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PHOTOPHASE AND ILLUMINATION EFFECTS ON THE SWIMMING PERFORMANCE AND BEHAVIOR OF FIVE CALIFORNIA ESTUARINE FISHES

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Running head: YOUNG ET AL.---LIGHT EFFECTS ON FISH SWIMMING
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Abstract.---Photophase and illumination affect many fish activities. In this study, we examined their effects on the critical swimming velocities (U_{crit}), swimming gait patterns, and oral grasping behavior of five California estuarine fishes. All species (4-5 cm SL) swam similarly (mean U_{crit} range:30-36 cm/s) under day/light conditions. However, both nighttime photophase and darkness decreased Delta Smelt (*Hypomesus transpacificus*) swimming velocities. Congeneric Wakasagi (*H. nipponensis*) swimming performance also decreased at night/dark conditions. Regardless of photophase and illumination, Delta Smelt, Wakasagi, and Splittail (*Pogonichthys macrolepidotus*) exhibited three swimming gaits: intermittent stroke-and-glide at low velocities, continuous stroking at moderate velocities, and intermittent burst-and-glide at high velocities near U_{crit}. In contrast, Chinook Salmon (*Onchorhynchus tshawytscha*) used only two swimming gaits: continuous stroking and burst-and-glide under all conditions. Inland Silversides (*Menidia beryllina*) used these two gaits under light conditions and all three gaits under dark conditions. Some Wakasagi, Splittail, and Chinook Salmon orally grasped the upstream screen in the flume at moderate to high water velocities. Oral grasping does not require jaw teeth and may represent adaptive behavior in natural habitats. Regarding vulnerability to water diversions that operate in the dark at night, the threatened Delta Smelt and introduced Wakasagi, comparatively, may be more at risk than the other species.

INTRODUCTION

Photophase and illumination play a fundamental role in the daily behavior of fishes, and many fish activity patterns vary with photophase (reviewed by Woodhead, 1966; Eriksson, 1978) and light intensity (Levine et al., 1980). The classification of fish as nocturnal, diurnal, or crepuscular is based mainly on their swimming activity peak throughout the day (Begout Anras et al., 1997), which has a strong relation to foraging (Helfman, 1978; 1981; 1986). Swimming activity in Perch (*Perca fluviatilis*) increased following a change from light to dark, and decreased following a change from dark to light (Alabaster and Scott, 1978). American Shad (*Alosa sapidissima*), which under normal light conditions were capable of swimming up to 45 cm/s, swam as slow as 8 cm/s under dark conditions (Katz, 1978). In an endurance and survival study using a fish treadmill with two-vector flows, R. M. Kano (Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary, Technical Report No. 4, 1982, unpubl.) found a markedly decreased swimming performance and survival of American Shad under dark conditions. Using a 15-m long flume, Doyle, R. T., D. N. Wallace, R. K. Dias, and J. V. Merriner (N. Y. Fish and Game, 1984, unpubl.) also demonstrated reduction in swimming ability of larval and juvenile Striped Bass (*Morone saxatilis*) and White Perch (*M. americana*) under dark conditions. They suggested that reduced performance in the dark was associated with the lack of visual stimuli. Visual stimuli under light conditions interacted with rheotactic responses mediated by the lateral line system. Juvenile Walleye Pollock (*Theragra chalcogramma*) and juvenile and adult Sablefish (*Anoplopoma fimbria*) were more readily impinged in the mesh of a tow net at lower light intensities (Olla et al., 1997). Cod (*Gadus morhua*) showed indications of a heightened sensory awareness at a greater light level (Engas et al., 1998), and Roach (*Rutilus rutilus*) showed increased orientation ability under lighted conditions making them better

swimmers against the water current (Van Anhollt et al., 1998). However, larval and juvenile Sole (*Solea solea*) had better rheopositive responses in dim light or total darkness than under bright light (Champalbert and Marchand, 1994). Significant effects of photophase on swimming performance have not been demonstrated in many other fishes, although G. R. Parsons (Mississippi Department of Wildlife, Fisheries, and Parks, Freshwater Fisheries Report Number 136, 1994, unpubl.) showed slight decreases in swimming performance of White Crappie (*Pomoxis annularis*) at night under light conditions compared to that during the day.

Fishes that inhabit the water column of estuarine ecosystems are often capable swimmers that must successfully deal with river and tidal currents, predator and prey movements, and human-derived engineering systems to transport or remove water. In California's Sacramento-San Joaquin "Delta" Estuary, the native and resident fishes share space and resources with introduced and migratory species. Scattered throughout this large estuary are >2,000 water diversions for agricultural, industrial and municipal uses (J. R. Herren, and S. S. Kawasaki, California Department of Fish and Game, Fish Bulletin 179, 2001, unpubl.). Entrainment losses of fish eggs, larvae and juveniles at water diversions are considered to be among the factors contributing to the population decline of many Delta fishes (California Department of Water Resources and U. S. Bureau of Reclamation Biological Assessment, 1994, unpubl.). Most of these diversions operate 24 h/d. At those diversions where fish entrainment is monitored, more fish are diverted during the night than during the day (U. S. Bureau of Reclamation, Tracy Fish Collection Facility Studies Vol. 4, 1996, unpubl.). It is unknown whether more fish are entrained at night because they cannot adequately detect the diversion, or because they cannot swim and avoid entrainment as effectively as during the day. Reduced swimming performance may be due to the absence of light (i.e., disorientation from inadequate visual cues) or a photophase-dependent swimming ability (i.e., performance-related circadian rhythms). Our objective was to determine the effects of photophase and light on the swimming performance and behavior of several Delta fishes to better understand their responses to these important illumination-related variables and to assist the conservation efforts of California's fish and water resources managers.

MATERIALS AND METHODS

Experimental design.—The experiments were conducted under two photophase (day or night) conditions: daytime (0800 to 1700 h) and nighttime (1900 to 2200 h) at 17°C during fall and early winter. At each photophase, experiments were conducted under two light conditions: light (50-60 lux) and complete darkness (0 lux) for a total of four combination treatments: Day/Light (D/L), Day/Dark (D/D), Night/Light (N/L) and Night/Dark (N/D). Young-of-the-year of five fish species from the Sacramento-San Joaquin Delta were selected to represent fish of special concern (Table 1). Delta Smelt (*Hypomesus transpacificus*, Osmeridae), Splittail (*Pogonichthys macrolepidotus*, Cyprinidae), and Chinook Salmon (*Oncorhynchus tshawytscha*, Salmonidae) representing native species that are listed under the federal or state Endangered Species Act as threatened; and, Wakasagi (*Hypomesus nipponensis*, Osmeridae) and Inland Silversides (*Menidia beryllina*, Atherinidae) representing fish that are introduced and potential competitors

of the native species. To facilitate comparison among different treatments and different species, similar size fish were used. Analyses of variance (ANOVA) showed no significant differences in the standard length (SL, range:4.0-5.4 cm), fork length (FL, range:4.2-5.9 cm), total length (TL, 4.6-6.6 cm) and wet weight (Wt, 0.6-1.6 g) of fish used in different treatments and among different species.

Fish collection and maintenance.—Splittail and Chinook Salmon were collected during summer, while Delta Smelt, Wakasagi and Inland Silversides were collected during fall. Delta Smelt, Splittail, and Inland Silversides were collected (purse and beach seines) from various Delta sites; Chinook Salmon came from the Nimbus State Hatchery; and Wakasagi were collected from Folsom Lake Reservoir (purse seine). Water temperature from these different sources were between 15 to 17°C. All fish were quickly transported in aerated containers to the University of California, Davis, Center for Aquatic Biology and Aquaculture. Except for Chinook Salmon, all fish were transported in 8-10 L polyethylene bags containing 4-6 ppt NaCl in water with 2-5 ml/l NovAqua (Novalek, Inc.) as described in Swanson et al. (1996). Chinook Salmon parr were transported in aerated fresh water without salt or NovAqua. All fish were maintained in continuously flowing air-equilibrated well water (water hardness: 294 mg/l, pH: 8.0, ammonia-nitrogen: <0.50 mg/l, total alkalinity: 314 mg/l; specific conductance: 660 μmho/cm) under a simulated natural photoperiod regime (38° 32' N), and fed a combination of live *Artemia* nauplii and a commercial diet (Biokyowa, Inc.). All fish were acclimated at 17°C at least 14 d before an experiment. Holding tanks were cleaned daily to remove fecal matter and uneaten food, and they were shielded with semi-opaque plastic sheets to minimize disturbance.

Experimental protocols.—Individual swimming performance under each treatment was measured using a modified Brett-type (Brett, 1964) recirculating swimming flume (9 l total volume) incorporating a pump with a calibrated (Marsh-McBirney, Inc. Model 523 electromagnetic flow meter) variable-speed motor. The swimming chamber (9 cm diameter, 24 cm long) included upstream and downstream polypropylene screens (1 mm mesh; 3×4 mm mesh spaces) and was immersed in a temperature-controlled water bath (17°C). Water velocity measurements from 4 to 54 cm/s (at 2.5 cm/s increment) made at ten locations (including within 1 cm from the chamber wall) varied by <10% (S.D.). Because the cross-sectional area of the fish was <<10% of the cross-sectional area of the swimming chamber, no corrections for solid-blocking effect were necessary (Brett, 1964). A light source with two 40-watt fluorescent bulbs was directed towards a white reflecting panel to provide a light intensity (LI-COR photometer Model LI-185A) of 50-60 lux in the swimming chamber during lighted experiments. This light intensity was chosen because preliminary observations showed that Delta Smelt preferred the darker areas in their holding tank, and 50-60 lux was the lowest light intensity at which reliable fish observations could be made through the video (visible light) camera. Two video cameras, one of which incorporated a pair of infra-red sensitive, night vision goggles, were mounted above the swimming chamber and connected to a video monitor and recorder for observing and measuring fish swimming performance and behavior. All experiments were video recorded at 60 frames/s. The flume and water bath were enclosed in a $3.2 \times 3.2 \times 3.2$ m box with overlapping black polyethylene sheets to exclude outside light and visual distractions to the fish.

Before each experiment, an individual fish was placed in the chamber and, after 5 min, water velocity was increased to approximately 4 cm/s for the remaining 55 min of chamber acclimation. During each experiment, water velocity was increased step-wise every 10 min at 2.5 cm/s ($\pm$ 0.04 SEM) starting at 4 cm/s (acclimation velocity) until the fish fatigued (indicated by three consecutive impingements at the downstream screen within the 10-min period). Swimming performance was calculated as critical swimming velocity (U_{crit}), the maximum velocity a fish can maintain for a specified period of time (Beamish, 1978) using:

$$U_{crit} = U_i + [U_{ii} \times (T_i / T_{ii})]$$

where U_i = highest velocity maintained for the prescribed period of time;

U_{ii} = velocity increment;

T_i = time elapsed at fatigue velocity; and

T_{ii} = prescribed time period.

After each experiment, the fish was lightly anesthetized (0.7 ppm MS-222), measured (SL, FL, TL), and weighed in a tared beaker of water.

Fish (n = 5-12/treatment) were used only once, and those exhibited any visible abnormalities or experienced prolonged or repeated loss of equilibrium in the flume during acclimation were removed and no data were collected.

Visual observations on swimming behavior, including willingness to swim, position in the chamber, rheotaxis, swimming gaits, oral grasping on the upstream screen, and caudal bracing or impingement on the downstream screen, were continuously made during all experiments. Because cessation of caudal undulations accompanied the oral grasping events, the timer was turned off to exclude grasping time from swimming time. An experiment was terminated when a fish grasped for >120 s.

Skeletal examination.—We hypothesized that oral grasping would require presence of jaw teeth. Therefore, we examined and compared the jaws of the different test species.   Fish (3-6 per species) were over-anesthetized in MS-222, fixed in 95% alcohol, dissolved (soft tissues) in 1% KOH, stained with alizarin red S, and stored in glycerin for skeletal examination (dissecting microscope) of the jaws.

Measurements.—Swimming performance was measured as U_{crit} (cm/s; see above for calculation). For swimming gait pattern measurements, the swimming gaits were identified (also see Swanson et al. 1998) as: a) stroke-and-glide: intermittent active stroking with passive gliding; b) continuous: continuous active stroking with no intermittent gliding; and c) burst-and-glide: intermittent active stroking with darting burst forward then gliding backward.   Stroke-and-glide gait was characterized by one or several small-amplitude body undulations followed by a straightening of the body and passively coasting; while burst-and-glide gait was characterized by a forward movement consisted of a single rapid, large-amplitude body undulation followed by a straightening of the body and passively coasting for a short duration. Video tape of each experiment was analyzed and at each velocity, the predominant swimming gait was identified and reported as velocity ranges (minimum, maximum) for each gait.

Analyses of video tapes were also made when oral grasping behavior was observed and the following were measured: a) water velocity ranges based on minimum and maximum water velocities at which oral grasping events were observed; b) total number of oral grasping events per experiment; and c) duration (in seconds) of each oral grasping event. Grasping duration for >120 s was not included in the calculation for mean grasping duration.

Statistical Analyses.—One-way ANOVA, Kruskal-Wallis, and Bonferroni t-tests (SigmaStat software) were used to compare results for experimental treatments, species, U_{crit}, velocity ranges (based on minimum and maximum velocity), number of oral grasping events and duration. ANCOVA (Systat software) was used to determine if standard length and wet weight were covariates of U_{crit}. G-tests of Independence (Sokal and Rohlf, 1995) were used to determine species effects on willingness to swim, treatment effects on willingness to swim in each species, and treatment effects on number of fish exhibiting grasping behavior for each species. Statistical differences were considered significant at $P < 0.05$.

<center>RESULTS</center>

Critical Swimming Velocity.—ANCOVA did not show significant covariant effects of standard length or wet weight on critical swimming velocity for each fish species at each light/photophase treatment. During D/L conditions, mean U_{crit} of all species were not significantly different (range: 30-36 cm/s; Fig. 1). G-tests of Independence showed that willingness to swim in each species was not affected by photophase or illumination. However, G-test showed that significantly more Delta Smelt were unwilling to swim (30-33%; $P = 0.003$) than the other species.

Regardless of photophase and light condition, 67-70% of Delta Smelt were willing to swim in the flume. Their D/L mean U_{crit} was significantly higher ($P<0.001$ to 0.023) than those under all other conditions, which were not statistically distinguishable. Under N/L conditions, their mean U_{crit} was significantly less ($P<0.001$ to 0.024) than all other species at the same photophase and light conditions; and under N/D condition, significantly less ($P<0.001$ to 0.004) than all other species except Wakasagi at the same photophase and light condition. Wakasagi, which is almost identical morphologically to its congener, Delta Smelt (Swanson et al. 2000, Moyle 2002), had 88-100% per treatment willing to swim. Further, the Wakasagi's mean U_{crit} under N/L conditions was significantly greater ($P<0.001$) than that of Delta Smelt and was statistically indistinguishable from those of the Splittail, Chinook Salmon and Inland Silversides (Fig. 1) under similar conditions. Photophase did not affect Wakasagi swimming performance, as long as light was present. However, under N/D conditions, mean U_{crit} was significantly lower than those under D/L ($P=0.013$) and N/L ($P=0.004$) conditions. Under D/D conditions, Wakasagi mean U_{crit} was intermediate and did not differ statistically from the mean U_{crit}s under the other conditions. Young-of-the-year Splittail, Chinook Salmon parr and young Inland

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Silversides all swam well, with 88-100% of fish per treatment willing to swim. Their U_{crit}s were not affected by photophase or light conditions.

Swimming gaits.—Delta Smelt, Wakasagi and Splittail used three different swimming gaits (Fig. 2): an intermittent stroke-and-glide at low velocities, continuous stroking at moderate velocities, and intermittent burst-and-glide at high velocities and near U_{crit}. Under the four photophase and light conditions, there were no significant differences in the mean swimming velocity ranges over which Delta Smelt used the intermittent stroke-and-glide gait. However, under N/D conditions, Delta Smelt and Wakasagi shifted significantly sooner to burst-and-glide than under other conditions (Delta Smelt; P<0.001 to 0.020) or under D/L and N/L (Wakasagi; P=0.034 and 0.039, respectively).

For Splittail, statistical analyses indicated no significant difference in the swimming gait patterns at different photophase and light combinations. However, mean maximum water velocity at which Splittail used intermittent stroke-and-glide swimming gait was slightly but significantly extended from 14 cm/s velocity under D/D conditions (P=0.013) and 16 cm/s velocity under N/L conditions (P=0.037), to 21 cm/s under N/D conditions.

Chinook Salmon used a continuous stroking swimming gait at low and moderate velocities, and a burst-and-glide swimming gait at high velocities and near U_{crit} (Fig. 2). Although no intermittent stroke-and-glide gait was used, some of the young salmon were observed near the bottom, or showed negative rheotaxis (facing downstream) and swam backwards with their pectoral fins to maintain position in the swimming chamber at the lowest velocities. Photophase and light did not have a significant effect on the swimming gait pattern of Chinook Salmon.

Inland Silversides' swimming gait pattern under light conditions (day or night) was similar to that of the Chinook Salmon; i.e., continuous stroking swimming gait at low and moderate velocities, and a burst-and-glide swimming gait at high velocities and near U_{crit} (Fig. 2). However, under dark conditions (day or night), Inland Silversides used an intermittent stroke-and-glide swimming gait at low velocities and frequently appeared disoriented. At moderate and high velocities, the Inland Silversides employed continuous stroking swimming gait, switching to burst-and-glide swimming gait near U_{crit}.

Oral grasping behavior.—At intermediate and high velocities (including velocities near U_{crit}), some Wakasagi, Splittail, and Chinook Salmon were observed to burst forward and attach themselves to the upstream screen with their mouth (termed "oral grasping"). From a close-up underwater video camera situated in the water bath, we observed the fish's mouth clamped on a single screen mesh (1 mm thick, 4 mm long). Ten Wakasagi (of 24 fish) were observed to grasp the upstream screen, and their longest duration (>120 s) occurred during the day at mean velocities > 25 cm/s (Fig. 3). However, none were observed to grasp at N/L conditions. G-tests

results indicate that illumination significantly affected the number of Wakasagi that exhibited grasping behavior (P = 0.03). Six Splittail (of 28 fish) were observed to grasp the upstream screen and none grasped for >10 s. Photophase and illumination did not significantly affect (G-test) the number of Splittail that exhibited grasping behavior. No Chinook Salmon were observed to grasp under light conditions, while 57% (day) to 50% (night) of the tested fish were observed to grasp under dark conditions (representing 7 of 25 total fish used). Result of G-test indicates that illumination significantly affected the number of Chinook Salmon that exhibited grasping behavior (P = 0.02). Four of the Chinook Salmon grasped the screen for >120 s, after which the experiments were terminated. A few (<10%) Delta Smelt and Inland Silversides appeared to attempt but were unable to grasp the screen.

Skeletal examination.—Jaw examinations showed that Delta Smelt, Inland Silversides and Wakasagi all have many fine teeth, and Chinook Salmon have many larger teeth. In contrast, Splittail have no jaw teeth (Table 1).

<center>DISCUSSION</center>

This was the first study to examine the important combined effects of photophase and light on the swimming performance and behavior of fishes. Delta Smelt, Wakasagi, Splittail, Chinook Salmon, and Inland Silversides of similar sizes had comparable, moderate swimming performance (mean U_{crit} range: 30-36 cm/s) during the day and under light conditions (although 33% of Delta Smelt were unwilling to swim). Delta Smelt, Wakasagi and Splittail swimming performance under these conditions were consistent with previous studies' (Young and Cech, 1996; Swanson et al., 1998; Swanson et al., 2000). The two osmerid fishes, Delta Smelt and Wakasagi, were the only species with U_{crit} significantly affected by photophase and light. Delta Smelt swimming performance was affected by both photophase and light separately and in combination, while Wakasagi swimming performance was significantly affected by a combination of photophase and light. Further, the lowest U_{crit} measured was at night under dark conditions, showing that the photophase and light effects are additive in Delta Smelt.

Regardless of photophase and illumination, Delta Smelt, Wakasagi and Splittail exhibited three velocity-dependent swimming gaits: intermittent stroke-and-glide at low velocities; continuous stroking at moderate velocities; and burst-and-glide at high velocities and near U_{crit}. Swanson et al. (1998) gave a detailed description and kinematic analysis of Delta Smelt swimming gaits during the day under light conditions. In our study, Delta Smelt and Wakasagi shifted from continuous stroking to burst-and-glide swimming gaits at lower velocities during the night under dark conditions. This shifting was probably linked to the decreased overall swimming performance at night under dark conditions.

Chinook Salmon and Inland Silversides under light conditions used only two velocity-dependent swimming gaits: continuous stroking at low and moderate velocities; and burst-and-

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glide at high velocities and near U_{crit}. However, under dark conditions, Inland Silversides used three velocity-dependent swimming gaits similar to those of Delta Smelt and Splittail. Inland Silversides was the only species in which the swimming gait pattern was dramatically affected by light. Under dark conditions, instead of the continuous stroking swimming gait at low velocities, Inland Silversides used an intermittent stroke-and-glide swimming gait and in many instances, seemed disoriented. This is the first report of a light-mediated change in vertebrate locomotory gait pattern.   Doyle, R. T., D. N. Wallace, R. K. Dias, and J. V. Merriner (N. Y. Fish and Game, 1984, unpubl.) suggested that disorientation in fish may be associated with lack of visual stimuli, and Deliagina et al. (1993) showed light as an orientation stimulus in lampreys *(Ichthyomyzon unicuspis*, *Petromyzon marinus*, and *Lampetra fluviatus*). In his review, Webb (1994) described other environmental factors (i.e., temperature, pressure) that are known to compress the general gait recruitment sequence. Why do the Inland Silversides include the intermittent stroke-and-glide gait at low or moderate velocities during darkened swims and exclude it during lighted ones? One possibility is that using the stroke-and-glide gait may be more energetically and hydrodynamically advantageous at low velocities (Weihs, 1974). Thus Inland Silversides may be compensating behaviorally while swimming in the dark, when foraging is unlikely (Bennett and Moyle, 1996). Another possibility is that this species probably relies to a greater degree upon its extravisual sensory acuity in the dark, and the pauses between the intermittent movements in the dark may significantly stabilize its perceptual field (e.g., to increase effectiveness of its acoustico-lateralis system; Kramer and McLaughlin, 2001). The presence of light may reduce reliance for extravisual acuity (e.g., for prey or predator detection).

Species varied in their tendency and ability to orally grasp the upstream screen in the swimming chamber. Oral grasping obviated swimming-related body undulations, presumably decreasing the energy requirements while avoiding impingement on the downstream screen. A few Delta Smelt and Inland Silversides appeared to attempt oral grasping on the upstream screen but were unable to accomplish it.   In contrast, some Splittail, Chinook Salmon and Wakasagi were observed to burst forward and grasp the upstream screen with their mouth usually at high velocities, including velocities near U_{crit}. Our results suggest that Chinook Salmon and Wakasagi are more likely to orally grasp under dark conditions than under light conditions.   For Wakasagi, this may correspond with the lower U_{crit} at night in the dark, and is further evidence of decreased performance during this time period.

Jaw examination on our five species indicated that oral grasping did not require jaw teeth. Oral grasping in species such as Wakasagi, young Splittail and Chinook Salmon parr may represent adaptive behavior in natural habitats. Wakasagi are found in reservoirs and tributary rivers and are subjected to periodic high stream flows (Aasen et al., 1998). Young Splittail forage in periodically flooded vegetation (Caywood, 1974), and Chinook Salmon parr thrive in streams with much debris (Naiman and Turner, 2000). In contrast, Delta Smelt and Inland Silversides occur in large numbers in open surface waters (W. A. Bennett, Interagency Ecological Program for the Sacramento-San Joaquin Estuary Newsletter 8, 1995, unpubl.; Moyle, 2002). Adams (2003) reported oral grasping behavior in nine species of minnows from North America and

investigated this behavior in relation to the species' environment. In nature, Wakasagi, young-of-the-year Splittail, and Chinook Salmon parr may orally grasp vegetation or other structures, perhaps to hold their position in swift currents. This may represent adaptive behavior by minimizing displacement and decreasing energy requirements. Such behavior may give Wakasagi, Splittail, and Chinook Salmon an advantage over Delta Smelt and Inland Silversides in maintaining position near water diversion structures.

Young-of-the-year Splittail oral grasping activity was first reported in our previous study (Young and Cech, 1996), but we did not quantify oral grasping events or duration, nor effects of photophase and illumination. Childs (1998) described a similar behavior (he termed "mooring and parking") in Scrawled Filefish (*Aluterus scriptus*), Orangespotted Filefish (*Cantherhines pullus*) and Whitespotted Filefish (*C. macrocerus*) wherein fish were observed to orally attached themselves to sponges in order to maintain their position. Adams et al. (2000) described oral grasping in Topeka Shiner (*Notropis topeka*) on swim tunnel wire mesh at moderate velocities (35-50 cm/s) and concluded that this behavior might retard downstream displacement of shiners. Recently, Adams et al. (2003) also examined oral grasping behavior in nine species of North American minnows and speculated that these minnows use oral grasping in high water velocities such as during flood.

Regarding vulnerability to entrainment and impingement at water diversions that operate in the dark at night, the threatened Delta Smelt and introduced Wakasagi may be more at risk, compared with the other species studied. Their decreased U_{crit} during darkened periods is consistent with the greater numbers of fish (especially Delta Smelt) salvaged at California State and federal fish salvage facilities during the night than during the day (U. S. Bureau of Reclamation, Tracy Fish Collection Facility Studies Vol. 4, 1996, unpubl.). Elimination or reduction of pumping rates and fish-screen approach velocities during the night and/or illumination of areas around water diversions should be considered to minimize harm to threatened species such as Delta Smelt. Additional studies should be conducted to examine whether nighttime illumination of water diversions: a) attracts these small fish, increasing entrainment and impingement, as in Gizzard Shad (*Dorosoma cepedianum*) and Rainbow Smelt (*Osmerus mordax*; Haymes et al.,1984); b) attracts predators, increasing predation-related mortality in these small fishes; or c) deflects these small fish as in Silver Eels *(Anguilla anguilla)* from hydropower stations (Hadderingh et al., 1999).

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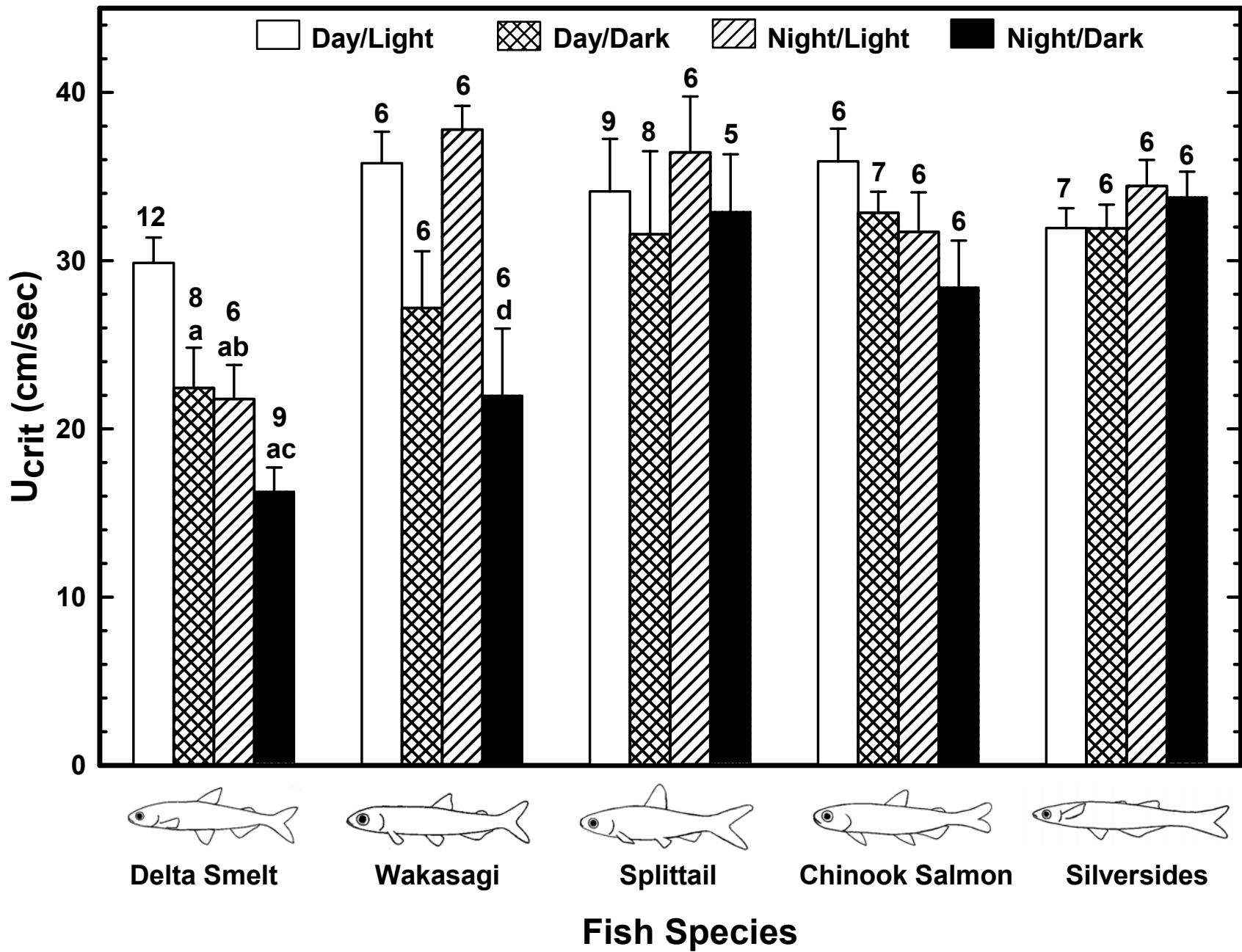
Fig. 1. Mean (± SEM) critical swimming velocity (U_{crit}) of different California estuarine fishes under the four photophase and light conditions. Superscripted letters show significant differences: a: <Delta Smelt at D/L conditions; b: <all other species at N/L conditions; c: <all other species except Wakasagi at N/D conditions; d: <Wakasagi at D/L and N/L conditions; number on top of bar indicates sample size.

Fig. 2. Mean (± SEM) swim velocity ranges (from minimum to maximum velocities) at which different swimming gaits were exhibited by different California estuarine fishes under the four photophase and light conditions.
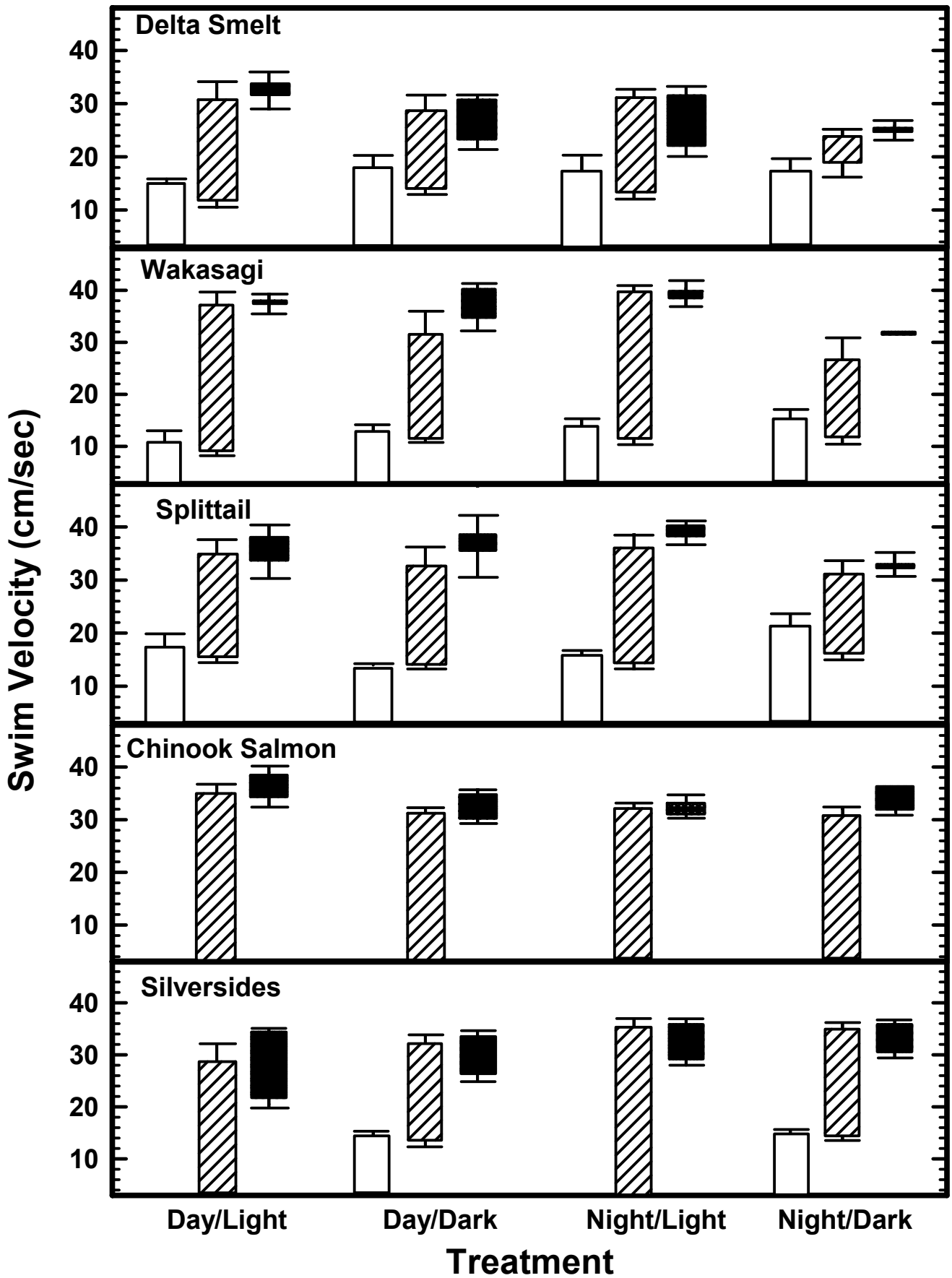
Fig. 3. Mean (± SEM) water velocity range, number of events and duration at which oral grasping behavior was observed in Wakasagi, Splittail, and Chinook Salmon under various photophase and light conditions. Fractional number indicates the number of fish that exhibited oral grasping behavior over number of total fish used; white circle indicates the mean U_{crit} value for total fish used; #: one fish grasped for > 120 s; ##: two fish grasped > 120 s.

TABLE 1. FISH SPECIES USED FOR THE PRESENT STUDY WITH PERTINENT INFORMATION. SL = standard length; Wt = wet weight; Native/Introduced and Resident/Transient: pertain to the species' status in the Sacramento-San Joaquin Delta System.

	Fish Species				
	Delta Smelt	Wakasagi	Splittail	Chinook Salmon	Silversides
SL range (cm)	4.0-5.0	4.1-5.4	4.0-5.0	4.0-5.3	4.1-5.0
Wt range (g)	0.6-1.1	0.6-1.4	0.7-1.6	0.8-1.5	0.6-1.1
Jaw teeth	Fine teeth	Fine teeth	No jaw teeth	Large teeth	Fine teeth
Oral grasping behavior	No	Yes	Yes	Yes	No
Native/Introduced	Native	Introduced	Native	Native	Introduced
Resident/Transient	Resident	Transient	Resident	Transient	Resident
General habitat	Open surface waters	Reservoir and tributaries	Shallow water and flood plains	Streams	Open surface waters

Figure showing U_{crit} (cm/sec) for five fish species under four conditions: Day/Light, Day/Dark, Night/Light, Night/Dark.

Delta Smelt: 12, 8 a, 6 ab, 9 ac
Wakasagi: 6, 6, 6, 6 d
Splittail: 9, 8, 6, 5
Chinook Salmon: 6, 7, 6, 6
Silversides: 7, 6, 6, 6

Y-axis: U_{crit} (cm/sec)
X-axis: Fish Species