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Tracy Series Volume 52 – Master's Thesis Excerpt

Effects of Temperature and Simulated Loading Stress on the Oxygen Consumption and Ammonia Production Rates of Fishes of the Sacramento-San Joaquin River Delta, California

U.S. Department of the Interior
Bureau of Reclamation
Mid-Pacific Region and
Denver Technical Service Center

July 2015

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1. REPORT DATE *(DD-MM-YYYY)*	**2. REPORT TYPE**	**3. DATES COVERED** *(From - To)*
July 2015	Final	

4. TITLE AND SUBTITLE

Effects of Temperature and Simulated Loading Stress on the Oxygen Consumption and Ammonia Production Rates of Fishes of the Sacramento-San Joaquin River Delta, California

5a. CONTRACT NUMBER

5b. GRANT NUMBER

5c. PROGRAM ELEMENT NUMBER

6. AUTHOR(S)

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5d. PROJECT NUMBER

5e. TASK NUMBER

5f. WORK UNIT NUMBER

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

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Fort Collins, Colorado 80523-1474

8. PERFORMING ORGANIZATION REPORT NUMBER

Volume 52

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

Bureau of Reclamation,
Tracy Fish Collection Facility
16650 Kelso Road, Byron, CA 94514

10. SPONSOR/MONITOR'S ACRONYM(S)

11. SPONSOR/MONITOR'S REPORT NUMBER(S)

12. DISTRIBUTION/AVAILABILITY STATEMENT

Available from the National Technical Information Service (NTIS)
Operations Division, 5285 Port Royal Road, Springfield, VA 22161

13. SUPPLEMENTARY NOTE

14. ABSTRACT

Total ammonia nitrogen production rates (M_{TAN}) and oxygen consumption rates (MO_2) were measured before and after simulated fish-loading stress (30-s air exposure), at 12, 15, 18, and 21ºC for delta smelt (*Hypomesus transpacificus*), 12, 16, 21, and 24 ºC Chinook salmon (*Oncorhynchus tshawytscha*), and 12, 18, 24 and 28 °C for striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*). Pre- and post-stress MO_2 and M_{TAN} of all species generally increased with temperature. Simulated fish-loading stress did not affect threadfin shad or delta smelt MO_2 and M_{TAN}, likely because their stress levels had already plateaued from the combination of handling and confinement in the respirometry chambers. Mean MO_2 for delta smelt ranged from 0.05 to 0.08 mg O_2/g/h and M_{TAN} ranged from 0.002 to 0.01 mg TAN/g/h over the tested temperature range. Threadfin shad MO_2 increased from 0.05 to 0.19 mg O_2/g/h and M_{TAN} increased from 0.001 to 0.01 mg TAN/g/h as temperature increased from 12 to 28 °C. Simulated loading stress increased striped bass (13–40%) and Chinook salmon (17 – 34%) MO_2 and M_{TAN} rates. Striped bass pre-stress MO_2 ranged from 0.03 mg O_2/g/ h at 12 °C to 0.09 mg O_2/g/h at 28 °C, and M_{TAN} ranged from 0.001 to 0.004 mg TAN/g/h. Chinook salmon tested between 12 and 28 °C had MO_2 and M_{TAN} values that ranged from 0.04 to 0.13 mg O_2/g/h, and from 0.001 to 0.003 mg TAN/g/h, respectively. These results indicate fish-loading stress affected Chinook salmon and striped bass MO_2 and M_{TAN}, though the magnitude of response was species-specific. Also, Chinook salmon and striped bass experienced a reduced ability to cope with simulated fish-loading stress, and return to pre-stress MO_2 and M_{TAN}, as temperatures increased.

15. SUBJECT TERMS

loading stress, respirometry, ammonia production, oxygen consumption, delta smelt, Chinook salmon, threadfin shad, striped bass

16. SECURITY CLASSIFICATION OF:			**17. LIMITATION OF ABSTRACT**	**18. NUMBER OF PAGES**	**19a. NAME OF RESPONSIBLE PERSON**
					Donald E. Portz, Ph.D.
a. REPORT	**b. ABSTRACT**	**a. THIS PAGE**		40	**19b. TELEPHONE NUMBER** *(Include area code)*
					303-445-2220

Tracy Fish Facility Studies
California

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by

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Bureau of Reclamation
Mid-Pacific Region and
Denver Technical Service Center

July 2015

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EXECUTIVE SUMMARY

Total ammonia nitrogen production rates (M_{TAN}) and oxygen consumption rates (MO_2) were measured before and after simulated fish-loading stress (30-s air exposure), at 12, 15, 18, and 21ºC for delta smelt (*Hypomesus transpacificus*), 12, 16, 21, and 24 ºC Chinook salmon (*Oncorhynchus tshawytscha*), and 12, 18, 24 and 28 °C for striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*). Pre- and post-stress MO_2 and M_{TAN} of all species generally increased with temperature. Simulated fish-loading stress did not affect threadfin shad or delta smelt MO_2 and M_{TAN}, likely because their stress levels had already plateaued from the combination of handling and confinement in the respirometry chambers. Mean MO_2 for delta smelt ranged from 0.05 to 0.08 mg O_2/g/h and M_{TAN} ranged from 0.002 to 0.01 mg TAN/g/h over the tested temperature range. Threadfin shad MO_2 increased from 0.05 to 0.19 mg O_2/g/h and M_{TAN} increased from 0.001 to 0.01 mg TAN/g/h as temperature increased from 12 to 28 °C. Simulated loading stress increased striped bass (13–40%) and Chinook salmon (17–34%) MO_2 and M_{TAN} rates. Striped bass pre-stress MO_2 ranged from 0.03 mg O_2/g/h at 12 °C to 0.09 mg O_2/g/h at 28 °C, and M_{TAN} ranged from 0.001 to 0.004 mg TAN/g/h. Chinook salmon tested between 12 and 28 °C had MO_2 and M_{TAN} values that ranged from 0.04 to 0.13 mg O_2/g/h, and from 0.001 to 0.003 mg TAN/g/h, respectively. These results indicate fish-loading stress affected Chinook salmon and striped bass MO_2 and M_{TAN}, though the magnitude of response was species-specific. Also, Chinook salmon and striped bass experienced a reduced ability to cope with simulated fish-loading stress, and return to pre-stress MO_2 and $M_{TAN,}$ as temperatures increased.

INTRODUCTION

Transportation of wild fish is used as a management tool in the Western United States to bypass facilities (*e.g.*, dams), that are barriers to fish migration, or water diversion structures that would otherwise entrain or injure fish (Nemeth and Kiefer 1999, Helfrich *et al.* 2001). Transportation of fish is also a key phase in many fish culture operations. Although maximizing fish survival during transport is highly valued, typical transportation procedures expose fish to a number of stressors, including handling (Barton *et al.* 1980, Barton 2000), confinement (Carmichael *et al.* 1984a), social stress (Sloman *et al.* 2000a, Sloman *et al.* 2001) and adverse water quality conditions (Wedemeyer 1996, Carmichael *et al.* 2001). Any of these stressors, or their combination, may, in actuality, reduce fish health and survival (Iwama *et al.* 2005). In this study, the effects of handling or loading (as would occur during transfer of fish to hauling tanks) on oxygen consumption (MO_2) and ammonia production rates were examined.

Fish continuously consume oxygen (O_2) to meet aerobic metabolic requirements, and as a byproduct, continuously excrete carbon dioxide [CO_2; carbon dioxide production (MCO_2)]. Oxygen consumption rates (MO_2) increase when fish are stressed, which can lead to reduced available O_2 in transport tanks, and hypoxic (and possibly anoxic) conditions. Hypoxia (low O_2 partial pressures) induces respiratory stress (Hughes 1973), resulting in tissue hypoxia and impairment of performance (Crocker and Cech 1997, Herbert and Steffensen 2005, Vagner *et al.* 2008), health (reduced growth and fecundity, unconsciousness) and ultimately reduced survivability (Weber and Kramer 1983, Cech and Crocker 2002). Transport stress also increases production of CO_2, and if the tank is not well-ventilated can produce hypercapnic conditions (Moyle and Cech 2000, Forsberg and Summerfelt 1999). Because increased oxygen consumption rates result in increased production of CO_2, effects of environmental hypercapnia during fish transport should also be considered.

Environmental hypercapnia can rapidly lead to physiological hypercapnia (elevated plasma CO_2), resulting in a decrease in blood pH and respiratory acidosis (Eddy *et al.* 1977, Portz *et al.* 2006), along with a reduction in MO_2 (Cruz-Neto and Steffensen 1997). Hypercapnia, and the subsequent development of respiratory acidosis, reduce the oxygen binding capacity and affinity of hemoglobin (Moyle and Cech 2000), resulting in hypoxemia, with the short- and long-term effects mentioned above. If fish are not fasted prior to transport, which may be the case when wild fish are captured and transported to culture facilities or are moved around potential barriers to migration, catabolism continues. The excretory byproducts of catabolism, largely nitrogenous compounds, result in steady accumulation of total ammonia nitrogen (TAN), a combination of ionized (NH_4^+) and unionized ammonia (NH_3). Elevated TAN, and particularly NH_3, the most toxic form, can cause gill corrosion, nerve damage, reduced swimming

performance (Shingles *et al.* 2001, Wicks *et al.* 2002, McKenzie *et al.* 2003), disease resistance (Ackerman *et al.* 2006), and ultimately unconsciousness and death (Meade 1985, Russo and Thurston 1991, Randall and Tsui 2002).

Fish health may be compromised during transport operations because loading and transport induced stress likely alter the physiological state of the fish (Maule *et al.* 1988, Davis and Schreck 1997, Congleton *et al.* 2000). Exposure to stress elicits a general adaptive physiological and behavioral stress response in most fishes (Pickering 1981), consisting of primary and secondary levels, and if the stressor persists, a tertiary level (Schreck 1981, Wendelaar Bonga 1997, Barton *et al.* 2002). The primary stress response can be thought of as the detection or perception of the stressor and initiation of neuroendocrine signaling systems that trigger the secondary response. The secondary response is a series of physiological changes that can result in increased heart rate, blood flow, and metabolic rate (Mommsen *et al.* 1999, Barton *et al.* 2002), and, in the short term, provide the fish with a greater ability to cope with the stressor. Prolonged exposure to a stressor leads to the tertiary stress response where the physiological changes have the net effect of reducing the overall survivability of the fish. In the case of fish transport, both loading and transport procedures may lead to elevated MO_2, MCO_2, and M_{TAN} rates, accelerating the rate of water quality decline, and possibly pre-disposing fish for the maladaptive effects of the tertiary stress response.

Biologists working in concert with state and federal fish salvage facilities in California's Sacramento-San Joaquin River Delta (SSJRD) have recognized the importance of developing fish-hauling guidelines as a means to maintain healthy water quality conditions during transport operations. Many SSJRD fishes, including the commercially cultured Chinook salmon (*Oncorhynchus tshawytscha*), and striped bass (*Morone saxatilis*), along with the federally endangered delta smelt (*Hypomesus transpacificus*), and the introduced threadfin shad (*Dorosoma petenense*), have incurred precipitous declines in population abundance in recent decades (Moyle *et al.* 1992, Yoshiyama *et al.* 1998, Moyle 2002, Feyrer *et al.* 2007). Striped bass and threadfin shad are two of the most abundance species salvaged and transported from the fish collection facilities, while Chinook salmon and delta smelt are ESA listed species salvaged at the facilities (NMFS 1997, Sweetnam 1999). As a result, it is widely suspected that operations at fish collection facilities contribute to the ongoing declines in fish populations in the SSJRD (Moyle 2002, Kimmerer 2008).

The goal of the study was to evaluate effects of fish loading, and provide data for the development of an improved set of fish loading and transporting guidelines for the Bureau of Reclamation's (Reclamation) Tracy Fish Collection Facility. A primary concern during fish-transport is maintaining appropriate fish densities, because stocking density directly contributes to the rate at which transport water quality and fish health are degraded (Carmichael *et al.* 2001, Hasan and Bart 2007). The primary objective of this study was to measure the effects of

temperature on the MO_2 and M_{TAN} rates, and calculated MCO_2 rates, of Chinook salmon, delta smelt, striped bass, and threadfin shad exposed to simulated fish-loading stress. Temperature was included as a variable because fish salvage operations in the SSJRD occur year round and encompass a temperature range of 5.4 to 29.0 °C (Craft *et al.* 2008). Secondary objectives were to assess the energetic cost of simulated fish-loading stress (short-term partial atmospheric exposure) to SSJRD fishes, and to measure the time required for MO_2 and M_{TAN} to achieve homeostasis, typically by returning to pre-stress (resting-routine) rates.

METHODS

Fish Source and Care

All fish holding tanks were covered with black shade cloth to reduce exposure to external stressors. Fish were maintained on natural photoperiods equivalent to those at their testing sites using timer-controlled halogen light sources (delta smelt and threadfin shad: 37°52'N; striped bass and Chinook salmon: 39°45'N). Water inlet pipes were angled to create a circular pattern of flow in each tank, and a velocity gradient of 4–10 cm/sec. Water temperatures were generally constant in all holding tanks, and were maintained at target holding temperatures ± 0.4 °C (± SD). All fishes were acclimated for at least four weeks prior to experimentation.

Delta Smelt

Age-1 delta smelt, cultured and reared at the University of California at Davis Delta Smelt Culture and Conservation Laboratory (Byron, California), were transported to Reclamation's Tracy Aquaculture Facility (TAF; Byron, California) between May–September 2007. Smelt were held in black 757-L cylindrical fiberglass tanks (120 cm diameter × 76 cm deep) receiving continuous flows (11.3 ± 0.8 L/min, mean ± SD) of recirculated water. Total ammonia nitrogen, nitrite, pH, salinity and O_2 were monitored daily and maintained at the following levels: 0.2–0.8 mg/L, < 0.05 mg/L, 7.8–8.1, 1.0–2.0 ‰, and 9.4– 10.5 mg/L, respectively. Smelt were continuously hopper fed satiation rations (3 % body weight/d) of a 2:1 mixture of 600–800 micron Lancy Feed and 370 micron Hikari plankton feed (Hikari Inc., Hayward, California). All experiments testing delta smelt were conducted between July 9 and August 13, 2007.

Threadfin Shad

A sub-sample of threadfin shad were removed by dip net from a shoal of wild fish entrained at Reclamation's Tracy Fish Collection Facility (TFCF; Tracy,

California) in a fish holding tank, and immediately transferred to the TAF during the summer of 2007. Threadfin shad were held under essentially the same conditions as delta smelt, but the interior of shad holding tanks were white. Total ammonia nitrogen, nitrite, pH, salinity and O_2 levels were 0.0–0.2 mg/L, < 0.05 mg/L, 7.9–8.2, 1.0–3.0 ‰, and 7.94–10.13 mg/L, respectively. Shad were fed satiation rations (3 % body weight/d) of a 1:1 mixture of 370 micron Hikari plankton feed and 0.6–0.8 mm Silver Cup sinking trout feed (Nelson & Sons, Inc., Murray, Utah). Threadfin shad experiments were completed between July 27 and August 6, 2007.

Striped Bass

Wild juvenile striped bass were collected from the TFCF and held at the TAF in the same manner as delta smelt and threadfin shad. In January 2008 approximately 600 striped bass were transported to Reclamation's Denver Aquaculture Facility (DAF; Denver, CO). Striped bass were held in black 757-L cylindrical fiberglass tanks receiving continuous flows (12.1 ± 1.0 L/min) of well water. Total ammonia nitrogen, pH, NaCl, conductivity and O_2 were monitored daily and maintained at the following levels: 0.0–0.1 mg/L, 7.7–8.2, 0.0–0.3 ‰, 414–565 µs/cm, and 7.6–10.4 mg/L, respectively. Striped Bass received satiation rations (3 % body weight/d) of 1.4–2.0 mm Silver Cup crumbled sinking trout feed (Nelson & Sons, Inc., Murray, Utah). Experiments testing striped bass were completed between February 23 and April 17, 2008.

Chinook Salmon

Hatchery-reared juvenile fall-run Chinook salmon from California Department of Fish and Game's Mokelumne River Fish Hatchery (Clements, California) were transported to the DAF in January 2008. Chinook salmon were held under the same conditions and provided the same food and feeding regime as striped bass. During holding TAN, pH, NaCl, conductivity and O_2 were monitored daily and maintained at the following levels: 0.0–0.2 mg/L, 7.5–8.1, 0.0–0.4 ‰, 296–722 µs/cm, and 7.82–10.19 mg/L, respectively. Chinook salmon experiments were completed between April 25 and May 28, 2008.

Fish Feeding Regime

Test fish used in this study were fasted for 12 h. This feeding regime was chosen to simulate typical pre-transport conditions at SSJRD fish collection facilities. Fish salvaged at the TFCF are normally held in fish-holding tanks for up to 8 h, when smelt are present at the facility, and up to 12 h, when salmon are present at the facility, prior to loading and transport (Sutphin and Wu 2008). The pre-test fasting period was selected because employees at fish salvage facilities have

no control over the feeding regimes of salvaged fish; there is even anectodal evidence at the TFCF that some fishes continue to feed as they transit the facility until they reach the holding tanks (B. Bridges, Bureau of Reclamation, personal communication). Given the possible variation in stomach fullness and temperature-mediated gastric evacuation rates of test fish, it is likely these experimental methods resulted in increased variance. Three to four days fasting is generally recommended to ensure all consumed food has been absorbed or evacuated (Barton and Schreck 1987). However, given the applications of this research, it was deemed more important to mimic conditions at the TFCF.

Experimental Methodology

Fish were acclimated at ≤ 1 °C/d to temperatures encompassing the seasonal range encountered at the TFCF (Craft *et al.* 2008). Delta smelt were acclimated to 12, 15, 18, and 21 °C, threadfin shad were acclimated to 12, 18, 24, and 28 °C, Chinook salmon were acclimated to 12, 16, 20 and 24 °C, and striped bass were acclimated to 12, 18, 24, and 28 °C. Experiments were conducted during the day within the same general diel period daily (0700–1400) to minimize the effects of diel variation in MO_2 and M_{TAN} (Fivelstad *et al.* 1990, Lyytikainen and Jobling 1998a). Because water pH can have a significant effect on M_{TAN} (Wright and Wood 1985, Randall and Tsui 2002) pre-experimental and experimental pH levels were monitored carefully and maintained between 7.3–8.2 to simulate water pH conditions (mean annual pH = 7.5) occurring at the TFCF (Craft *et al.* 2008).

Measurements of MO_2 and M_{TAN} rates were made on individual fish placed in acrylic flow-through respirometers (volume = 225 ml, length = 180 mm) submerged in a temperature-controlled water bath. Threadfin shad and delta smelt trials were replicated 12–13 times per temperature/treatment combination, and striped bass and Chinook salmon trials were replicated 11–12 times per temperature/treatment combination. At the onset of the loading period fish were held in water containing NaCl (5 ‰) and Polyaqua^{TM} (0.2 ml/L; Kordon LLC., Hayward, California) to reduce osmoregulatory imbalances associated with handling stress, in addition to aiding the regeneration of the slime coat (Carmichael *et al.* 1984b, Swanson *et al.* 1996).

Test chambers were covered with shade cloth to maintain semi-dark conditions, minimizing fish activity and stress, and, to an extent, to simulate conditions present in fish-hauling trucks during transport. Though never directly measured, given the design, it is assumed the inside of the TFCF transport truck is completely dark. Light levels in experimental respirometers were not measured. Prior to the initiation of data collection, delta smelt and threadfin shad were given a 6-h respirometer adjustment period, while Chinook salmon and striped bass were given a 12-h adjustment period. Adjustment periods were based on pilot data suggesting Chinook salmon and striped bass would achieve baseline resting-routine MO_2 within 12 h. Pilot work with delta smelt and shad determined

that they would generally survive chamber confinement for 6-h, but it was not possible to get a consistent resting-routine MO_2 for these species, so a 6-h period was used.

Following the adjustment interval, water flow (ml/min) was adjusted until differences in O_2 concentrations between effluent and affluent water was approximately 1.0 mg/L, as recommended by Cech (1990). Effluent and affluent water samples were simultaneously collected using twice-flushed 1-ml and 5-ml syringes for measurement of oxygen and TAN concentrations, respectively. Dissolved oxygen concentrations were measured with Strathkelvin 1302 electrodes connected to a Strathkelvin O_2 Interface Model 928 (detection limit 0.01 mg/L; North Lanarkshire, Scotland). A pH probe (LaMotte pHPLUS digital pH meter, Chestertown, Maryland) and ammonia nitrogen electrodes (Lamotte) were used to measure TAN concentration (detection limit and accuracy of 0.01 mg/L).

After the measurement of pre-stress MO_2 and $M_{TAN,}$ respirometry chambers were partially drained until the water depth was approximately 1 cm (mean volume = 60 ml), a process that took an average of 7.9 sec (Figure 1). Fish were partially air-exposed for 30 sec and then the chambers were refilled. This standardized stressor exposed fish to a process that simulated the fish loading process at SSJRD facilities where salvaged fish are removed from holding tanks in a partially dewatered bucket and transferred to a fish transport truck. Measurements of MO_2 and M_{TAN} were resumed 20 min after the partial air-exposure (sufficient time for at least one full exchange of water through the experimental chambers) and continued at 20-min intervals for an additional 80 min. The 80-min test periods were selected because the mean time for the completion of fish-loading, fish-transport, and fish-release procedures at the TFCF is approximately 80 min (Sutphin and Wu 2008).

Oxygen consumption rates were calculated using the standard flow-through respirometry equation (Cech 1990). Ammonia excretion rates were calculated using the modified flow-through respirometry equation shown below:

$$M_{TAN}\ (\text{ml/min}) = Q \times (TAN_i - TAN_e) \qquad \text{Equation 1}$$

where Q is the flow rate of water passing through the respirometry chamber (ml/min), TAN_i is the TAN concentration (mg/L) of the affluent water, and TAN_e is the TAN concentration (mg/L) of the effluent water. The temperature coefficient values for both MO_2 and M_{TAN} were also calculated. Temperature coefficient (Q_{10}) defines rate of biological change (change in MO_2 and M_{TAN}) resulting from increasing temperature 10 °C.

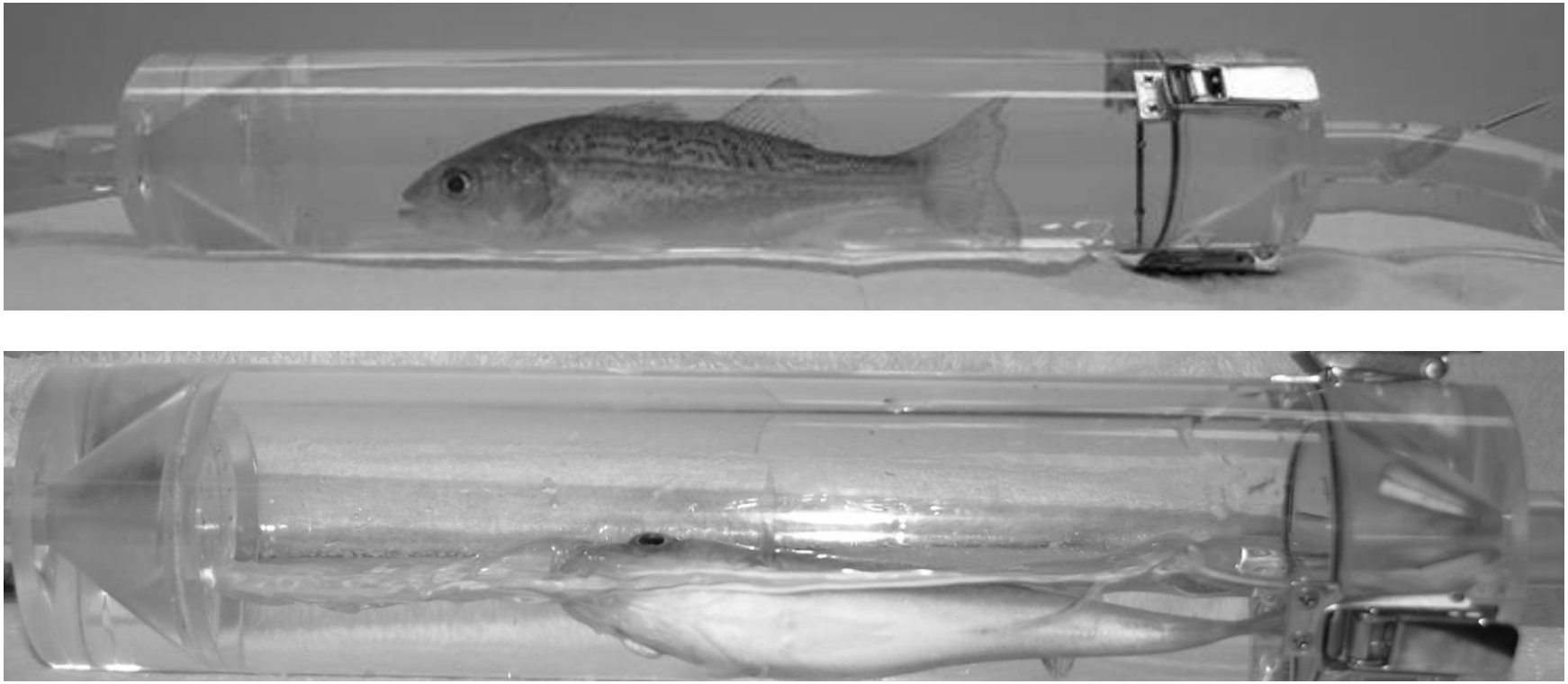

Figure 1.—Respirometry chamber (volume = 225 mL, length = 180 mm) used to measure oxygen consumption and ammonia production rates of test fish (striped bass shown in image; top image). Standardized stressor, constituting nearly complete draining of respirometer water and exposure to the atmosphere, used to simulate fish loading stress during testing (bottom image).

Ammonia Quotient

The primary end product of protein metabolism in most freshwater fish is ammonia (Eddy 2005). Therefore, when fish are exposed to aerobic conditions, an estimate of the amount of the fish's total energy production contributed by protein catabolism can be made by comparing the ratio of oxygen consumption to ammonia production, and is termed the ammonia quotient. The ammonia quotient (AQ) is defined as a pollution loading rate, because it provides an indication of the amount of ammonia produced per unit of oxygen consumed, and is of particular interest when establishing appropriate diets and water requirements during fish culture and fish-transport operations (Lyytikainen and Jobling 1998b). The AQ was calculated as the mean moles of ammonia produced divided by the mean moles of O_2 consumed for each individual species tested (see Kutty 1978).

RESULTS

Delta Smelt

Delta smelt WW and total lengths (TL) ranged from 4.1–8.6 g, and 70–103 mm, respectively, and did not differ significantly across test temperatures (ANOVA, $P > 0.05$; Table 1). Delta smelt exhibited behavior symptomatic of confinement stress when placed in the test chamber, and frequently swam forcefully into the screen at the upstream end of the respirometer. Even with a reduced acclimation period, some smelt mortality occurred at all temperatures, including two fish at 12 °C, four at 15 °C, five at 18 °C, and five at 21 °C.

Delta smelt MO_2 values were significantly affected by water temperature and time (RMANOVA, $P < 0.05$). Mean pre-stress MO_2 of Delta Smelt at 15 and 18 °C were 1.17 and 1.61 times higher than 12 °C values, but at 21 °C the difference was only 1.04; similar differences were observed for the other sampling times (Figure 2). Smelt MO_2 increased following the simulated loading stress, peaking at 20 min and slowly declining to near pre-stressor levels at 80 min, irrespective of temperature (Figure 2). Mean pre-stress M_{TAN} of delta smelt increased with temperature between 12 and 21 °C (Figure 3). Smelt M_{TAN} were positively correlated with increasing temperature, increasing by up to 2.45 times between 12 °C and 24 °C values. The M_{TAN} for the smelt was generally unaffected by time (post-stress), with the exception of the 24 °C treatment where M_{TAN} values were substantially elevated at 20 and 40 min post-loading stress and slowly declined to near pre-stressor values by 80 min. The calculated smelt MO_2-Q_{10} values were 1.7 (12–15 °C) and 2.9 (15–18 °C), while $M_{TAN}Q_{10}$ values were 3.8 (12–15 °C) to 8.0 (15–18 °C); the 21 °C treatment was excluded from Q_{10}

Table 1.—Experimental conditions and sizes of fish used in measurements of changes in MO_2 and M_{TAN} as a function of simulated loading stress (30-sec dewatering) of four fishes from California's Sacramento-San Joaquin River Delta. Striped bass weight at 28 °C was significantly different then weights at all other test temperatures ($P < 0.05$, ANOVA). No other statistical differences were detected across test temperatures within species. Interspecific comparisons were not made due to differences in experimental conditions and sampling methodology. Values are expressed as means ± 1 SD.

Species	Sample size	Temperature (°C)		Wet weight (g)	Total length (mm)
		Target	Actual		
Delta smelt	12	12	12.1 ± 0.3	6.2 ± 2.2	94 ± 10
	13	15	15.1 ± 0.3	5.9 ± 1.5	92 ± 7
	15	18	18.0 ± 0.3	6.3 ± 1.0	95 ± 3
	13	21	21.2 ± 0.3	6.2 ± 1.8	93 ± 9
Threadfin shad	12	12	12.0 ± 0.1	5.9 ± 1.2	84 ± 6
	11	18	18.0 ± 0.2	6.1 ± 0.9	83 ± 3
	11	24	24.2 ± 0.3	5.8 ± 0.6	83 ± 4
	12	28	27.6 ± 0.4	6.0 ± 1.2	83 ± 5
Striped bass	13	12	12.0 ± 0.2	9.7 ± 1.5	105 ± 6
	13	18	17.9 ± 0.1	9.5 ± 1.6	106 ± 5
	13	24	24.1 ± 0.1	11.1 ± 1.7	108 ± 4
	13	28	28.2 ± 0.2	14.4 ± 3.6	115 ± 7
Chinook salmon	13	12	12.0 ± 0.2	9.1 ± 1.4	99 ± 5
	13	16	16.3 ± 0.1	9.7 ± 0.9	101 ± 1
	13	20	21.2 ± 0.1	9.5 ± 2.6	100 ± 9
	13	24	24.1 ± 0.1	10.5 ± 2.0	101 ± 7

calculations because of the drop in MO_2. Ammonia quotient (AQ) levels for delta smelt ranged from 0.05 at 12 °C to 0.12 at 21 °C, suggesting the percent of smelt energy production covered by protein catabolism is positively linked to temperature, and ranges from 17–44 %. Smelt carbon dioxide production rates at 12, 15, 18 and 21 °C were estimated to be 0.08, 0.11, 0.13, and 0.10 mg CO_2/g/h, respectively.

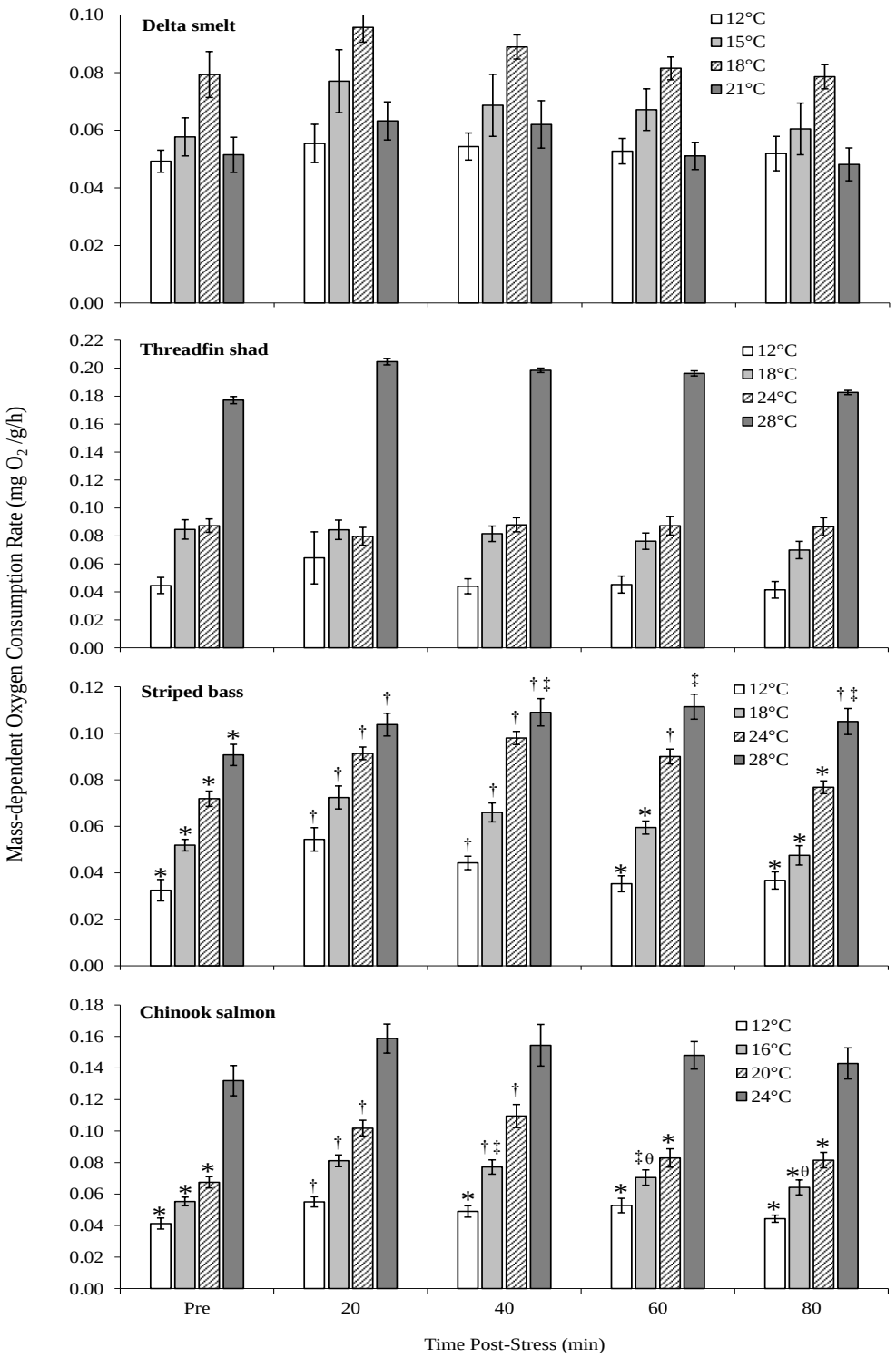

Figure 2.—Pre-stress and post-stress (20–80 min) mass-dependent oxygen consumption rates (mean ± 2 SE) of delta smelt, threadfin shad, striped bass, and Chinook salmon exposed to four temperatures. Different symbols above treatment means indicate significant differences across treatment medians (RMANOVA, $P < 0.05$).

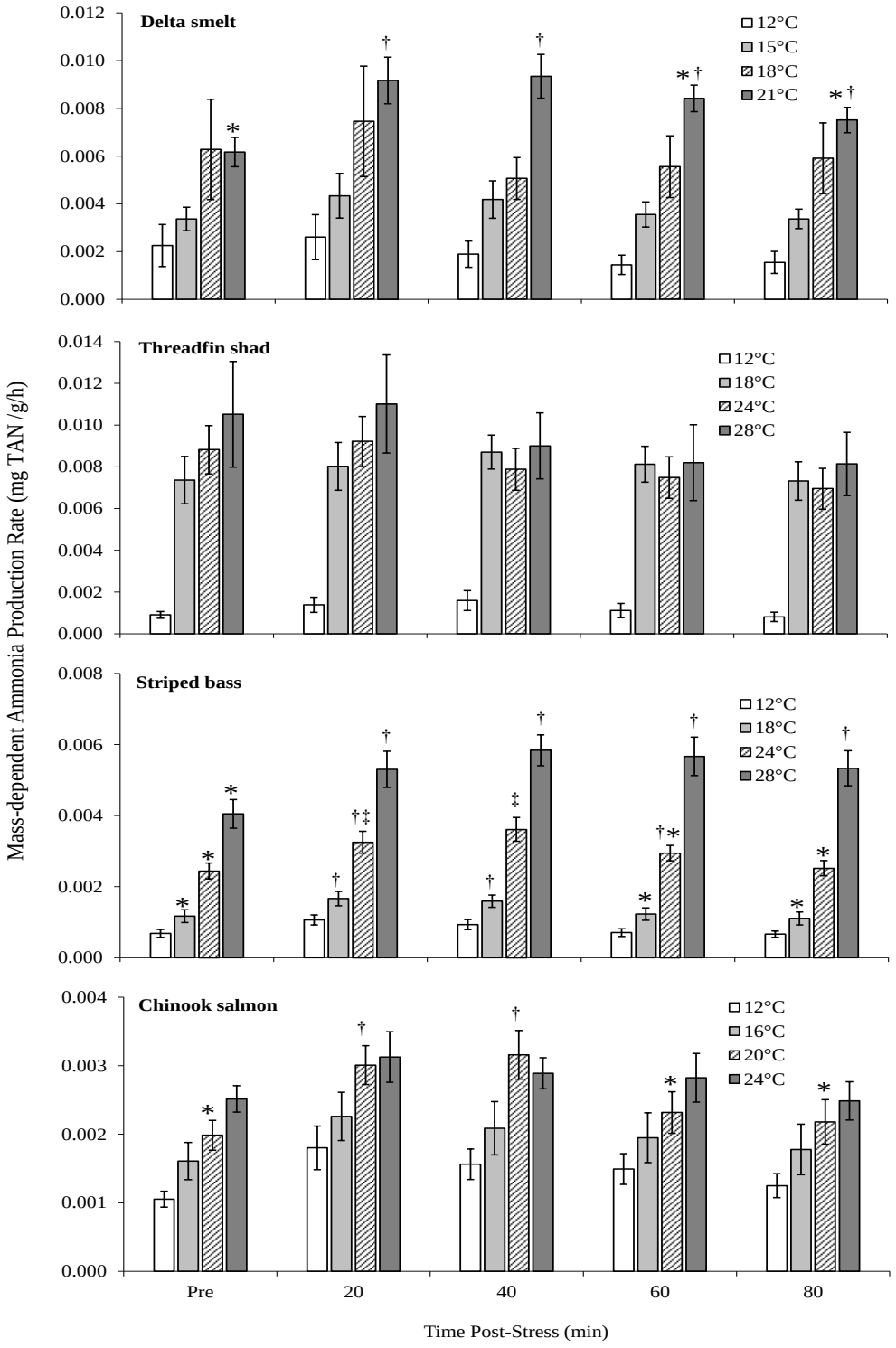

Figure 3.—Pre-stress and post-stress (20–80 min) mass-dependent ammonia production rates (mean ± 2SE) of delta smelt, threadfin shad, striped bass, and Chinook salmon exposed to four temperatures. Different symbols above treatment means indicate significant differences across treatment medians (RMANOVA, $P < 0.05$).

Threadfin Shad

Threadfin shad WW ranged between 3.2–8.2 g and TL ranged from 73–92 mm, and both were statistically similar across test temperatures (ANOVA, $P > 0.05$; Table 1). Threadfin shad behaved similarly to delta smelt when confined to the respirometers. Throughout testing, one, two, four, and four shad died when exposed to 12, 18, 24, and 28 °C, respectively. Both mean pre-stress MO_2 (Figure 2), and M_{TAN} increased (Figure 3) as temperature increased from 12 to 28 °C (RMANOVA, $P < 0.01$). Shad MO_2-Q_{10} values ranged from 1.1 (18–24 °C) to 5.9 (24–28 °C). Shad M_{TAN}-Q_{10} ranged from 1.4 (18–24 °C) to 32.9 (12–18 °C). Ammonia quotient (AQ) for threadfin shad ranged from 0.02 at 12 °C to 0.10 at 18 °C, indicating percent of shad energy production covered by protein catabolism ranges from 8–37 %. Carbon dioxide production rates of shad exposed to 12, 18, 24 and 28 °C were estimated as 0.09, 0.12, 0.11, and 0.29 mg CO_2/g/h, respectively. Simulated loading stress affected both MO_2 (Figure 2) and M_{TAN} (Figure 3) of threadfin shad tested at all temperatures (RMANOVA, $P < 0.05$), though the differences were likely not biologically significant, as, of all species tested threadfin shad MO_2 and M_{TAN} tended to remain the most uniform pre- and post-stress, with slight increases at 20 min post-loading stress and then a slight decline to values close to the pre-stressor range.

Striped Bass

Striped bass WW ranged between 6.2–22.1 g, and TL ranged between 92–133 cm (Table 1). Striped bass acclimated readily to the respirometry chambers, exhibited minimal activity during experiments, and no fish died during testing. There were no differences in mean TL of striped bass compared across treatments (ANOVA, $P > 0.05$), however, fish tested at 28 °C averaged 9% heavier than those tested at 12 and 18 °C (ANOVA, $P < 0.05$). Striped bass mean resting-routine MO_2 and M_{TAN} increased as test temperatures increased from 12 to 28 °C (RMANOVA, $P < 0.05$; Figure 2; Figure 3). Striped bass MO_2-Q_{10} values ranged from 1.7 (18 –24 °C) to 2.2 (12–18 °C). Striped bass M_{TAN}-Q_{10} ranged from 2.5 (12–18 °C) to 3.6 (24–28 °C). Ammonia quotients for striped bass ranged from 0.02 at 12 °C to 0.04 at 21 °C, indicating the percentage of energy production covered by protein catabolism generally increased with temperature and ranged from 8–17 %. Carbon dioxide production rates of fish exposed to 12, 18, 24 and 28 °C were estimated as 0.08, 0.10, 0.13, and 0.15 mg CO_2/g/h, respectively. Both oxygen consumption rates and M_{TAN} of striped bass increased when exposed to simulated loading stress, at all temperatures, 20 min post-stress (RMANOVA, $P < 0.05$; Figure 2 and 3), except at 12 °C, when no difference in pre- and post-stress M_{TAN} levels were detected. Interestingly, the rate at which striped bass recovered (*i.e.*, time required for fish to achieve pre-stress MO_2 and

M_{TAN}) decreased as temperature increased (Figure 2). However, when exposed to the warmest test temperature (28 °C) striped bass MO_2 and M_{TAN} did not recover from simulated loading stress within the 80-min test period.

Chinook Salmon

Chinook salmon WW ranged from 5.7–14.5 g, and TL ranged from 86–117 mm, and both were not significantly different across test temperatures (ANOVA, $P > 0.05$; Table 1). Chinook salmon appeared to acclimate readily to the respirometers, exhibited minimal activity during acclimation, and experienced no experimental mortality. Mean resting-routine MO_2 and M_{TAN} of Chinook salmon increased with increasing temperatures between 12–24 °C (RMANOVA, $P < 0.05$; Figures 2 and 3). Salmon MO_2-Q_{10} ranged from 1.7 (16–20 °C) to 5.4 (20–24 °C). M_{TAN}-Q_{10} values ranged from 1.7 (16–20 °C) to 2.9 (12–16 °C). Ammonia quotients for salmon ranged from 0.02 at 24 °C to 0.03 at all other test temperatures, indicating the percentage of energy production covered by protein catabolism was generally unaffected by temperature and ranged from 7–11 %. Carbon dioxide production rates of fish exposed to 12, 16, 20 and 24 °C were estimated as 0.08, 0.11, 0.14, and 0.22 mg CO_2/g/h, respectively. Chinook salmon MO_2 and M_{TAN} were affected by simulated loading stress at all temperatures except 24 °C, and 12 and 24 °C, respectively (RMANOVA, $P < 0.05$). However, M_{TAN} of Chinook salmon tested at 24 °C did not drop to pre-stress routine rates within the 80-min test period.

DISCUSSION

This study demonstrated mean routine and post-stress MO_2 and M_{TAN} of delta smelt, threadfin shad, striped bass and Chinook salmon generally increased with increasing temperature, a response common to most freshwater fish (Brett and Groves 1979, Alsop *et al.* 1999). Study results also indicated thirty seconds of partial air exposure affected delta smelt, Chinook salmon, and striped bass MO_2 and M_{TAN}, though the significance and magnitude of stress appears to be species–specific. Interestingly, while both Chinook salmon and striped bass displayed rapid increases in MO_2 and M_{TAN}, these species also displayed the most rapid recovery, while threadfin shad and delta smelt values tended to change less, suggesting they may have already experienced a high level of physiological stress, so the added effect of the simulated loading stressor did not appear to have an additive impact. Also, Chinook salmon and striped bass experienced a reduced ability to cope with simulated fish-loading stress, and return to pre-stress MO_2 and $M_{TAN,}$ as temperatures increased.

Of the species tested delta smelt and threadfin shad tended to have the highest "resting-routine" MO_2 and M_{TAN} over the tested temperatures, and exhibited

similar MO_2 and M_{TAN} when tested at 12 and 18 °C. Also, delta smelt, and threadfin shad in particular, broadly showed the most muted response to simulated fish-loading stress. This is illustrated by relatively low mean changes in MO_2 and M_{TAN} following simulated loading stress for delta smelt (+11–32 %) and threadfin shad (-10–+35 %). This is possibly evidence of a higher level of sensitivity to general physiological stress, as is supported by other findings on smelt (Swanson *et al.* 1998, Swanson *et al.* 2005, Swanson and Cech 1995) and shad (B.Bridges 2009, Bureau of Reclamation, personal communication). In response to confinement in respirometers, both delta smelt and threadfin shad displayed escape behaviors throughout the recovery period. Stress (Barton *et al.* 1986, Barton and Schreck 1987), increased activity (Rychly and Marina 1977) and swimming (Kutty 1969, Beamish 1970), result in increased MO_2, and likely increased M_{TAN} (Wiggs *et al.* 1989, Alsop *et al.* 1999, Randall and Tsui 2002) in fish. Therefore the elevated threadfin shad and delta smelt pre-stress MO_2 and M_{TAN}, and their limited response to simulated loading stress were probably a function of heightened stress and activity during the post handling recovery period, and throughout testing, as has been reported in other species (Barton *et al.* 1986, Randall and Tsui 2002). A direct corollary of this assumption is that pre-stress MO_2 and M_{TAN} of delta smelt and threadfin shad should not be considered routine rates as defined by Cech (1990), but are more analogous to active rates. Nevertheless, these rates are likely representative of the MO_2 and M_{TAN} salvaged delta smelt and threadfin shad experience at fish collection facilities, given the confined nature of the loading and transport tanks. Chinook salmon and striped bass typically had lower routine MO_2 and M_{TAN} than delta smelt and threadfin shad; these fish did become quiescent within the test chambers, and therefore these measured rates could be considered resting-routine as defined by Cech (1990). Interestingly, Chinook salmon tended to have slightly higher MO_2 and M_{TAN} compared to striped bass when tested at 12 and 24 °C.

Of the factors that can affect MO_2 and M_{TAN}, a likely source of high variation in the observed rates was our pre-test feeding regime. Gut fullness can have a significant effect on both MO_2 and M_{TAN} of fish (Jarboe 1995, Forsberg 1997), and rate of gut evacuation is dependent upon meal size and temperature (Persson 1981, He and Wurtsbaugh 1993). Fish used in the study actively fed in their holding tanks, but because individual fish were not isolated prior to testing, the degree of gut fullness of randomly selected specimens following the 12-h fasting period cannot be estimated. Gut fullness is commonly not of concern in similar studies, as a lengthy pre-experimental period is typically provided to assure all gut contents have been evacuated (Cech 1990). When fish are exposed to warm temperatures (> 20 °C) complete gut evacuation generally occurs within 12 h (Windell *et al.* 1976, Persson 1979, Persson 1982), but at cooler temperatures (2–10 °C) gut evacuation generally takes > 20 h (Elliot 1972, Garcia and Adelman 1985). If applicable, this scenario would result in variations in the proportion of energy allocated for specific dynamic action (SDA), and a subsequent variation in metabolic rates, biased towards over-estimates of resting-routine energy consumption. The magnitude of the over-estimation could range

from 5 to at least 23 % based on literature (McCue 2006). However, because using an upwardly biased estimate of MO_2 and M_{TAN} to set wild fish holding and transport criteria would result in recommendations to hold fewer fish because of assumptions of higher levels of oxygen demand or ammonia production per kg of handled fish, this is not seen as a detrimental finding for this particular application.

Chinook salmon, delta smelt, and striped bass MO_2 and M_{TAN} tended to increase in response to simulated loading stress. It is generally accepted that increases in MO_2 resulting from stress or exhaustive activity (*e.g.* swimming and struggling) result from a need to repay an oxygen debt (Scarabello *et al.* 1992, Brick and Cech 2002). However, mechanisms behind stress-induced increases in M_{TAN} are relatively untested on freshwater teleosts, and probable explanations include increased blood cortisol levels, an osmoregulatory response, or ammonia production as a result of increased activity of muscle fibers.

Another possible explanation for the observed M_{TAN} response to simulated loading stress is osmoregulatory in nature. Exposure to stress can increase gill permeability (Wendelaar Bonga 1997). This secondary stress response results in reduced plasma sodium and chloride ion levels (Congleton *et al.* 2000, Forsberg *et al.* 2001). It is hypothesized that specialized cells in gills of freshwater teleosts function in exchanging NH_4^+ (essentially H^+) for Na^+, maintaining internal homeostasis (Wood and Marshall 1994, Marshall 1995). This hypothesis is supported by pioneering research conducted by Maetz and Garcia Romeu (1964), whom indicated NH_4^+ injections resulted in an influx of Na^+ ions in goldfish. However, Lin and Randall (1995) suggested the primary mechanism driving Na^+ diffusion is likely not a result of exchange with NH_4^+, but due to H^+-ATPase secreted protons in gill epithelial cells that function in creating favorable channels for Na^+ diffusion. Considering these results, the most likely mechanism responsible for stress-induced increases in M_{TAN} observed in our test organisms are a combined result of increased muscle fiber ammonia production, due to increased struggling and associated elevations in metabolism, as well as elevated cortisol levels, during simulated loading stress.

Exposure to simulated loading stress elicited a similar qualitative behavioral response in all test fish, which included rapid caudal fin movement and gill ventilation, as well as body undulations. Mommsen and Hochachka (1988) indicated a major portion of ammonia production during extensive exercise in fish is a result of deamination of adenlyates in fish muscle. This hypothesis is supported by research indicating M_{TAN} of fish increase with increased activity (Holeton *et al.* 1983, Sukumaran 1986). However, it is clear that further research on ammonia production in the muscle tissue of fish under transport conditions would help to confirm if this is indeed the source of the ammonia.

As previously discussed, Chinook salmon and striped bass MO_2 and M_{TAN} tended to increase post stress, but there was some variation in how temperature affected

each species. The rate at which an organism repays an oxygen debt, and returns to homeostasis post-stress or post-exercise, is a function of the time required for the body's conversion of lactate to glycogen (Brick and Cech 2002); the rate at which a fish returns to pre-stress M_{TAN} levels after stress is most likely related to the time required to flush excess internal ammonia produced by muscles. Chinook salmon and striped bass exposed to their lower range of test temperatures were able to achieve internal homeostasis within the 80-min test period. To our knowledge, this is the first study to measure freshwater fish's M_{TAN} response to stress so rapidly after exposure to the stressor and over such short time intervals. However, Elliot (1969) reported MO_2 of juvenile Chinook salmon exposed to handling stress at temperatures between 5–14.3 °C and tested in a raceway pond (2.4 × 24.4 m) returned to mean pre-stress levels within 30 min post-stress. Similarly, Davis and Schreck (1997) reported MO_2 of juvenile Coho salmon (*O. kisutch*) exposed to handling stress at 13 °C returned to pre-stress levels within 4 h post-stress; and Brick and Cech (2002) reported MO_2 of handled young-of-year striped bass returned to pre-stress levels within 2 h post-stress.

Though fish MO_2, and likely M_{TAN}, recover rapidly from simulated loading stress, it is important to realize fish may still be recovering from more subtle stress effects well after MO_2 and M_{TAN} have declined, as stress-induced fluctuations in plasma electrolyte and solute concentrations may take much longer to return to pre-stress levels (Hille 1982, Nikinmaa *et al.* 1983, Schreck *et al.* 1989). Given the potential effects of predation at fish release sites, and the negative impacts of stress on fish swimming performance (Portz 2007), fish collection facility managers should recognize that plasma constituents such as circulating glucose and cortisol levels, and not MO_2 and M_{TAN}, are likely the "safest" measure of time required for fish to fully recover from loading stress. Nevertheless, it is even less practical to attempt to measure these plasma constituents as part of an adaptive management approach than it is to measure MO_2 and M_{TAN} levels, so the most prudent approach would be to look for combinations of loading and handling scenarios that minimize the changes in the homeostatic state of the fish while simultaneously remaining feasible from a facility management standpoint.

Striped bass required more time to recover from the simulated loading process as temperature increased, and did not recover at 28 °C within the observed time interval. The same thermal effect was observed with Chinook salmon MO_2 as temperatures increased from 12–16 °C. A possible explanation for the observed result is that the higher temperatures moved the fish out of their optimal thermal ranges. Chinook salmon are a coldwater species, displaying optimal growth and preferring temperatures between 11–18 °C (Marine 1997, Myrick and Cech 2002), and are generally unable to tolerate water temperatures above 24 to 25 °C for lengthy periods (Baker *et al.* 1995, McCullough 1999). In comparison, striped bass are a coolwater species preferring temperatures between 13–25 °C (Coutant *et al.* 1984, Stickney 1994), displaying optimal growth at temperatures between 17.8–28.5 °C (Cox and Coutant 1981, Kellogg and Gift 1983), and tolerating temperatures as high as 33.9 °C when acclimated to 30 °C (Stickney 1994, Cook

et al. 2006). Considering the thermal preferences of our test fish, it is likely our experimental thermal regimes exposed Chinook salmon to temperatures well outside of their preferred range, and fish in the higher treatments experienced some thermal stress throughout testing, muting or masking the effects of our standardized stressor. A similar explanation may also apply to striped bass tested at 28 °C.

The effects of stress on MO_2 of Chinook salmon from this study are similar to Elliot's (1969) finding that the MO_2 of juvenile Chinook salmon exposed to non-descript handling stress increased 9–25 % compared to control levels. Interestingly, other species of fish tend to display a greater MO_2 response to similar standardized stressors in comparison to our test fish. Juvenile steelhead and Coho salmon MO_2 increased approximately two-fold when forced to struggle in a vertically oriented test chamber and when exposed to 30-sec of atmospheric exposure in a dip-net, respectively (Barton and Schreck 1987, Davis and Schreck 1997). It is possible differences in response to stress are simply a function of species variation (Pickering *et al.* 1989, Barton 2000), the nature of the stressor (Davis and Schreck 1997), or because our test fish had been exposed to a culture environment for a prolonged period, perhaps reducing their sensitivity to culture-related stressors (Woodward and Strange 1987).

When compared to the results of studies on species related to those described here, the pre-stress MO_2 of delta smelt and juvenile Chinook salmon were slightly lower than reported, but similar to those reported for juvenile striped bass. Swanson and Cech (1995) reported that delta smelt had routine MO_2 of 0.23 at 12 °C and 0.22 mg O_2/g/h at 17 °C, with a Q_{10} of 1.6. Barton and Schreck (1987) and Gallaugher *et al.* (2001) reported juvenile Chinook salmon routine MO_2 of 0.10 mg/h at 8 °C and 0.12 mg O_2/g/h at 10 °C. Elliot (1969) reported group MO_2 of juvenile Chinook salmon increased from 0.1–0.28 mg O_2/g/h as pond raceway temperatures increased from 5.0–14.3 °C, respectively. Kruger and Brocksen (1978) reported MO_2 of juvenile striped bass increased from approximately 0.04 – 0.22 mg O_2/g/h, as temperatures increased from 8–24 °C, and also reported MO_2-Q_{10} levels ranging from 1.4 (16–24 °C) to 8.1 (12–16 °C). Brick and Cech (2002) reported similar results, and indicated when exposed to freshwater and tested at temperatures of 15 and 25 °C, mean MO_2 of juvenile striped bass were approximately 1.8 and 2.8 mg O_2/h.

There are limited published data on the M_{TAN} of freshwater teleosts, and of the species used in this study only the M_{TAN} of striped bass have been previously published. Altinok and Grizzle (2004) reported M_{TAN} of juvenile striped bass similar to those reported in our research. Also, comparisons across conspecifics indicate our measured M_{TAN}, for all species, are generally similar, and our calculated AQ values are slightly lower (Colt *et al.* 2009), when compared to other freshwater teleosts.

Fish salvage and transport operations at SSJRD fish collection facilities expose fish to a multitude of stressors (Raquel 1989, Sutphin and Wu 2008). Based on prior studies on fish transport and handling, the most stressful portion of the process are likely the methods used to transfer fish into fish-transport trucks (Barton *et al.* 1980, Maule *et al.* 1988; Portz 2007). The results of this study support this prediction, and suggest, as other authors have, that MO_2 is an appropriate means to measure effects of stress on freshwater fish (Barton and Schreck 1987, Cech and Brick 2002). The results also provide evidence that M_{TAN} of fish is an appropriate measure of metabolic rate, as observed Dabrowski (1986), and therefore is also a promising indicator of stress.

When such data are to be applied to fish transport operations, the recommended strategy should be to use a pair of mass balance approaches to determine whether oxygen or TAN will be the limiting factor for the transport containers in question. Oxygen can be rapidly replenished using a well-designed aeration system, as is common on most fish transport vehicles, but TAN is generally not removed from the water (though one could design a physicochemical system using zeolite to do so). Therefore, the oxygen mass balance equation could be used to set target O_2 delivery rates to compensate for the anticipated fish biomass. However, the actual amount of biomass that can be safely transported may be dictated by the M_{TAN} mass balance equation, because the accumulation of ammonia may reach levels of concern; exactly what those levels are would be a function of temperature, pH (Avault 1996) and the species-specific tolerance of ammonia.

The metabolic cost of fish-loading stress, coinciding with possible increases in TAN and CO_2 and reductions in O_2 levels during fish transport operations, should be a concern to fish collection facility managers. Even if measures are taken to ensure adequate fish densities and appropriate water quality levels are maintained during transport, facility mangers would be advised to consider that fish-loading stress (Wicks, unpublished data as cited in Randall and Tsui 2002), and reduced oxygen concentrations (Alabaster and Lloyd 1982, Alabaster *et al.* 1983) likely increase the toxicity of ammonia to fish. Similarly, stress (Portz 2007), elevated ammonia (Shingles *et al.* 2001, Wicks *et al.* 2002, McKenzie *et al.* 2003), elevated carbon dioxide (Dahlberg *et al.* 1968), and reduced oxygen (Jones 1971, Domenici *et al.* 2000), reportedly affect the swimming performance and activity of fish, and therefore their ability to evade predation at release sites (Mesa 1994, Domenici *et al.* 2007). This may be of a greater concern than observed in this study because it only simulated stressors associated with one phase of the fish salvage and transport process, and Barton *et al.* (1986) showed how multiple repetitive stressors can have a cumulative effect on the physiological response in fish.

RECOMMENDATIONS

If conditions are quiescent, the short-duration truck transport that occurs from the TFCF may provide sufficient time for fish to recover from loading-stress when transported in cool to moderately warm (~12–20 °C) water temperatures. However, elevated densities, sloshing, and deteriorating water quality conditions likely do not contribute to a quiescent environment that promotes fish recovery. Also, when exposed to warmer water temperatures, our results suggest it takes fish prolonged periods (> 1 h) to recover from loading stress. If it is a goal to release fish that have fully recovered from stress, a significant (~2 h) post-transport holding period may be required. This approach is not efficient, as it requires a Fish Diversion Worker to remain at the release site while fish recover, and a means to ensure water quality doesn't worsen during this period would need to be devised. Therefore, instead, fishery managers should take all necessary measures during fish-loading to reduce handling and confinement stress, and use water-to-water transfers during fish-loading. Facility personnel should take the necessary precautions to attempt to minimize overloading of fish in fish-loading buckets that may expose fish to dewatering, overcrowding, and possibly atmospheric conditions. Employing the use of multiple fish holding tanks when fish are entering the facility in elevated densities (splitting total fish across multiple tanks), or transferring a portion of fish using a vacuum-type pump (Transvac Fish Vacuum Pump, www.transvac.com/) from a single tank may permit transference and loading (and transport if necessary) of fish at lower densities.

When logistically appropriate, fish should be transported near their lower range of tolerable temperatures, as a means to reduce MO_2 and M_{TAN}, and possibly limit the effects of fish-loading stress. Because TFCF fish are salvaged and maintained in holding tanks at the same temperature as the southern SSJRD, there is no control over the temperature fish enter the facility. However, at elevated temperatures (> 20 °C) 18 °C well water, mixed with salt to achieve 8 ‰ NaCl levels, could be utilized to gradually drop transport tank water temperatures. This will likely placate fish stress response, but could also allow internal transport tank temperatures to be more similar to the slightly cooler temperatures commonly measured at Sacramento River release sites. It is commonly accepted that rates of temperature change, to maintain fish health, should not exceed 1°C/d (Wedemeyer 1996; Portz *et al.* 2006). Given TFCF operations, this is likely an unacceptable consideration, and a more rapid rate of temperature decrease (~1 °C/5 min) would be necessary. If this technique is utilized further investigation regarding rate of thermal change and maximum decrease in temperature should be considered. Another means to maintain cooler temperatures, particularly when atmospheric temperatures exceed SSJRD water temperatures, is to ensure the transport tank is not filled too early prior to a haul-out, thereby minimizing increases in internal temperatures prior to fish loading.

Recently, the TFCF began utilizing newer and higher volume (9,462 l) fish-haul tanks. The TFCF fish-haul trucks can be provided pure oxygen via oxygen cylinders (the rate of O_2 production in the truck still needs to be determined), likely making low O_2 levels not a limiting factor during transport. Also, these trucks are equipped with a degassing system, and though this system also needs to be evaluated, it may make elevated CO_2 levels of lesser concern and not the limiting factor during transport. However, the current truck needs to be evaluated to determine O_2 production, CO_2 degassing, and to measure the true transport water volume (*i.e.*, volume of water at start and volume of water lost during transport). Once these parameters have been evaluated, the data collected during the current study can be utilized, considering optimal or maximum/minimum levels of TAN, CO_2, and O_2 that can be achieved during transport, to determine which water quality parameter is likely most limiting and what is the temperature dependent density of fish that can be transported without achieving harmful levels of said parameter. Considering the cumulative and interacting effects of stress and adverse water quality conditions, we recommend maintenance of fish transport water quality levels well within recommended limits (see Wedemeyer 1996) during fish-transport operations. However, a well-informed panel of managers and biologists should be utilized to select "optimal" water quality conditions that should be established as the standard when determining maximum densities of fish during transport.

ACKNOWLEDGMENTS

Funding for this project was provided by the Bureau of Reclamation, Tracy Fish Collection Facilities Research Program and Materials and Standards Program. We thank Dr. B. Johnson, Dr. N. Grigg, and two anonymous reviewers for suggestions that have helped to improve this document. The study design was improved with input from R. Silva, B. Bridges, B. Bridges, S. Hiebert, Dr. D. Portz and members of the Tracy Technical Advisory Team. M. Brandt, C. Hueth, B. Wu, R. Reyes, D. Reed, M. Trese and M. Trask provided technical support while caring for fish and conducting laboratory studies. We thank the Tracy Fisheries Research Group for providing threadfin shad and striped bass, the Mokelumne Fish Hatchery for providing Chinook salmon, and University of California at Davis's Delta Smelt Culture and Conservation Laboratory for providing delta smelt.

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