 metric tons) and 1999 (average 2.3 metric tons) (Fig. 18.31). In 2007 the Cowlitz Indian Tribe in Washington petitioned the National Marine Fisheries Service (NMFS) to protect the Eulachon under the U.S. Endangered Species Act. After extensive and detailed review (Gustafson et al. 2010, 2012), the NMFS listed all Eulachon stocks south of the U.S.–Canada border (i.e., waters under U.S. jurisdiction) as Threatened (NMFS 2010; Reynolds & Romano 2013). They recognized a Southern Distinct Population Segment (DPS) that included Eulachon populations spawning in the Klamath, Columbia, and Fraser Rivers and British Columbia coastal rivers south of the Nass River. The review team considered climate change to ocean condition as the most serious threat to the southern DPS; climate change impacts on freshwater habitat and Eulachon bycatch from shrimp fisheries were scored as moderate to high risk in all areas of the DPS. Dams and water diversions in the Klamath and Columbia Rivers and predation in the Fraser and British Columbia coastal rivers also ranked as top threats to Eulachon persistence (Gustafson et al. 2010, 2012). In British Columbia, the Central Pacific Coast and Fraser River populations of Eulachon are considered Endangered and the Nass and Skeena River populations as Special Concern (COSEWIC 2014). In the Fraser River, similar to the Columbia River, spawning biomass declined 98% in a 10-year period (about 1998–2008) (COSEWIC 2011). In the Central Pacific Coast of British Columbia, many rivers have also experienced drastic declines in run size, some to the point of virtual extirpation, including the Kitimat, Kemano, and Bella Coola Rivers

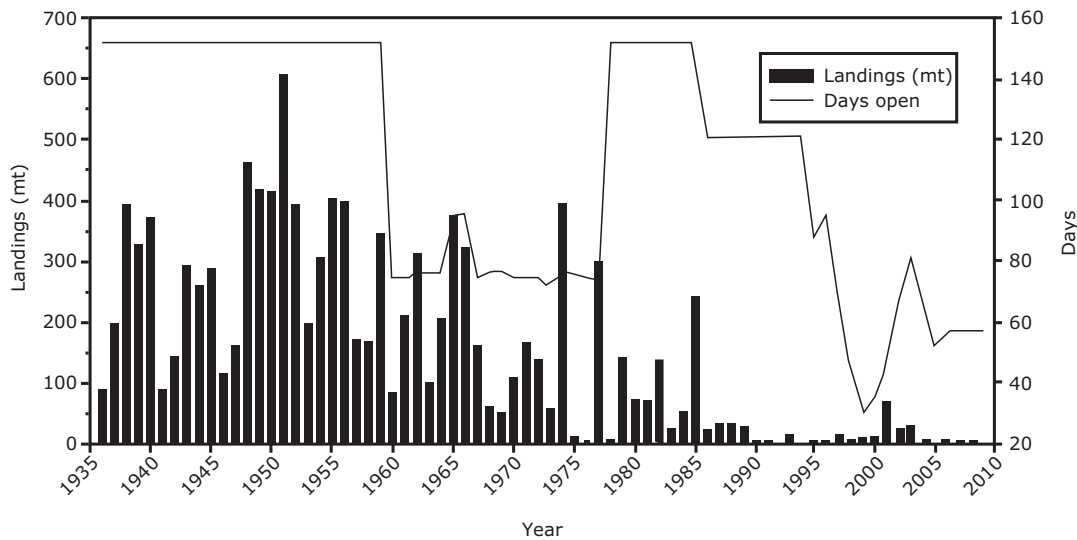


Figure 18.31. Commercial landings (metric tons, mt) of Eulachon, *Thaleichthys pacificus*, and estimated total number of days the fishery was open in the Columbia River from 1935 to 2009 illustrating the collapse of the fishery since about 1985. Similar patterns of decline are documented for the Cowlitz and Fraser Rivers (redrawn from Gustafson et al. 2010).

and those in Rivers Inlet. Substantial declines are also documented for the Kingcome and Klinaklini Rivers, but modest returns remain in those rivers.

Even though other Smelt species are not currently of conservation concern, all anadromous and stream spawning fishes are confronted with increasing problems of habitat degradation. For anadromous populations, the most important concern is the modification of flow regimes of rivers and streams, which can be caused by barriers or climate change. Dams and weirs physically limit upstream migration of these fishes to spawning grounds and create lentic conditions in traditionally lotic habitats, impeding spawning success. Channel modification and sedimentation are also imminent threats to Smelt populations, destroying available spawning grounds and creating adverse conditions for early egg development.

COMMERCIAL IMPORTANCE

Although most species were historically or are abundant across their ranges, few Smelt sustain commercial fisheries. Most are caught by average sportsmen (mostly during the spawning runs) and are consumed locally with a few being important food sources to indigenous tribes. For example, even though historical fisheries once existed, the Delta Smelt is not presently commercially valuable in North America. Moreover, the current Endangered status

of this species prohibits any sportfishing or commercial catches, but they are frequent in the by-catch of commercial fisheries (Moyle 2002). The introduced Wakasagi also has no direct commercial value in North America, though they are extremely valuable in Asia where they support a strong commercial fishery and are cultivated. Populations were introduced in California in 1959 to improve reservoir fisheries. Wakasagi are a good source of food for stocked salmonid species and create larger than average catches of those species. However, foraging shoals of Wakasagi can have significant negative effects on zooplankton communities. Other native fishes, especially Delta Smelt, which are dependent on zooplankton for food, can be adversely affected (Moyle 2002).

The abundance of Pond Smelt, especially during the spawning season in Alaskan and Canadian streams, provides a local food source for many rural communities (Morrow 1980). Scott & Crossman (1973 citing Turner 1886) indicated the Pond Smelt has a sweet taste and is an excellent food fish. Natives in Alaska catch the fish with dipnets in a subsistence fishery during the spawning runs. However, the species is so restricted in range that no commercial fishery can be supported (Scott & Crossman 1973; Morrow 1980). Likewise, Longfin Smelt are abundant and like other Smelt, can be easily caught during their spawning runs, but the meat of the fish is described as oily, soft, and easily spoiled (Scott & Crossman 1973; Morrow 1980; Moyle 2002). Longfin Smelt are undoubtedly

consumed in areas of local abundance, but no known commercial fishery exists; however, Longfin Smelt do compose part of the bycatch of other commercial fisheries.

Historically, Eulachon supported subsistence fisheries by Pacific Northwest Indian Tribes and First Nations, and some harvesting still continues (see conservation section; reviewed by Gustafson et al. 2010; Figs. 18.32–18.34). Because Eulachon arrived in late winter and early spring when other fresh food resources were scarce, they were referred to as savior fish or salvation fish. Besides a food source, the fish have such a high lipid content that dried fish were used as candles by Native Americans and were referred to as candle fish (Morrow 1980; Reynolds & Romano 2013; Fig. 18.35). Tribes along the lower Columbia River used dried or smoked Eulachon for trade with other inland tribes because Eulachon were only available from the lower reaches of large tributaries (Wydoski & Whitney 2003). The oil, or Eulachon grease, was boiled and removed from the fish and sold separately by the gallon where it brought a high price in British Columbia (Scott & Crossman 1973; Wydoski & Whitney 2003). The highly nutritious oil was solid at room temperature and was a common year-round condiment with many foods and was used as a medicine for skin rashes and internal ailments by many First Nations peoples (Kuhnlein et al. 1982, 1996). Similarly, up to the early 1900s, Alaskan Tlingits or other native peoples caught Eulachon (or hooligan) for food, extracted oil from their flesh with simple presses, and used them to barter with inland tribes of southeastern Alaska (Fig. 18.32). Another term applied to Eulachon was fathom fish because they were laid side by side, head to tail, dried or smoked and sold by the fathom (1.8-m lengths) (Wydoski & Whitney 2003). Subsistence fisheries for Eulachon oil and flesh (e.g., smoked) still exist today in many areas of the northwest and Alaska (Moffitt et al. 2002; see conservation section; Figs. 18.33 and 18.34). The oily flesh of fresh Eulachon is described as mild in flavor (Wydoski & Whitney 2003). Meriwether Lewis, who consumed Eulachon while overwintering at Fort Clatsop during the Lewis and Clarke expedition (Fig. 18.32), described the flesh as superior to any he had ever tasted, even more delicate and luscious than white fish of the lakes which formed his standard of excellent fish flesh (Reynolds & Romano 2013).

Commercial fisheries for Eulachon in the Columbia River, Washington (formerly the largest osmerid fishery in North America), which dates to the late 1800s (Wydoski & Whitney 2003), produced catches of 1,270 metric tons (Moyle 2002) in 1990 and 327 metric tons in 2002 (Moffitt et al. 2002). Morrow (1980) reported average annual

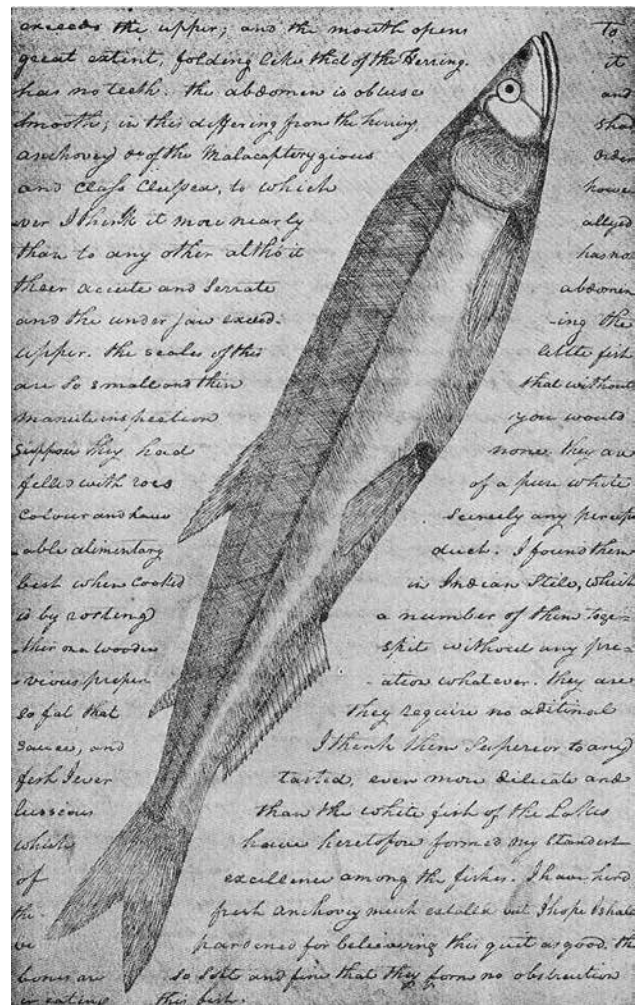


Figure 18.32. A page of William Clark's handwriting from his journal on the Lewis and Clark Expedition with his sketch of the Eulachon, *Thaleichthys pacificus*, giving the first written notice of the species. The Eulachon was brought to Clark by Native Americans seeking trade goods on the Columbia River, 28 February 1806 (from Jordan 1907a; image is in the public domain; source, digital image collection of Freshwater and Marine Image Bank, University of Washington Libraries, Seattle).

catches of 455 metric tons for Washington and Oregon and also mentioned that the fishery in British Columbia was of similar size. Between 1938 and 1997 the total annual commercial catch varied between 2,594 metric tons (1945) and 4 metric tons (1996). The fishery essentially collapsed in 1990 and has not recovered (Gustafson et al. 2010, 2012; Fig. 18.31). The catch during that time was indicative of variation in spawning run size but also was influenced by market demand and harvest restrictions when spawning runs are low. For example, the eruption of Mount St. Helens in 1980 resulted in poor spawning suc-



Figure 18.34. Eulachon, *Thaleichthys pacificus*, being smoked for later consumption in a Haisla Nation fish camp along the Kemano River, British Columbia (Living Landscapes 2012) (courtesy of Dave Gordon).



Figure 18.33. Native fishers of Pacific Northwest coastal rivers have long sought and valued the Eulachon, *Thaleichthys pacificus*, for their rich, pure oil and flesh (Figs. 18.34 and 18.35). In the Kemano River, British Columbia, native fishers (upper) of the Haisla Nation remove Eulachon from a large seine during the 2003 spring spawning run (March–April) (see conservation section). In specially outfitted grease camps set up along the river, the catch is transferred from punts to storage bins (middle), known as stink boxes, where the fish ripen (decompose) for about a week. The ripened fish are then cooked in open, wood-fired boilers, and as the boilers cool, the pure, clear oil rises to the top and is skimmed off (lower). Traditionally, the oil, or hooligan grease, was a highly valued and powerful commodity that was traded to inland tribes. The inland trade routes were aptly named the grease trails (Cambria Gordon Ltd. 2006; Living Landscapes 2012) (courtesy of Dave Gordon).



Figure 18.35. Dried Eulachon, *Thaleichthys pacificus*, which are rich in oil, were often burned and used as light sources by Native Americans, thus, earning the name candle fish (courtesy of Chad Hood, Tongass Minerals Group).

cess and a poor return of adults in 1984 (Wydoski & Whitney 2003). Sport fisheries, using long-handled dipnets, are also significant, and landings sometimes equal that of the commercial fishery (Morrow 1980; Wydoski & Whitney 2003). Besides being used as human food, Eulachon are also processed mechanically and used for animal feed.

Rainbow Smelt have supported both sport and commercial fisheries in North America for >100 years. Accessible spawning aggregations of these fish make them particularly vulnerable to fishing (Marston et al. 2002). Commercial fishers regularly capture Rainbow Smelt with bag nets, trawls, traps, and gill nets. In Lake Michigan, commercial Rainbow Smelt fishing began around 1940; however, soon after (1942–1943) the production dropped to zero due to a purported communicable disease (although the exact cause is unknown), which resulted in nearly total mortality of Rainbow Smelt in Lake Huron and Lake Michigan (Becker 1983). However, stocks recovered quickly and annual catches ranged between 4,490–9,072 metric tons in the Great Lakes region throughout the 1960s and 1970s (Morrow 1980). In the late 1960s, the Rainbow Smelt was the most abundant commercial fish caught by weight in the Great Lakes (Bailey 1964; Scott & Crossman 1973). In the 1980s, annual catches of 10,886 metric tons were realized for the Great Lakes region. Coastal catches of Rainbow Smelt are usually lower and average about 70 metric tons in the New England area (Morrow 1980; Buckley 1989) and 907 metric tons in the Canadian Atlantic (Scott & Scott 1988).

Anadromous stocks of *Osmerus*, due to their overall greater size than landlocked populations, have always supported higher market values (Morrow 1980; Scott &

Scott 1988). High market values and the resultant overfishing may explain declines in annual catches (Morrow 1980; Scott & Scott 1988). From the late 1970s to late 1980s, the annual catch of coastal Rainbow Smelt dropped from an average of 953 metric tons to just over 454 metric tons. Barriers to migration and poor water quality likely contributed to the decline.

Sportfishing for Rainbow Smelt with dipnets (Fig. 18.36), seines, or hook-and-line is also popular and annual catch estimates are thought to equal or exceed that of commercial fisheries (Bailey 1964; Morrow 1980; Buckley 1989). Rainbow Smelt are considered highly palatable and are eaten breaded and fried, baked, or even pickled (Becker 1983). Rainbow Smelt are often taken by hook-and-line by ice fishers in an annual ritual of fishing through the ice from heated Smelt shacks (Beckman 1942; Fig. 18.37), but anglers in the Gulf of St. Lawrence, New Brunswick, also use box nets to capture Rainbow Smelt under the ice (Scott & Scott 1988). After the ice melts and spawning runs commence, fishers then use seines and dipnets to catch the fish in large numbers. Along the Great Lakes, Rainbow Smelt fishing has become a spring ritual, although the level of seasonal excitement has waned since the smelt-mania of the 1930s and 1940s. During this period, ≤30,000 people would flock annually to the small towns of Onconto and Marinette, Wisconsin, for the spring Smelt run (Becker 1983). Banquets, dances, and even a wrestling competition in a ring covered with two tons of Rainbow Smelt, adorned the spring fishing season. In fact, the new-found cultural phenomenon injected vital revenue and afforded new employment opportunities to the region, furthering along recovery from the Great Depression.



Figure 18.36. Fishers along a river on Prince Edward Island dip for Rainbow Smelt, *Osmerus mordax*, during a spawning run (courtesy of Sean Landsman Photography).



Figure 18.37. Smelt shanties lining the frozen Kennebec River near Gardiner and Randolph, Maine, which lie just above the tide line on the river. The shanties symbolize the winter ritual of fishing for anadromous Rainbow Smelt, *Osmerus mordax*, during the spawning run, which usually lasts from about December to March. Best fishing is associated with a rising tide at night. The shanties, many of which are individualized, accommodate 2–6 fishers, are heated by small stoves (note the chimneys), and often have electricity for light. Rainbow Smelt are caught through a trough on one or both sides of the shanty through which baited fishing lines are dropped (courtesy of Bob Trapani, www.momentsinmaine.com).

LITERATURE GUIDE

The preponderance of general information available on Smelt in North America is in Scott & Crossman (1973), Morrow (1980), Becker (1983), Scott & Scott (1988), Page & Burr (1991, 2011), and Moyle (2002) (see also Nellbring 1989). These authors provide syntheses of life history, taxonomy, and distributional data in the form of descriptive species accounts. McAllister's (1963; Fig. 18.38) paper is one of the earliest, most complete works on the family and is a classical reference. Gustafson et al. (2010, 2012) provided a

comprehensive and detailed status review for the Eulachon and Bennett (2005) and Moyle et al. (2016) for the Delta Smelt, summarizing biological, ecological, and conservation information for each respective species. Sommer & Mejia (2013) provided a highly detailed and quantified characterization of habitat of the Delta Smelt. CDFW (2009) in an unpublished report provided similar review for the Longfin Smelt. McAllister et al. (1981), Wilson & Williams (1991), and Cavender (1986) are principle references for the Smelt fossil record. Chapman (1941) provided detailed illustrations of various osteological features of Smelt, and Torao (2000) provided useful figures showing developmental stages of Wakasagi. Research on the distinctive cucumber odor in Smelt is limited to McDowall et al. (1993). Much detailed information of antifreeze properties in Smelt is available, particularly the work by Driedzic and colleagues (e.g., Driedzic & Ewart 2004; Driedzic & Short 2007; Richards et al. 2008; Ditelcadet et al. 2011; Robinson et al. 2011b; Hall et al. 2012; Clow & Driedzic 2012; Ditelcadet & Driedzic 2013) and other references in the physiology section. Myriad genetic studies, mostly investigating biogeography and population structure, were conducted on various Smelt species (e.g., Taylor & Bentzen 1993ab; Taylor & Dobson 1994; Stanley et al. 1995; Bernatchez 1997; McLean et al. 1999; McLean & Taylor 2001; Coulson et al. 2006ab; Bradbury et al. 2006a, 2008abc, 2010, 2011; Fisch et al. 2009 and other references cited herein).

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Figure 18.38. Over a professional career spanning 45 years, Don E. McAllister (1934–2001) published widely in ichthyology and in later years developed expertise on aquatic conservation issues. His 1963 revision of the Osmeridae laid the groundwork for much of the literature that followed on Smelts and their allies (courtesy of ichthyologist photograph collection of Brooks M. Burr).

photographs of Rainbow Smelt. Gordon McWhirter and Ken Sterling patiently reviewed text, figures, tables, and literature cited. René Reyes superb photographs of Smelt development sequences greatly enhanced the chapter. Tom Palmer gave us a close-up photograph of Rainbow Smelt eggs in the wild and a Massachusetts coastal spawning run. Bob Trapani provided us photographs of the Smelt shanties in Maine. Scott Wickard and Tom

Kline provided us with stunning photographs of Eulachon spawning runs under generous licensing agreements. Dave Gordon helped us document the perhaps now vanishing artisanal fishery for Eulachon with well-crafted photographs of the fishers and processing of the species. Chad Hood provided a flaming Eulachon (candle fish) photograph. Gayle Henderson redrew many of the figures.