RECLAMATION
Managing Water in the West

Effects of Short-term Holding on Fishes: A Synthesis and Review

Volume 29

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

December 2005

REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. REPORT DATE *(DD-MM-YYYY)*
December 2005

2. REPORT TYPE
Final

3. DATES COVERED *(From - To)*

4. TITLE AND SUBTITLE
Effects of Short-Term Holding on Fishes: A Synthesis and Review

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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One Shields Avenue, Davis CA 95616-8751
Bureau of Reclamation, Technical Service Center, Fisheries Applications and
Research Group, D-8290, PO Box 25007, Denver CO 80225-0007

8. PERFORMING ORGANIZATION REPORT NUMBER
Volume 29

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
Bureau of Reclamation, Tracy Fish Collection Facility, TO-410,
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

Collecting, handling, sorting, holding, and transportation in aquaculture, stocking programs, fish salvage, and commercial and sport fisheries can be stressful to the affected fishes. Stress-related effects of short-term holding are influenced by water quality, confinement density, holding container design, and agonistic and predation-associated behaviors. These effects can be manifested as suppressed immune systems, decreased growth, poor swimming performance, loss of reproductive capacity, or death. Holding tolerance may depend upon the species, life stage, genetic background or strain, previous exposure to stress, and behavior of the held fish. Temperature, dissolved oxygen, salinity, carbon dioxide, pH, alkalinity, hardness, ammonia and nitrite are the most common water quality parameters affecting physiological stress. High fish densities and holding container designs may also compromise survival and immune function by affecting water quality and aggressive fish interactions. Lastly, fishes held for relatively short durations are influenced by agonistic behaviors associated with competition, cannibalism, predation, and nascent dominance hierarchies. This synthesis summarizes literature concerning the effects of short-term holding on the condition of fishes and provides a review to assist researchers and managers in working towards implementing improvements for fish collection, holding, and transport, especially at fish salvage facilities in the South Delta, California.

15. SUBJECT TERMS
fish physiology, stress, holding, transport, literature review, synthesis, review, summary, water quality, tolerance, reproductive capacity, aquaculture, sorting, confinement density, predation, container design swimming performance

16. SECURITY CLASSIFICATION OF:			**17. LIMITATION OF ABSTRACT**	**18. NUMBER OF PAGES**	**19a. NAME OF RESPONSIBLE PERSON**
					Doug Craft
a. REPORT	**b. ABSTRACT**	**a. THIS PAGE**			**19b. TELEPHONE NUMBER** *(Include area code)*
					303-445-2182

Tracy Fish Facility Studies
California

Effects of Short-Term Holding on Fishes: A Synthesis and Review

Volume 29

by

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December 2005

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Series Editor

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Denver CO 80225-0007

Cover

Fish photography by Rene Reyes, Tracy Fish Collection Facility, Tracy, California.
Design by Doug Craft.

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TABLE OF CONTENTS

Page

Executive Summary v

Introduction 1

Section 1: Water Quality 5
Holding Water Sources 9
Flow Rate and Loading Density 10
Temperature 12
Dissolved Oxygen 14
Ammonia, Nitrite, and Nitrate 16
Salinity 19
pH 20
Carbon Dioxide and the Carbonate Cycle 23
Alkalinity 25
Hardness 26

Section 2: Stocking Density and Confinement 27
Metabolism and Growth 29
Corticosteroid Response 30
Health and Immune Function 32
Survival 33

Section 3: Holding Container Design 34
Circular Tanks 36
Square Tanks 38
Raceway-Type Ponds/Tanks 38
Rectangular Cross-Flow Tanks and Rectangular Mixed-Cell Tanks 41
Oval, Foster-Lucas, and Rectangular Circulating Tanks 41
Silo and Upwelling Tanks 43

Section 4: Behavioral and Predatory Impacts 45

Conclusion and Final Considerations 49

Acknowledgements 50

References 50

Table of Contents—continued

Tables

Table *Page*

1 Water quality variables for different species 6
2 General water quality recommendations for holding of fishes 7
3 Advantages and disadvantages of different tank designs................................35

Figures

Figure ***Page***

1 Physiological responses to stressors during holding and transport....................3
2 CO2, H^+, and ion movement across fish gills from a high pH in water...22
3 Gill permeability and leakage effects at different pH conditions 22
4 Relation between pH and relative proportions of inorganic carbon species of CO_2: H_2CO_3, HCO_3^-, and CO_3^{2-} in solution 24
5 (a) Circular tank design and (b) resulting dead zones, cross-section view......37
6 Square tank design 39
7 Raceway design...39
8 Oval tank design..42
9 Foster-Lucas design 42
10 Rectangular circulating tank design..43
11 Silo tank design..44

EXECUTIVE SUMMARY

Most sources of stress in aquaculture, fish salvage, stocking programs, and commercial and sport fisheries may be unavoidable. Collecting, handling, sorting, holding, and transporting are routine practices that can have significant effects on fish physiology and survival. Nevertheless, an understanding of the stressors affecting fish holding can lead to practices that reduce stress and its detrimental effects.

The stress-related effects of short-term holding are influenced by water quality, confinement density, holding container design, and agonistic and predation-associated behaviors. Physiological demands (e.g., resulting from confinement-related stresses) exceeding a threshold level where the fish can no longer compensate may lead to debilitating effects. These effects can be manifested as suppressed immune systems; decreased growth, swimming performance, or reproductive capacity; even death. Furthermore, holding tolerance may depend upon the species, life stage, genetic background, and behavior of the held fish.

Teleost fishes manifest stress responses, which are categorized primary, secondary, and in some cases tertiary. The primary stress response of teleost fishes involves the release of catecholamines. The primary stress response triggers sequential secondary responses, (e.g., increases in plasma glucose, hematocrit, lactate, heart rate, gill blood flow, gill permeability, lamellar recruitment; decreases in plasma chloride, sodium, potassium, liver glycogen, muscle protein, and metabolic rate). Another key primary stress response is the release of corticosteroids (e.g., cortisol) responsible for physiological preparations to protect against the effects of stressors. Cortisol also maintains long-term hyperglycemia after the catecholamine effects have subsided. Elevation of plasma cortisol induces a wide range of secondary physiological responses in fishes including the stimulation of metabolic and osmoregulatory responses, and immunosuppression, even after recognition of an actual or perceived stress. The secondary responses from catecholamines and corticosteroids may ultimately cascade to tertiary stress responses, which include reduced growth rate, reduced metabolic scope for activity, decreased disease resistance, decreased reproductive capacity, as well as altered behavior and survivability.

Water quality is one of the most important contributors to fish health and stress level. Fish may be able to tolerate adverse water quality conditions; however, when combined with other stressors, fish may be quickly overcome by the resulting physiological challenges. The effects of water quality vary considerably with species, life stage, and previous exposure to stress. Temperature, dissolved oxygen, salinity, carbon dioxide, pH, alkalinity, hardness, ammonia and nitrite are the most common water quality parameters affecting physiological stress. Secondly, high fish densities in holding containers are the most common problem throughout aquaculture facilities, live-fish transfers, and fish salvage operations. Furthermore, the holding container design may also compromise the survival and immune function by affecting water quality, density

and confinement, and aggressive interactions. Design-related factors are controllable. Sufficient oxygen, proper flow or filtering requirements, and holding container shape are some of the most important attributes of holding container design for fishes. Lastly, fishes held for relatively short durations are also influenced by negative interactions, associated with intraspecific and interspecific competition, cannibalism, predation, and determining nascent hierarchies. These interactions can be lethal (i.e., predation) or may act as a vector for pathogens to enter (i.e., bites and wounds). Predation may be a significant source of mortality for fisheries practices that do not sort by size or species while holding.

Stress associated with short-term holding of fishes can have negative effects on overall health and well-being. This review and synthesis identifies and summarizes some of the noteworthy findings on four aspects of short-term holding of fishes: water quality, density/confinement, holding container design, and agonistic behaviors/predation. These four aspects are major factors contributing to the physiology, behavior, and survival of fishes held for a relatively short-term basis. A goal of this paper is to assist researchers and managers in developing improvements for fish collection, handling, and transportation associated with State and Federal fish salvage facilities in the South Delta, California.

INTRODUCTION

There is continuing concern for fish survival when holding fishes for short durations, whether in commercial fishing vessels, sport fishing live-wells, stocking programs, or in fish salvage facilities associated with large water diversions (Burrows and Chenoweth, 1970; Pankhurst and Sharples, 1992; Clearwater and Pankhurst, 1997; Pedersen and Amble, 2001; Cooke et al., 2002). This concern has led to innovations in fish holding container design and reassessment of designs already in use. However, physiological constraints and behavioral characteristics of held fishes have been frequently overlooked when designing new fish holding structures. Understanding the biological processes that occur while fishes are held in tanks or ponds and implementing optimal holding methods should decrease stress and disease susceptibility, thereby increasing survival.

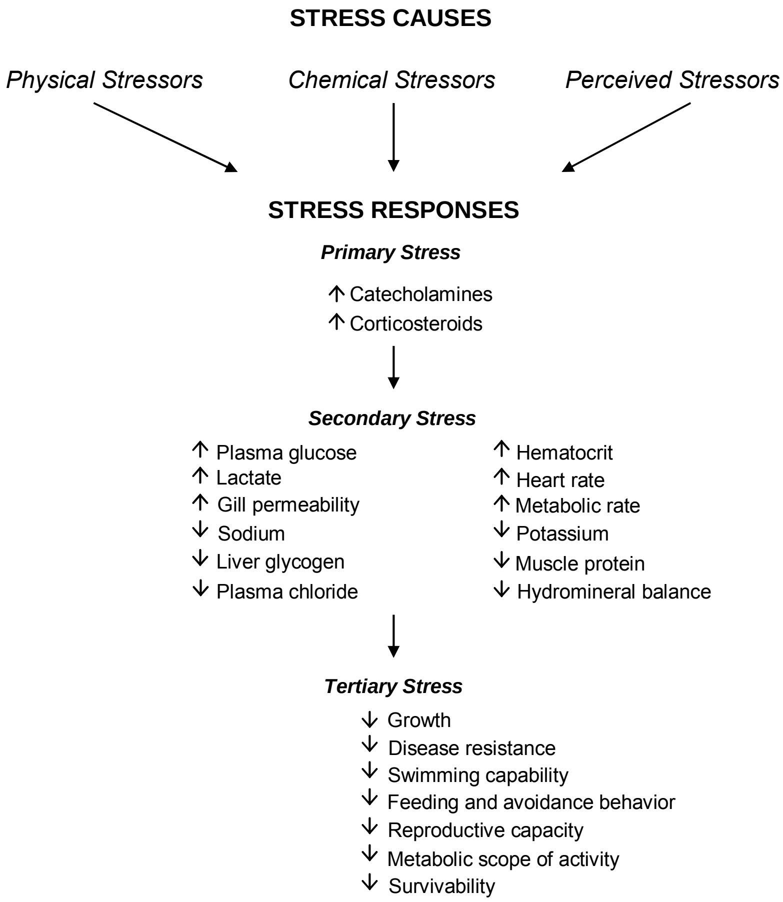
The effects of short-term holding (i.e., a few hours up to 2 weeks) may be influenced by water quality, confinement density, holding container design, predation, and agonistic behaviors. Additional physiological demands (e.g., resulting from confinement-related stresses) that exceed a threshold level can overcome physiological coping mechanisms and lead to debilitating effects. These effects can be manifested as suppressed immune systems, decreased growth, swimming performance, or reproductive capacity, and death (Barton and Iwama, 1991; Barton et al., 2002). Most of the factors (e.g., water quality) influencing stress while fish are detained in a holding structure are, to some degree, under the control of the biologist/culturist. Furthermore, holding tolerance may depend upon the species, life stage, genetic background, and behavior of the held fish (Woodward and Strange, 1987; Kjartansson et al., 1988; Barry et al., 1995; Barton and Iwama, 1991; Barton, 2002). Some species may be unusually sensitive to stress (e.g., quick to startle and jump from tanks, or slow to resume feeding once confined; Clearwater and Pankhurst, 1997). Many fishes survive exposure to stressors, but later die of disease or osmotic dysfunction (Mazeaud et al., 1977). In this review, stress is defined as a condition where a fish's internal homeostasis is impaired from a stressor (Wendelaar Bonga, 1997; Barton et al., 2002).

Stress responses in teleost fishes are manifested as primary, secondary, and in some cases tertiary (figure 1). The primary stress response of teleost fishes involves the release of catecholamines (e.g., epinephrine, norepinephrine) into the circulatory system from chromaffin cells. This stress response also stimulates the hypothalamic-pituitary-interrenal (HPI) axis to release corticosteroids (e.g., cortisol) from the interrenal tissue (Mazeaud and Mazeaud, 1981; Randall and Perry, 1992; Wendelaar Bonga, 1997; Mommsen et al., 1999; Barton et al., 2002). The release of catecholamines into the bloodstream is rapid (Randall and Perry, 1992), while cortisol synthesis has a temperature-related delay of minutes (Wedemeyer et al., 1990; Lankford et al., 2003). Because blood sampling procedures are invasive and thus stressful, these temporal characteristics make it difficult to use plasma catecholamine concentrations as a measurement of stress in cultured or wild fishes. In contrast, the inherent delay of cortisol formation makes it a more useful measurement. In freshwater and marine fishes, plasma cortisol, plasma glucose, hemoglobin, and hematocrit may increase over a 15 minute to 4 hour period in response to capture, handling, and transportation stresses (Robertson et al., 1988; Frisch and Anderson, 2000; Grutter and Pankhurst, 2000).

The primary stress response triggers sequential secondary responses, (e.g., increases in plasma glucose, hematocrit, lactate, heart rate, gill blood flow, metabolic rate; decreases in plasma chloride, sodium, potassium, liver glycogen, and muscle protein; Pickering, 1981; Mommsen et al., 1999; Barton et al., 2002). Secondary responses generally appear within a few minutes to an hour. These changes often remain for longer periods of time compared to the catecholamine and corticosteroid increases, and assist the fish in mobilizing fuels to meet increased energy demands. Hyperglycemia after stress results, in part, from glycogenolysis stimulation from catecholamines to satisfy increased energy demands for a “flight or fight” response (Mazeaud and Mazeaud, 1981). In addition, catecholamines function to regulate some cardiovascular and respiratory functions, including increased blood flow, gill permeability, and lamellar recruitment (Booth, 1979; Randall and Perry, 1992; Wendelaar Bonga, 1997). The resulting increase in gas exchange also increases gill permeability to water and some ions. This can be manifested as a gain in water and loss of small ions from the blood of freshwater fishes and as a water loss and ion influx for marine fishes (Mazeaud et al., 1977; Wendelaar Bonga, 1997).

Along with the catecholamines, cortisol is also responsible for physiological preparations to combat the effects of stressors. An elevation of plasma cortisol induces a wide range of secondary physiological responses in fishes including the stimulation of metabolic and osmoregulatory responses, and immunosuppression after recognition of an actual or perceived stress (Barton and Iwama, 1991). Cortisol is essential to the long-term maintenance of hyperglycemia after the catecholamine effects have subsided (Barton and Iwama, 1991; Mommsen et al., 1999). However, chronic stress (stress that persists over a long period of time) can be maladaptive, resulting in severely compromised immune function and/or energy stores. Non-specific immune function is extremely important serving as a first line of defense, and can be suppressed as a result of increased corticosteroids in the blood (Yin et al., 1995; Clearwater and Pankhurst, 1997; Montero et al., 1999; Ortuño et al., 2001).

The secondary responses may ultimately cascade to tertiary stress responses, which include reduced growth rate, reduced metabolic scope for activity, decreased disease resistance, decreased reproductive capacity, as well as altered behavior and survivability (Wedemeyer et al., 1990; Barton and Iwama, 1991; Mommsen et al., 1999). The extent of tertiary responses may be directly related to the severity and duration of the stressor. Physiological compensation to stress may be achieved, but chronic stress, even at low levels, may impair performance by diverting energy resources that might otherwise be used for routine activities, growth, immune function, and/or reproduction (Barton and Iwama, 1991; Barton et al., 2002). (See figure 1.)



Modified from Barton et al. 2002

FIGURE 1.—Physiological responses to stressors during holding and transport.

Water quality is one of the most important contributors to fish health and stress level. Fish may be able to tolerate adverse water quality conditions; however, when adverse conditions occur from a concert of environmental and biological variables, fish may be quickly overcome by the resulting physiological challenges. The effects of water quality vary considerably with species, life stage, and previous exposure to stress (Wedemeyer, 1996). Therefore, effective management of fishes under confinement commands species-specific knowledge of their biological requirements with respect to water quality and an understanding of their previous exposures or condition when introduced to holding containers.

High fish density in holding containers is the most common problem throughout aquaculture facilities, live-fish transfers, and fish salvage operations (Wedemeyer, 1996). Crowding (i.e., nearing or in excess of the maximum density of fishes in a confined space) depends on a fish's behavioral and physiological requirements for space as the carrying capacity for a given volume of water is approached. Crowding is often the result of an attempt to maximize profits and minimize financial costs of holding fish.

Carrying capacity is greatly governed by water quality and when it is approached or exceeded, may contribute to lowered metabolism, immunosuppression, increased disease transmission, and lowered survival rates.

The design of the structure used to hold the fishes may also compromise the survival and immune function by affecting water quality, fish density and confinement, and agonistic interactions and predation. Fortunately, many of the design-related factors are controllable by engineers, fish managers, and biologists. Sufficient oxygen must be present in the holding structure and proper flow or filtering requirements must be met to remove metabolic wastes. Stress associated with handling during transfer into these fish holding containers can also be severe and have both immediate and long-term effects (Barton and Iwama, 1991). Therefore, it is crucial that holding containers not add additional stress to already compromised fish.

Some additional stresses on fishes held for relatively short durations include predation, cannibalism, and agonistic interactions. These interactions must be effectively managed, keeping losses and damages minimized and stresses at low levels so that immunological function is not impaired (Pickering and Pottinger, 1989; Pottinger and Pickering, 1992; Kubitza and Lovshin, 1999). Negative interactions between fishes in holding tanks can result from intraspecific and interspecific competition, predation, and determining dominance hierarchies. While some of these interactions may not be directly lethal to the fish, fighting-related wounds in the skin can act as a vector for pathogens to enter. Predation may also play a role in mortality for fisheries practices that do not sort fish by size or species while holding (Chang and Liao, 2003a). This is seldom a problem in culture, because there tends to be a continuous grading process that eliminates the size disparity. However, fishes screened and/or salvaged at electrical power plants, irrigation diversions, and municipal water facilities, as well as those fishes harvested and held in containers aboard commercial fishing vessels are likely commingled with larger conspecifics and predators. The presence and perceived threat of these fishes may have detrimental stress effects (Berejikian et al., 2003; Chang and Liao, 2003a).

Our knowledge about short-term holding effects on fishes comes from studies on relatively few species often represented by cultured animals that have not been exposed to a natural environment. Of the more than, 20,000 species of teleost fishes, the salmonids are vastly over represented, and may not have an identical stress response as other fishes (Wendelaar Bonga, 1997). This review was compiled to organize and synthesize current knowledge of short-term holding effects of fishes from literature that either directly or indirectly have incorporated short-term holding and confinement of fishes. Very few studies directly investigate short-term holding effects examining related physiological and behavioral responses. Consequently, there is a need for well-structured investigations of the effects of short-term holding on feeding, growth, swimming ability, immune response, health, reproduction, and survival. Further development and application of techniques for monitoring related physiological effects is also important to evaluating fishes under confinement and culture. The four primary sections of this review and synthesis (water quality, density/confinement, holding container design, and behavioral and predatory impacts) are the major factors contributing to the physiological and behavioral responses, and consequent survival, of fishes held for a relatively short time period.

SECTION 1: WATER QUALITY

Most fishes are dependent on water for the exchange of gases and ions across the gills, and as a diluting agent for metabolic wastes. Yet, water's physical and chemical properties (herein referred to as water quality) are strongly influenced by the atmosphere, sediments, organisms and their wastes, and the flow or exchange rate of a water body. Water quality can be affected by the condition and/or deterioration of the holding systems. Fishes may incur additional energetic costs associated with stress responses from physical and chemical fluctuations in aquatic systems (Barton and Iwama, 1991). Poor water quality, as determined by each species, can prompt the reallocation of energy from secondary (non-essential) physiological processes (e.g., growth, reproduction) towards primary (essential) processes (e.g., metabolism, immune function). Thus, adequate, or preferably "optimal", water quality is essential for holding fish in an environment that will neither activate their stress responses nor alter their normal energy budget. Short-term exposure to poor water quality can result in permanent damage or mortality if physical or chemical variables are allowed to reach lethal levels and/or synergize in a deleterious manner (Carmichael et al., 1984a; Robertson et al., 1987; Erickson et al., 1997; Pavlidis et al., 2003).

Optimal water quality for short-term holding is dependent upon the species, water source, water flow rate, and the fish density in holding containers. A species' water quality requirements will vary with fish health, including previous exposure and life history. When a fish's past exposure and health are not known, water quality remains the most controllable factor for short-term holding. Lethal and stressful physiological limits are known for many aquaculture species to specifically enhance economic gains; however, few experiments have explored the "optimal" water quality for fishes. (See tables 1 and 2.) There are many water quality information sources for long-term and intensive culture of fishes (Pickering, 1981; Cech et al., 1994; Wedemeyer, 1996; Adams, 2002; Timmons et al., 2002). Unfortunately, the information relating to short-term care (specifically, less than 2 weeks) is sparse. Our goal is to highlight the most common water quality-related problems associated with short-term holding and care of fishes.

TABLE 1.—Water quality variables for different species. Note the lack of information about species optimum ranges

Species	Common name	Optimum range	Lower range	Upper range	Reference
Temperature (ºC)					
Salmo trutta	brown trout		0–4	19–30	Spaas, 1960; Frost and Brown, 1967
Acanthopagrus latus	yellowfin sea bream		4.9–9.4	34.8–38.2	Jian et al., 2003
Ictalurus punctatus	channel catfish	25–30			Tucker and Robinson, 1990
Lota lota	burbot		3.3 ± 0.06	31.5 ± 0.12	Hofmann and Fischer, 2002
Fundulus zabrinus	plains killifish			40.5 ± 0.4	Ostrand and Wilde, 2001
Hybognathus placitus	plains minnow			38.8 ± 0.8	Ostrand and Wilde, 2001
Pogonicthys macrolepidotus	splittail		6.5–7.3	29–33	Young and Cech, 1996
Dissolved oxygen (mg/L)					
Fundulus zabrinus	plains killifish		1.25 ± 0.09		Ostrand and Wilde, 2001
Hybognathus placitus	plains minnow		2.08 ± 0.14		Ostrand and Wilde, 2001
Pogonicthys macrolepidotus	splittail		0.6–1.3		Young and Cech, 1996
Scopthalmus maximus	turbot	5–6	3.2 ± 0.3		Pichavant et al., 2001
Dicentrarchus labrax	European Sea bass	5–6	4.5 ± 0.2		Pichavant et al., 2001
Coryphaena hippurus	dolphin fish		4.5–5.5		Lutnesky and Szyper, 1990
Oncorhynchus spp.	salmon/trout		5–6		Westers and Pratt, 1977
Ictalurus punctatus	channel catfish		3		Carter and Allen, 1976
Salinity (ppt)					
Acanthopagrus latus	yellowfin sea bream			54–69	Jian et al., 2003
Fundulus zabrinus	plains killifish			43 ± 0.05	Ostrand and Wilde, 2001

TABLE 1.—Water quality variables for different species. Note the lack of information about species optimum ranges—continued

Species	Common name	Optimum range	Lower range	Upper range	Reference
Hybognathus placitus	plains minnow			16 ± 1.94	Ostrand and Wilde, 2001
Pogonicthys macrolepidotus	splittail			20–29	Young and Cech, 1996
Cyprinus carpio	common carp			15	Payne, 1983
pH					
Gila bicolor bicolor	Klamath tui chub			10.75 ± 0.48	Falter and Cech, 1990, Wood and McDonald, 1982
Catostomus snyderi	Klamath largescale sucker			10.73 ± 0.41	Falter and Cech, 1990, Wood and McDonald, 1982
Chasmistes brevirostris	shortnose sucker			9.55 ± 0.43	Falter and Cech, 1990, Wood and McDonald, 1982

TABLE 2.—General water quality recommendations for holding of fishes (modified from Timmons et al., 2002). Every species has an “optimal” range that may not be represented by this broad spectrum

Water quality variable	Safe holding concentrations, mg/L	APHA-AWWA-WPCF standard methods number
Alkalinity (as $CaCO_3$)	50–300	2320
Aluminum (Al)	< 0.010	3111, 3113, 3120
Ammonia (NH_3–N un-ionized)	< 0.0125 (Salmonids)	4500–NH_3
Ammonia (NH_3–N Total)	< 1.0 (cool-water fish) < 3.0 (warm-water fish)	4500–NH_3
Arsenic (As)	< 0.05	3114
Barium (Ba)	< 5.0	3111, 3120, 3125
Cadmium (Cd) Alkalinity < 100 mg/L (as $CaCO_3$) Alkalinity > 100 mg/L (as $CaCO_3$)	< 0.0005 < 0.005	3113, 3125
Calcium (Ca)	4–160	3114, 3120

TABLE 2.—General water quality recommendations for holding of fishes (modified from Timmons et al., 2002). Every species has an "optimal" range that may not be represented by this broad spectrum—continued

Water quality variable	**Safe holding concentrations, mg/L**	**APHA-AWWA-WPCF standard methods number**
Carbon Dioxide (CO_2) Tolerant species (tilapia) Sensitive species (salmonids)	< 20 < 60	4500–CO_2
Chlorine (Cl_2)	< 0.003	4500–Cl
Copper (Cu) Alkalinity < 100 mg/L (as $CaCO_3$) Alkalinity > 100 mg/L (as $CaCO_3$)	0.006 0.030	4500–
Hardness, total (as $CaCO_3$)	> 100	2340
Hydrogen cyanide (HCN)	< 0.005	4500–CN^-
Hydrogen sulfide (H_2S)	< 0.002	4500–S^{2-}
Iron (Fe)	< 0.150	
Lead (Pb)	< 0.020	3113, 3125
Magnesium (Mg)	< 15.0	3120
Manganese (Mn)	< 0.010	3120, 3125
Mercury (Hg)	< 0.00002	3112, 3500–Hg
Nitrogen (N_2) Total gas pressure As N_2 gas	< 110 percent < 103 percent	2810
Nitrite (NO_2)	< 1 0.1 in soft water	4500–NO2-
Nitrate (NO_3)	0–400 or higher	4500–NO3-
Nickel (Ni)	< 0.1	3113, 3125
Oxygen dissolved (DO)	> 5 (pO_2 > 90 mm Hg)	4500–O A-G
Ozone (O_3)	< 0.005	4500–O_3
PCB's	< 0.002	6431
pH	6.5–8.5	4500–H^+
Phosphorous	0.01–3.0	4500–P
Potassium (K)	< 5	3111, 3120
Salinity	species dependent	2510, 2520
Selenium (Se)	< 0.01	3114
Silver (Ag)	< 0.003	3113, 3125
Sodium (Na)	< 75	3120
Sulfate (SO_4)	< 50	4110, 4120, 4130
Total gas pressure (TOP)	< 105% (species dependent)	2810

TABLE 2.—General water quality recommendations for holding of fishes (modified from Timmons et al., 2002). Every species has an "optimal" range that may not be represented by this broad spectrum—continued

Water quality variable	Safe holding concentrations, mg/L	APHA-AWWA-WPCF standard methods number
Sulfur (S)	< 1	–
Total dissolved solids (TDS)	< 400 (site and species specific; use as rough guideline)	2540 C
Total suspended solids (TSS)	< 80	2540 D
Uranium (U)	< 0.10	3113, 3125
Vanadium (V)	< 0.10	3113, 3125
Zinc (Zn)	< 0.005	3113, 3125

Holding Water Sources

Water from different sources, such as ground or surface, may differ in physical and chemical properties that could affect fishes during short-term holding.

Groundwater

Typically, groundwater sources, such as wells or springs have consistent temperatures within a few degrees, are low in dissolved oxygen (DO), but high in dissolved carbon dioxide (CO_2) and nitrogen (N_2), and may have elevated dissolved hydrogen sulfide (H_2S) and ferrous iron concentrations (Fe^{2+}) (Avault, 1996). Because groundwater percolates through soil and rock, it becomes enriched with minerals and nutrients through dissolution and biotic processes (Stumm and Morgan, 1996). Before using groundwater to hold fish, it should be equilibrated with the atmosphere by aerating the water to increase the DO content, and de-gas or release any CO_2, N_2 or H_2S.

Surface Water

Surface water sources, such as streams and lakes, are typically more variable in their physical and chemical properties, and are categorized into three broad types: freshwater (0 ppt), estuarine (brackish, 1–30 ppt), and saltwater (30+ ppt) (Avault, 1996). Compared to groundwater sources, surface waters frequently have higher DO content, atmospheric levels of CO_2 and N_2, but the held-fishes' exposure rate to pathogens and toxins also increases. The possibility of anthropogenic influences from substance penetration into the water table or local runoff (i.e., pesticides, thermal pollution) must be considered with surface and groundwater. Although groundwater is often preferred over surface waters, due to fewer biological nuisances and less chance of pollutant exposure (Avault, 1996), it is often not an option for brackish or marine water sources.

Flow Rate and Loading Density

The ability of the holding system to support a fish density largely depends on the water flow rate and the filtration system needed to maintain the optimal water quality required for the species.

Loading Density

Loading density refers to the actual fish carrying capacity of the water and is calculated as fish weight per water flow rate, which is the volume of water turnover in a given amount of time (i.e., kg/L/min or lb/gpm flow). Crowding or confinement (discussed more thoroughly in a later section) refers to fish behavioral responses to the density of fishes in a given volume (Wedemeyer, 1996; Timmons et al., 2002). The loading density for any given holding container changes with the species, average size of fish, and water quality variables (Haskell, 1941; Westers and Pratt, 1977; Avault, 1996; Timmons et al., 2002).

Effects of Loading Density

High fish loading densities can rapidly deplete DO, particularly if the fish are allowed to forage and are hyperactive or stressed. For example, fishes subjected to handling disturbances increased their oxygen consumption rates as a result of the metabolic cost associated with activity and stress (Barton and Schreck, 1987; Davis and Schreck, 1997). Also, fishes kept at high loading densities frequently incur more physical abrasions with loss of scales and mucus leading to decreased immuno-competence and increased disease persistence (see section 2: Stocking Density and Confinement and section 4: Behavioral and Predatory Impacts ; Pickering and Pottinger, 1989; Schreck, 1996; Iguchi et al., 2003).

High fish densities during short-term holding are often associated with transportation (hauling) processes. During transportation, water quality often deteriorates at an accelerated rate (potentially within 1–2 h after loading) due to the fishes' stress responses, physical reactions (i.e., regurgitation, excretions, and mucus production), release of breakdown products from organic matter, and microbial respiration. Stress responses are typically exacerbated by poorer water quality conditions from inadequate water exchange rates (Chow et al., 1994; Davis and Schreck, 1997; Paterson et al., 2003). For example, the capture, handling and hauling of fishes increases their metabolic activity and thus their oxygen consumption rates (Davis and Schreck, 1997). Fish respiration enhanced by crowding reduces DO and increases dissolved CO_2 concentrations, while metabolism-related secretions increase the ammonia (NH_3), total suspended solids (TSS) and total dissolved solids (TDS). Assuming the temperature remains the same, pH will decline with the increasing dissolved CO_2 (discussed more thoroughly later this section); while low pH will decrease the proportion of toxic NH_3, it favors increase of dissolved CO_2 (Randall, 1991). For example, short-term stress exposure from confinement and poor water quality on largemouth bass, *Micropterus salmoides*, (dissolved $CO_2 > 135$ mg/L, $NH_3 > 0.20$ mg/L, DO < 6 mg/L) resulted in increased plasma corticosteriods and glucose, and altered plasma chloride and osmolality during the recovery phase (Carmichael et al.,1984a, 1984b).

Water Flow Rate

Flow rates (L/h) within a holding structure should be sufficient to promote optimum water quality and the removal of fish wastes, without causing fish to become stressed and physically overwhelmed by the fast flows (Burrows and Chenoweth, 1970). Often, simple monitoring of in-line sensors or simply catching the water entering the tank for a given period of time can be used to estimate the flow rate.

Effects of Water Flow Rate

Excessive flow rates should be avoided, because it may fatigue fishes. There are various types of swimming activity that can produce exhaustion stress. Aerobic swimming activity, such as sustainable swimming, uses mostly oxidative red muscle, whereas anaerobic swimming activity, such as burst-type swimming, is largely powered by glycolytic white muscle for short periods of time. Burst swimming for extended periods (> 20 s) leads to physical exhaustion, resulting in muscle and blood pH decreases (Milligan 1996, 1997), ion- and osmo-regulatory problems (Wood et al., 1983; Moyes and West, 1995), and possible mortality (Black, 1958; Wood et al., 1983). Prolonged swimming and exhaustive exercise may stimulate erythrocyte swelling (Soivio and Nikinmaa, 1981), and elevate plasma cortisol, glucose and lactate levels (Wood et al., 1983; Tang et al., 1989; Cech et al., 1996; Milligan, 1997). Intense exercise for even short time periods (e.g., 5–10 min) can result in metabolic or mixed acidoses (Wood et al., 1983; Tang et al., 1989). Excessive lactate accumulation in the blood (Black, 1958) and associated intracellular acidosis (Wood et al., 1983) are most likely responsible for the deaths of fishes after intense exercise. Furthermore, fishes intensely exercised without proper recovery time and conditions (which is species-specific) may experience disorientation, buoyancy difficulties, and post-exercise mortality (Wood et al., 1983; Brick and Cech, 2002). Severe exercise as a result of tank flows beyond the maximum swimming ability may result in death several hours after the end of exercise (Black, 1958; Wood et al., 1983).

Exhaustive exercise, swimming performance, and recovery periods for fishes are affected by body size (Ferguson et al., 1993; Müller et al., 2000), past exposure (Houlihan and Laurent, 1987; Farrell et al., 1990; Davison, 1997), health (Leon, 1986; Scarabello et al., 1991; Kieffer and Tufts, 1998), and water quality (Dahlberg et al., 1968; Kieffer et al., 1994; Wilkie et al., 1997). Optimum water velocities for each type of holding container (see section 3: Holding Container Design) is governed by the species, size, and physical condition of the fish held. Holding various sizes and species of fish will result in different swimming performances making water flow rate a controllable variable. For example, Brett (1965) established a now-recognized trend that there is an increase in the absolute swimming speed of fish with size using sockeye salmon, (*O. nerka*). Hammer (1995) found that the maximum growth of various salmon occurs at 1 BL/sec versus a higher velocity of 3 BL/sec. After 5 min of exhaustive exercise, small rainbow trout, *O. mykiss*, (ca. 8–12 cm FL) have 50 percent less white muscle lactate concentration (16 µmol/g) compared with larger rainbow trout (ca. 50–60 cm FL; Ferguson et al., 1993). Fish that are forced to maintain a constant exercise level without becoming stressed and physically overwhelmed by flows are in better physical condition, with higher growth and survival rates (Burrows and Chenoweth, 1970; Watten and Johnson, 1990; Young and Cech, 1993; 1994). Water velocities, in which fish can maintain their position, also benefit in saving energy by ventilating their gills by the flowing water (i.e., ram ventilation) and reduce their oxygen demand (Losordo and Westers, 1994). Exercise conditioning has demonstrated increased red and white muscle activity, enhanced cardiac output and oxygen carrying capability in the blood (Nahhas et al, 1982; Woodward and Smith, 1982, Losordo and Westers, 1994).

High flow rates are also problematic, if particulate matter is not allowed to settle or removed via filtration before entering the holding containers. Particulate matter (5–20 µm size range), when continually suspended, tends to chronically irritate fish gills, predisposing fishes to bacterial and/or viral gill disease (Bullock et al., 1994; Schreck, 1996).

Temperature

Temperature affects the physical and chemical properties of water and all chemical reaction equilibria. Typically, a 10 ºC increase in water temperature results in the doubling of a chemical reaction rate (Stumm and Morgan, 1996). Water temperature influences gas solubility, and, therefore, the dissolved gas content in water. For example, as water temperature increases, the solubility of oxygen (O_2) and other gases decrease (i.e., N_2 and CO_2; Colt, 1984). Temperature directly affects the H^+ activity and must be taken into account when determining and recording pH measurements; for example, for pure water at 30 ºC, neutral pH is 6.92, while at 0 ºC neutral is 7.48 (Colt, 1984). Water temperature also modifies the carbonate cycle equilibrium and the proportion of toxic NH_3 present. The carbonate cycle (covered in a subsequent section) regulates pH, which in turn affects the NH_3–NH_4^+ equilibria (Stumm and Morgan, 1996). Water temperature also affects the lethality of pollutants on fish. For example, fish exposed to pollutants typically have a decreased survival time by a factor of 2 or 3 with each increase of 10 ºC (Alabaster and Lloyd, 1982; Heath, 1998).

Effects of Temperature

Fish are poikilotherms (or organisms whose body temperatures' change essentially with the environmental temperature), so their surrounding water temperature is critical to their physiological reaction rates and metabolic processes. Every species has an optimal temperature range in which the fish does not exhibit any signs of thermal stress and/or altered behavior. As a fish's body temperature increases, biochemical reaction rates generally increase for enzyme reactions and membrane transport flux dynamics, even relative to minute temperature shifts of less than 0.5 ºC (Elliot, 1981; Neill and Bryan, 1991). Consequently, a rise in water temperature often drives increased metabolic rates of fishes, assuming that there are no other limiting factors.

Thermal stress occurs when the water temperature exceeds the optimal temperature range, thus initiating changes that disturb normal physiological functions resulting in energy expended towards stress responses, and even a potential decrease in individual survivorship (Brett, 1958; Fry, 1971; Elliot, 1981). Optimal temperature ranges may change with ontogeny, body size (Brett, 1956; Fry, 1971), and the individual's health, including past thermal experiences (Elliot, 1981). For example, most fishes can acclimate to gradual temperature changes over months, such as with season. However, rapid water temperature changes or exposures to sustained temperatures outside the optimal range (thus, sub-optimal) often result in thermal stresses or lethal conditions. The severity of the thermal stress response may depend on other water quality constituents, for example, DO content and TDS concentration in the water (Hettler, 1976; Claireaux et al., 1995; Claireaux and Audet, 2000). Lipid reserves, plasma proteins, blood osmolality and serum electrolytes may decrease due to ion- and osmo-regulatory dysfunction creating physiological imbalances with thermal stress (Houston and Schrapp, 1994; Swanson et al., 1996; Claireaux and Audet, 2000). The additional metabolic costs from thermal stress responses subtract from immune function, reproduction and growth (Schreck, 1981; Barton and Schreck, 1987; Donaldson, 1990; Barton and Iwama, 1991). Thermal stress-related behaviors include a reluctance to feed, sudden or erratic movements with possible collision with the tank wall or other fishes, jumping, rolling, pitching, color and parental care change, and increased regurgitation, defecation and gill ventilation (Elliot, 1981; Alsop et al., 1999; Cooke et al., 2003a; Smith and Hubert, 2003).

Water temperature also affects swimming performance and related functions. For example, acute temperature changes have resulted in reduced swimming performance (Kieffer, 2000; Parsons and Smiley, 2003). Fishes often acclimated to a range of temperatures typically have the poorest swimming performance at the lowest temperature (Alsop et al., 1999; Myrick and Cech, 2000). Additionally, a predator's ability to forage and prey's ability to escape predation, as well as general migration and spawning capacities are affected by temperature (Moore and Townsend, 1998; Myrick and Cech, 2000; Cooke et al., 2003a; Parsons and Smiley, 2003; Marine and Cech, 2004). Though many captured fishes are not released back into their habitats, some governmental and private groups release fish after transport and/or short-term holding periods. With the possible additive or synergistic effects of water temperature changes associated with live transport and subsequent release, along with stressors attributed to handling, higher than expected fish mortality is likely due to decreased swimming ability, and increased predation vulnerability (Moore and Townsend, 1998; Parsons and Smiley, 2003).

Recommendation for Short-Term Holding

Water temperature in short-term holding tanks or vessels should be similar to the originating source, such as the water body or other tank system, to avoid thermal shock when fish are transferred to the holding system (Wedemeyer, 1996). The temperature tolerance ranges of many cultured species are known and could be used to gauge tolerance ranges for less-well-studied species (Alabaster and Lloyd, 1982; Avault, 1996; Wedemeyer, 1996; Timmons et al., 2002). For some fishes, transportation can be less stressful, if it takes place during cooler months or in chilled water (Carmichael et al.,1984a, 1984b; Robertson et al., 1987; Erickson et al., 1997; Pavlidis et al., 2003). Cooler water temperatures typically decrease metabolic processes (e.g., oxygen consumption rate, NH_3 excretion rates, activity levels), while oxygen solubility increases. If fishes are to be transported at a cooler temperature, their holding water should be slowly cooled (≤ 1 ºC/day) to match the desired temperature for transportation (Elliot, 1981; Wedemeyer, 1997). Likewise, when the fishes arrive to the new destination, the difference between the transportation temperature and new holding tank or vessels should be minimized. For more general reviews of behavioral and physiological effects of water temperature on fishes, see Brett (1956), Fry (1971), Elliot (1981), Neill and Bryan (1991), and Wedemeyer (1996).

Dissolved Oxygen

The oxygen concentration in water decreases with increasing water temperature, salinity, and decreasing atmospheric pressure. The freshwater DO concentration is the greatest at 14.60 mg/L (equivalent to "parts per million", ppm) at air saturation and 0 ºC, then declines to 9.26 mg/L at 19 ºC, and to 7.54 mg/L at 30 ºC (Colt, 1984) due to decreased gas solubility. Similarly, in saltwater at 19 ºC, DO is 8.5 mg/L at 15 parts per thousand (ppt; g/L) and 7.61 mg/L at 33 ppt (Colt, 1984) due to gas solubility decreases. At high elevations, the atmospheric pressure declines, decreasing the partial pressures of all gases, including that of oxygen (denoted as pO_2). Thus, even though oxygen remains 20.94 percent by volume of air, the "thinner" air (decreased barometric pressure) decreases pO_2, and consequently the maximum DO content at air equilibrium. For example, at 19 ºC, the expected air-equilibrated freshwater DO content decreases from 9.26 mg/L at sea level to 8.42 mg/L at 8000-m elevation, and to 7.65 mg/L at 1,600-m elevation (Colt, 1984). Conversely, water may become supersaturated (i.e., when a gas concentration is greater than that with air saturation) with DO when water is under pressure from deep wells or aquacultural technology (e.g., U-tubes), turbulently mixed in plunge pools below water falls or dams, or through intense photosynthesis in shallow pools with a "carpet" of macrophytes.

Effects of Dissolved Oxygen

Fish oxygen uptake typically consists of the following events: (1) Continuous branchial ventilation brings DO in inspired water near the gill lamellae; (2) DO diffusion down its partial pressure gradient from the ambient water across lamellar membranes into the blood; and (3) O_2 diffusion across erythrocytic membranes, binding with hemoglobin. The larger the pO_2 difference (i.e., gradient) between the inspired water and the blood (O_2-depleted, due to metabolism), the greater the O_2 diffusion rate across the gill lamellar membranes. The water-blood pO_2 gradient is maintained by gill ventilation, which replaces the water boundary layer outside the gill membranes, and gill perfusion, which replaces the blood boundary layer inside these membranes. Hyperventilation (increased gill ventilatory frequency and/or stroke volume) may signal low water pO_2 (hypoxia). For a more in-depth discussion of respiration, please refer to Hughes (1981), Wedemeyer (1996), Perry and Tufts (1998), and Moyle and Cech (2004).

Because water is the respiratory medium for most fish, its DO content is the most critical and limiting water quality variable (Fry 1947, 1971). DO is essential for aerobic activity, and thus DO concentrations below the species' aerobic limit (critical pO_2) require fishes to exploit anaerobic metabolic pathways, which are inefficient and useful only for short time periods. Cech et al.,(1979) showed that the critical pO_2 of a fish increases as temperature and metabolic demands for O_2 increase. When the ambient pO_2 is sub-optimal, respiratory stress can occur and be lethal (Neill and Bryan, 1991). Conversely, hyperoxic (supersaturation) conditions can decrease gill ventilation increasing blood pCO_2 with potentially severe consequences (see carbon dioxide and the carbonate cycle section). The oxygen consumption rate and the degree of respiratory stress is dependent upon the species, life stage, body weight, prior exposure, health, and activity levels (Elliot, 1969; Wedemeyer and McLeay, 1981; Alabaster and Lloyd, 1982).

Respiratory stress involves increased gill ventilation frequency and volume (Campagna and Cech, 1981; Lutnesky and Szyper, 1990), pituitary-interrenal activity (Wedemeyer and McLeay, 1981), and hematological changes (e.g., increased red blood cell capacity; Lochmiller et al., 1989). It also includes changes in cardiac rate, stroke volume and output, gill perfusion patterns, and oxygen consumption rates (Webber et al., 1998; Brodeur et al., 2001; Stecyk and Farrell, 2002). As a result, fishes can experience tissue hypoxia (hypoxemia), stunted or retarded growth (Weber and Kramer, 1983), reduced fecundity, or unconsciousness. In addition, fish exhibit altered behavioral patterns, such as erratic swimming, side-lying, aquatic surface respiration, reduced spawning activity, avoidance of low oxygenated areas, and movement into cooler water reducing their metabolic oxygen consumption (Hughes, 1981; Kramer, 1987; Lutnesky and Szyper, 1990; Love and Rees, 2002).

The effects of low DO content on swimming performance are important to consider when releasing fishes from holding systems and when selecting holding container flow rates. A fish in hypoxic conditions (e.g., associated with sub-optimal transportation system) may exhibit reduced swimming ability or performance, impairing foraging or predator avoidance. For example, largemouth bass, *M. salmoides*, and coho salmon, *Oncorhynchus kisutch*, have decreased maximum sustainable swimming speeds in hypoxic conditions (Dahlberg et al., 1968). Similarly, sockeye salmon, *O. nerka*, displayed a poor recovery after swim speed tests under moderately hypoxic conditions (water $pO_2 < 100$ mm Hg or ca. DO < 6.5 mg/L; Farrell et al., 1998).

Daily fluctuations and rapid depletions of DO can occur in short-term holding systems: (1) if algae is present, (2) when the loading densities are excessive, (3) as water temperature, TDS or salinity increases (Stecyk and Farrell, 2002), (4) if foraging is allowed (Timmons et al., 2002), and (5) where fish are hyperactive and/or stressed (Wilson et al., 1994; Carey and McCormick, 1998). A holding system designed to use eutrophic surface waters with large algal populations may dramatically affect the DO content. During daylight, water pO_2 can exceed air-saturation levels due to O_2 production (photosynthesis). O_2 can be produced faster than it diffuses out of solution (equilibrating with air), or is consumed by biological oxygen demand (BOD) (Heath, 1995). In contrast, DO can decrease dramatically during the night when photosynthesis stops and biological respiration continues.

The energetic costs of foraging and digestion can dramatically affect the DO content within a holding container. Specific dynamic action-related costs (SDA, including digestion, absorption, and assimilation) in channel catfish, *Ictalurus punctatus*, resulted in an increased oxygen consumption rate by 40 percent compared to resting levels (Brown and Cameron, 1991).

Metabolic expenditures during swimming activity, and thus the oxygen consumed during these activities are also important to consider. For example, rainbow trout had a 2.0 to 2.5-fold increase in their oxygen consumption after 5 min of exhaustive exercise, due to the "repaying of the oxygen debt" in the muscle tissues (Scarabello et al., 1991).

Recommendation for Short-Term Holding

Increased water flow rate and aeration, and lower loading densities can control DO content during short-term holding. Water exchange through holding systems should assist in mixing of oxygen-rich surface layers with more oxygen-depleted deeper layers. Maintaining dissolved oxygen levels throughout the water column can be accomplished by bubbling supplemental oxygen or air, increasing the influent rate of well-oxygenated water, or by the mechanical mixing action of a spray bar, baffle, or surface agitator. Generally, DO contents consistent with equilibrium with atmospheric O_2 at a particular temperature, salinity and elevation are usually optimal for short-term holding (Wedemeyer, 1996; Timmons et al., 2002). Usually, oxygen levels > 4 ppm (parts per million) are desirable, although tolerance to hypoxia is species specific (Thomforde, 2001).

Due to the large increase in oxygen consumption with increased SDA, fishes should not be excited, handled, or transported within 24 to 48 hours after feeding (while fishes are in a post-prandial state), if DO content cannot be increased.

Ammonia, Nitrite, and Nitrate

Nitrogen, acquired from food-based proteins, is continually turned over with synthesis of new proteins, used for development and growth acting as an amino acid "sink", and excretion of nitrogenous wastes such as urea and NH_3.

NH_3

In nature, the addition of total ammonia-nitrogen (TAN) to water occurs from bony fish wastes, the accumulation of dead organisms and other debris in the water column or from anthropogenic sources such as industries and agriculture (Alabaster and Lloyd, 1982; Meade, 1985; Russo and Thurston, 1991; Wilkie, 2002). NH_3 exists in two forms that are in equilibrium with each other:

$$NH_4^+ \Leftrightarrow NH_3 + H^+ \tag{1}$$

ionized ammonia nitrogen (NH_4^+–N; ammonium ion) and un-ionized ammonia nitrogen (NH_3–N), which together are referred to as TAN. NH_3 can be oxidized to nitrite (NO_2^-), then nitrate (NO_3^-) via aerobic nitrification by chemical and biological processes (Stumm and Morgan, 1996).

The ratio of NH_4^+ to NH_3 is dependent upon the temperature, pH, the carbonate cycle equilibrium, and salinity (or ion concentration) of the water. Of the two forms, the NH_3 is more toxic and thereby determines the toxicity of TAN. Increases in pH, temperature, or salinity will increase the amount of NH_3 (Spotte, 1970; Alabaster and Lloyd, 1982). For example, for water pH 7.0 at 10 ºC and 25 ºC, the percentages of NH_3 are 0.19 and 0.55, respectively. At pH 8.0, an increase of temperature from 10 ºC to 25 ºC substantially increases the percentage of NH_3 from 1.98 to 5.28, respectively (Spotte, 1970).

Effects of NH_3

Short-term exposure to elevated NH_3 concentration causes increased gill ventilation, erratic and quick movements, loss of equilibrium, coughing, convulsions, lack of foraging, and even mortality in fishes (Meade, 1985; Russo and Thurston, 1991). Other symptoms of excessive NH_3 (typically concentrations > 0.3 mg/L, though actual tolerance is species dependent) are skin and gill corrosion and nerve damage. High NH_3 in the tissues will also cause a blood pH elevation, and osmoregulatory disturbance. Chronically elevated NH_3 typically decreases growth rates, fecundity, disease resistance, and swim performance, and it increases metabolic rate (Russo and Thurston, 1991; Timmons et al., 2002). For example, rainbow trout, *O. mykiss*, exposed to elevated ammonia concentrations (50% of the 96-h LC for rainbow trout, ca. 288 ± 15 µmol/L) exhibited a decreased critical swimming speed (from 2.23 ± 0.15 body length [BL]/s to 1.61 ± 0.17 BL/s), and an increased metabolic rate (from 3.04 ± 0.86 to 5.65 ± 0.59 mmol O_2/kg-h), which severely decreased its aerobic activity scope (from 6.38 ± 2.58 to 2.41 ± 0.61; Shingles et al., 2001).

NO_2^-

NO_2^- is an intermediate product between NH_3 and NO_3^- via the nitrification process. In the presence of DO, nitrifying bacteria, such as *Nitrosomonas spp.*, can quickly oxidize NO_2^- to NO_3^-:

$$NH_4^+ + 1\tfrac{1}{2}\, O_2 \rightarrow NO_2^- + 2H^+ + H_2O \tag{2}$$

NO_2^- usually does not occur in great qualities in aerobic or oxidizing aquatic systems (typically < 0.005 mg/L), because it is often a quick intermediate step in the nitrification process. If nitrification is slowed, this toxic substance will increase in concentration. NH_3 can also be reduced to N_2 under anaerobic conditions. Environmental factors that affect the conversion of NO_2^- are pH, temperature, DO content, microbial density, and inhibiting compounds (Lewis and Morris, 1986; Russo and Thurston, 1991).

Effects of NO_2^-

NO_2^- is toxic to fishes, especially if allowed to accumulate or when fishes are chronically exposed to low NO_2^- levels, and its impact can be influenced by body size, species tolerances, and by other water quality variables (Lewis and Morris, 1986). During NO_2^- exposure, ion balance becomes disrupted as NO_2^- binds to active branchial uptake mechanisms reducing Cl^- efflux to the ambient water and a loss of potassium (K^+) from skeletal muscle to extracelluar fluid (thus increasing the K^+ in the plasma; Jensen et al., 1987; Stormer et al., 1996). A major effect of NO_2^- on fishes is the oxidation of blood hemoglobin iron (Fe^{2+}) to its ferric state, forming methemoglobin, which colors the blood brown and causes "brown blood" disease. Methemoglobin cannot reversibly bind oxygen and can result in hypoxemia and mortality (Lewis and Morris, 1986; Russo and Thurston, 1991). Increased gill ventilation and heart rate are also noted side effects of NO_2^- (Jensen, 2003).

NO_3^-

The NO_3^- is the final product of the nitrification process via bacteria like *Nitrobacter spp.* and *Nitrococcus spp.* (Timmons et al., 2002):

$$NO_2^- + \tfrac{1}{2}\,O_2 \rightarrow NO_3^- \qquad (3)$$

Although NO_3^- is present in most oligotrophic systems, it is found in higher concentrations (e.g., > 0.5 mg/L) in eutrophic systems.

Effects of NO_3^-

Though this compound is the least toxic, high concentrations of nitrate (e.g., 96-h LC > 1000 mg/L,) may affect fish osmoregulation and gas exchange (Lawson, 1995; Timmons et al., 2002).

Recommendation for Short-Term Holding

For short-term holding, we strongly encourage the monitoring of TAN, NO_2^- and NO_3 concentrations. percentage of free NH_3 can be determined from water pH, temperature, and TAN. There are commercially available kits to monitor TAN, NO_2^- and NO_3^- at low levels (i.e., TAN < 2.5 mg/L), which are preferable to the high concentration kits. TAN accumulation occurs in holding containers that have low water exchange, high fish load densities, foraging, and/or stressed fish. Biofiltration (i.e., nitrification with *Nitrosomonas spp.* and *Nitrobacter spp.*), converts TAN to less-toxic NO_3^-, but up to

40 days may be needed to fully activate a culture. Freshwater short-term holding systems have the option of using ion exchange minerals (i.e., zeolites) for TAN reduction, but this method is ineffective for brackish and saltwater systems. Designing short-term brackish and saltwater systems to use flow-through water would help ensure low TAN levels.

Salinity

Water may be classified based on the total concentration of dissolved ions in water (expressed as parts per thousand (ppt): freshwater (0 ppt), brackish (1–30 ppt), and saltwater (> 30 ppt). Seawater primarily contains chloride (Cl^-), sodium (Na^+), with lesser amounts of sulfate (SO_4^{2-}), magnesium (Mg^{2+}), calcium (Ca^{2+}), potassium (K^+), bicarbonate (HCO_3^-), bromide (Br^-), boron (B^{3+}) and strontium (Sr^{2+}) totaling approximately 35 ppt (Stumm and Morgan, 1996). The ion concentrations of fresh water depend on interactions between the water and the geology, hydrology, sediments, discharges/erosion, and climate of a watershed. Salinities in brackish, marine, and hypersaline habitats are affected by evaporation and dilution (via precipitation and land runoff) of water and may also vary seasonally. Salinities in estuarine environments may fluctuate significantly with daily tides and winds.

Effects of Salinity

Much like temperature and DO, each species and life stage has an optimal salinity range, beyond which osmoregulatory stress begins. Fish generally use one of four strategies to maintain an internal balance of dissolved ions and water: (1) osmoconformers, (2) users of substantial urea and trimethylamine oxide (TMAO), (3) hyposmotic regulators, or (4) hyperosmotic regulators (see Eddy, 1981; Wood and Shuttleworth, 1995; and Moyle and Cech, 2004 for more in-depth reviews). Because most bony fish are osmoregulators (either hyposmotic or hyperosmotic regulators), they will be the focus of this section. Fishes may be either euryhaline (exhibiting wide salinity tolerance ranges) or stenohaline (narrower salinity tolerance ranges). Additionally, freshwater fishes are hypertonic to the surrounding water, tending to diffusively “lose” ions to their environment and osmotically “gain” water; while saltwater fishes are hypotonic to their surroundings tending to “gain” ions and “lose” water. Thus, the internal total ionic concentrations of these fishes, regardless of their environment (freshwater, brackish and saltwater) is typically regulated within the 7–10 ppt salinity range (Stickney, 1991).

Outside of their optimal salinity ranges, fishes may increase the energy allocation towards osmoregulation and away from other processes such as activity, growth, and reproduction, if food intake or quality does not increase (Swanson, 1998). Conversely, the oxygen consumption rate of grass carp, *Ctenopharyngodon idella*, decreased from 0.16 to 0.11 mg O_2/g-h. The metabolic rate reduction is thought to be advantageous because it reduces blood circulation to the gills and external medium, thus assisting in the osmotic balance maintenance (Maceina et al., 1980). If water salinity is too high or low, mortality may occur because fish cannot maintain internal homeostasis. For example, tilapia showed a marked increase in plasma osmolality, Na^+, Cl^-, Na^+–K^+–ATPase, and the number of apoptotic cells when exposed to 75–95 ppt water (acclimated to 35 ppt; Sardella et al., 2004). Yet, the signs of osmoregulatory stress are not always obvious, and by the time the effects are observable, severe damage may have already occurred (Moser, 1985).

Capture and handling-related stresses stimulate physiological changes, such as increased lamellar recruitment and gill permeability (mediated by catecholamines, adrenergic neurons, and corticosteroids; Booth, 1979; Mommsen et al., 1999). When exposed to stressors, the gills become "leaky" to water and ions, often resulting in osmoregulatory imbalances (Mazeaud et al., 1977).

Recommendations for Short-Term Holding

For short-term holding, fish should be maintained within their salinity tolerance range. The practice of using brackish recovery environments enhances the survival of stressed, freshwater fish (Carmichael et al.,1984a; Mazik et al., 1991; Swanson et al.,1996) by decreasing the osmotic gradient between the water and the fish's internal fluids, slowing outward diffusion rates.

pH

The pH of water is defined as the logarithm of the reciprocal of the free hydrogen ions (H^+) activity. The *p* of pH refers to the power (puissance) of the H^+ activity (Wetzel, 2001). Activity is a thermodynamic analog of concentration, and at equilibrium pure water will have an H^+ concentration of 1×10^{-7} mol/L at 25 °C. This condition produces as pH 7.0, which is "neutral". The pH scale range below 7 is "acidic" while the range greater than 7 is "basic". At 25 °C, if the water pH is < 7.0, then the water has the capability to neutralize added hydroxyl ions (OH^-); whereas a pH > 7.0 provides the ability to neutralize added H^+. The usual pH range, 0 to 14, is buffered by bicarbonates and carbonates; however, most natural systems range over pH 5.0–10.0 for fresh water and 8.0–8.3 for saltwater.

Water pH has direct effects on other water quality variables (e.g., TAN) and, consequently, on fishes. Acidic water decreases the $NH_3{:}NH_4^+$ concomitantly as it increases the "carbonic acid complex" (H_2CO_3; which is the $[H_2CO_3]$ plus $[CO_2]$) to bicarbonate (HCO_3^-) ratio (further explained in the CO_2 and carbonate cycle section). Fishes maintain a plasma pH > 7.0 (typically, pH 7.8–8.0, depending on species and water temperature). Temperature increases will decrease the plasma pH in fishes (Randall and Wright, 1987), as well as other aqueous solutions that are not strongly buffered.

Effects of Acidic Water

At near-lethal or sub-lethal levels, such as pH 4.2–5.0 for various salmonids, H^+ acts directly on gill membranes, increasing ion permeability generally causing a loss of Na^+

and Cl^- ions (and other electrolytes; Randall, 1991). This change in membrane ion permeability causes decreased osmotic pressure, and increased hematocrit, plasma protein concentration, and blood viscosity (Wood and McDonald, 1990; Randall, 1991). Additionally, fish blood and extra-cellular fluids become acidified, dissolved CO_2 excretion and DO transport are altered, bone demineralization occurs, renal function and ammonia excretion are disrupted, migration of juvenile salmon may be delayed, and early mortality may occur (further reviewed by Wood and McDonald, 1982; Wood, 1988; McDonald, 1983). For example, the parr-smolt transformation of juvenile Atlantic salmon, *Salmo salar*, is seriously impaired at pH 4.2–4.7 (Saunders et al., 1983). Atlantic salmon exposed to acidic water migrated down the streams later than the non-exposed control salmon and the marine survival of acidic water-exposed salmon decreased 20 to 30 percent compared with the controls (Kroglund and Finstad, 2003). Also, acidic waters cause a depression of the non-specific immune activity by the immunosuppressive effects of cortisol (high cortisol levels compared with controls; Nagae et al., 2001). Exposure to acidic water also caused an increase in coughing and ventilation frequency in rainbow trout (Ye and Randall, 1991). Moreover, acidic water increases metal and H_2S toxicity (Rand and Petrocelli, 1985). For example, low water pH increases aluminum (Al^{3+}) dissolution rates, from rocks and soil, resulting in Al^{3+} toxicity (Sprague, 1985). This is a particular problem with egg through larval stages of fishes both in nature and in hatchery systems. Hydrogen sulfide ($H_2S \rightarrow HS^- + H^+ \rightarrow 2H^+ + S^{2-}$) toxicity is related to the dissociated ions, which comprise about 4 percent of the total solution at pH 8.4. However with a decrease in pH (ca. pH 6) the dissociated forms increase to 90 percent of the solution (Rand and Petrocelli, 1985). This increase in the concentration of dissociated ions (H^+ and S^{2-}) would increase the toxicity of the compound.

Effects of Basic Water

On the basic end of the pH spectrum, high pH (species dependent but generally pH > 9) reduces or curtails NH_3 excretion. Gill NH_3 excretion rate is facilitated by plasma pH greater than the neutral point (ca. arterial pH 7.8). Low NH_3 (95 percent of TAN exists as NH_4^+ at this pH) that allows for the maintenance of a positive pNH_3 diffusion gradient from blood to water across the gills (Wilkie et al., 1993; Goss et al., 1998; Wilkie, 2002; and figure 2). For example, Lahontan cutthroat trout (O. *clarki henshawi*) acutely exposed to water pH ≤ 10 (this is species dependent) depressed the gill NH_3 excretion rate which resulted in an increase in plasma NH_3 concentration (Wilkie et al., 1993). As plasma NH_3 concentration increases at high water pH, the blood-gill-water pNH_3 gradient is reestablished at the higher concentrations creating the "leakage effect" (when plasma NH_3 resumes diffusion; Wilkie et al., 1993; Claiborne et al., 2002; and figure 3). In extreme situations, when the plasma total NH_3 concentrations are too high due the high water pH, NH_3-assoicated neurotoxicity occurs, allowing for increased predation, or high pH-induced mortality (Wood et al., 2002). The effects of high pH environments also include increased blood pH, decreased gill membrane potential, white turbidity presence in skin mucus, fin and gill corrosion, and increases in the influx of sodium (Na^+) and chloride (Cl^-). (See figure 2.)

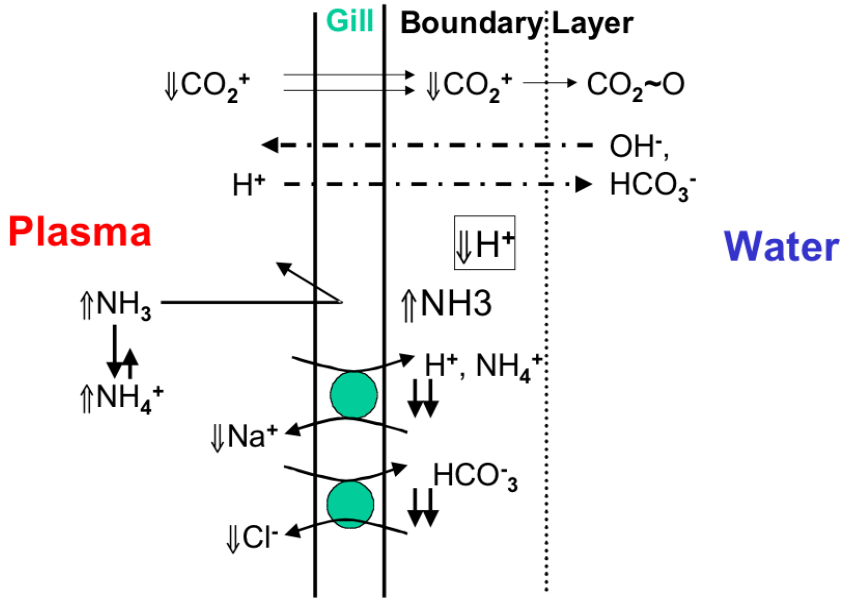


FIGURE 2.—CO_2, H+, and ion movement across fish gills from a high pH in water. (Solid arrow indicates active transports; hashed arrow indicates partial pressure passive transport).

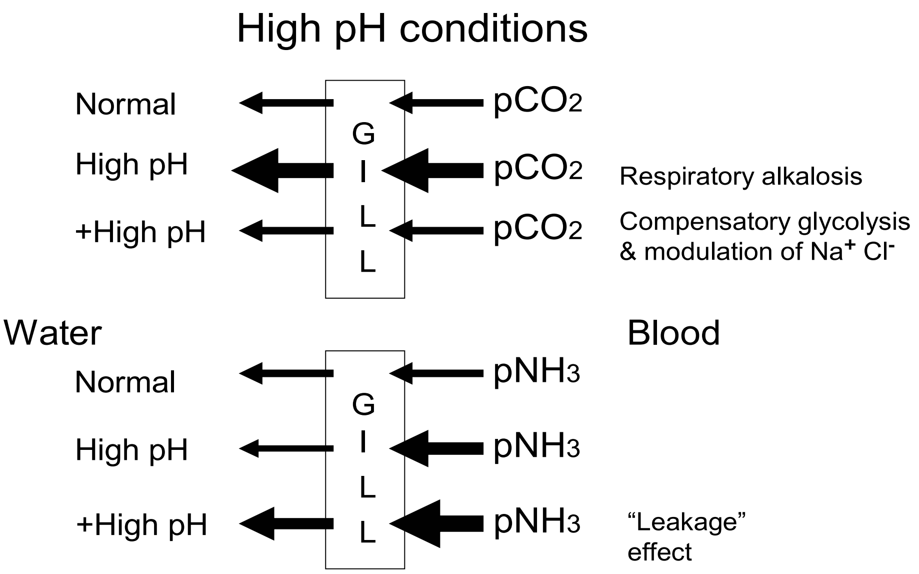


FIGURE 3.—Gill permeability and leakage effect at different pH conditions. (Thicker arrow indicates higher flux and + indicates very high pH).

Recommendation for Short-Term Holding

Short-term holding should involve pH monitoring within the holding containers and the source water. Circulation of the atmosphere above the holding containers and air equilibrating the water before it enters the holding container will prevent dissolved CO_2 levels from building, decreasing pH. With high fish densities, the TAN levels should be carefully monitored. At high pH levels the toxic form of ammonia will become more prevalent. Removal of TAN may be necessary, through source water exchange, chemical filtration with zeolites for freshwater systems, or biological filtration using bacteria for brackish and saltwater systems. The microbes involved in biological filtration consume both DO and alkalinity. The addition of bases (such as $NaHCO_3$) to maintain a level of alkalinity is often recommended. Such additions will also prevent the system's pH from declining to levels that would impact both the biological filtration and, potentially, the held species. The type of base used may have different solubility rates and carbonate-bicarbonate contents (Boyd, 1997; Timmons et al., 2002), and thus, treatments should be considered with caution.

Carbon Dioxide and the Carbonate Cycle

Although CO_2 is 20 to 38 times more soluble in water than is O_2, its concentrations are usually low in surface waters due to its low atmospheric concentration (0.3 percent of atmospheric air) and its rapid uptake by algae and macrophytes. Most dissolved CO_2 in holding situations is produced from fish respiration and the decomposition of organic matter (Timmons et al., 2002). Dissolved CO_2 in groundwater systems can vary widely depending on the location and biological activity in the system (Piedrahita, 2004). Typically, the amount of dissolved CO_2 in water from the air is 1.08 mg/L at 0 ºC, 0.63 mg/L at 15 ºC, and 0.31 mg/L at 30 ºC (Colt, 1984). Dissolved CO_2 is regulated by water pH and total dissolved inorganic carbon in the water. For example, dissolved CO_2 takes various forms as it hydrates and equilibrates:

$$CO_2\,(\text{air}) \Leftrightarrow CO_2\,(\text{dissolved}) + H_2O \Leftrightarrow H_2CO_3 \Leftrightarrow HCO_3^{1-} + H^+ \Leftrightarrow CO_3^{2-} + 2H^+ \tag{4}$$

which represents CO_2, carbonic acid (H_2CO_3), nontoxic bicarbonate ions (HCO_3^{1-}), and carbonate ions (CO_3^{2-}; see Grace and Piedrahita (1994), Piedrahita and Seland (1995), and Stumm and Morgan (1996)). If the pH is less than 6.43, the $CO_2 + H_2O \Leftrightarrow H_2CO_3$ reaction predominates. When the water pH is greater than 10.43, the $HCO_3^{1-} + H^+ \Leftrightarrow CO_3^{2-}$ reaction predominates. Because in most water, pH ranges between 7–9, HCO_3^- is the most common carbonate species. Carbonate systems are considered to be volatile (open) or non-volatile (closed) based on the ability of dissolved CO_2 to equilibrate with the atmosphere. To determine the dissolved CO_2 concentration, two of three variables need to be known: pH, total carbonate carbon, and/or alkalinity. (See figure 4.)

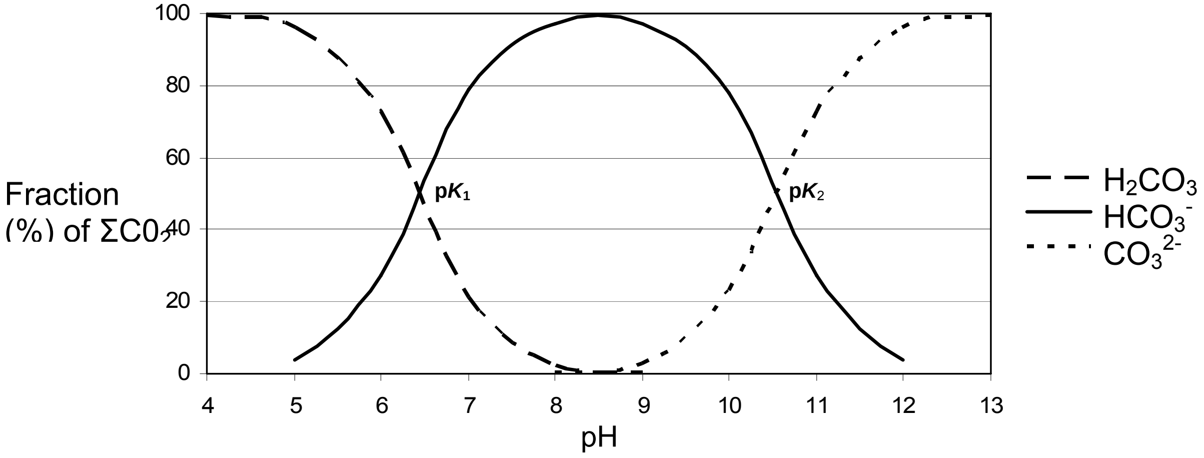


FIGURE 4.—Relation between pH and relative proportions of inorganic carbon species of CO_2: (H_2CO_3), HCO_3^-, and CO_3^{2-} in solution. (modified from Wetzel, 2001).

The carbonate system and equilibrium process are affected by the changes in temperature and ionic strength (Piedrahita and Seland, 1995). Increasing water temperature decreases the solubility of carbon dioxide in water and favors the equilibrium constants, the extent to which compounds dissociate, for carbonic acid (H_2CO_3). The carbonate system in freshwater is affected by the ionic strength of its composition (discussed later in the alkalinity and hardness sections) and pH; thus freshwater carbonate systems vary more than that of saltwater. Saltwater's high concentrations of Na^+ and Cl^- have a very low affinity for hydroxyl (OH^-) and hydrogen (H^+) ions, and its calcium ions (Ca^{2+}) have an affinity for the carbonate species (CO_3^{2-}; Stumm and Morgan, 1996). In saltwater, the pK_1 for HCO_3^- is an estimated 0.5 pH units lower, and pK_2 for CO_3^{2-} is approximately 1 pH unit lower compared to fresh water (Wetzel, 2001).

The carbonate system helps maintain pH by resisting changes in pH (buffering) through the absorption or the release of free H^+ ions. For example, if photosynthesis removes CO_2 from the water and its carbonate system, then the balance (Equation 4) is forced to the left removing H^+ from the system. Steady state can only be maintained then, if there is a source of H^+ from HCO_3^- and H_2CO_3; otherwise, pH of the water could be expected to increase. In nature, H_2CO_3 arises from the dissolution of carbonate rocks, increasing the CO_2 in groundwater.

Effects of CO_2 and the Carbonate Cycle

The accumulation of dissolved CO_2 in fish holding systems can be a greater danger to fishes than the accumulation of TAN. Fish generally produce 1.27 g CO_2 for 1.0 g of O_2 they consume (Grace and Piedrahita, 1994). Without proper control, the dissolved CO_2 will increase as a product of fish respiration and decomposition of organic material.

Excessive dissolved CO_2 concentrations slow CO_2 excretion from fish gills, causing increases in plasma CO_2 (hypercapnia). The immediate consequence is a blood pH decrease (respiratory acidosis), although this acidosis is compensated via plasma HCO_3^- increases over a period of hours (Janssen and Randall, 1975; Heisler and Neumann, 1980) to days (Crocker and Cech, 1998). Unless the intracellular pH of erythrocytes is protected (Nikinmaa et al., 1984), the ability of hemoglobin to bind O_2 at the gills is decreased producing hypoxemia (see Soivio and Nikinmaa (1981) for a further discussion on intraerythrocytic pH buffering). Oxygen sensors within the gill initiate increased ventilation frequencies and amplitudes during hypoxia (Daxboeck and Holeton, 1978). There is also evidence that gill structures sense CO_2 and pH within the blood (Perry and Gilmour, 2002). Hypercapnia can provoke vaso-constrictions, increased blood pressure, changes in aortic blood pressure (species-dependent), unconsciousness, and early mortality (Crocker et al., 2000; Perry and Gilmour, 2002).

The deleterious effects of dissolved CO_2 may be exacerbated by pH effects on fishes, making dissolved CO_2 management essential. For example, with increased photosynthesis, dissolved inorganic carbon rapidly decreases, shifting the dissociation equilibrium (Wetzel, 2001). A shift from CO_2 towards HCO_3^- and CO_3^{2-} decreases the pCO_2 in the water, and promotes a loss of CO_2 across the gills (Goss et al., 1998).

Recommendation for Short-Term Holding

For short-term holding, dissolved CO_2 needs to be monitored, particularly if the primary water source is groundwater. Typically dissolved CO_2 can be estimated by a meter but actual determination of the carbonates present requires subsequent calculations. If surface waters are used, high algal concentrations can produce hypercapnia along with hypoxia, particularly during the pre-dawn hours when respiration occurs at high levels from both algae and fishes, without O_2 production from photosynthesis. Air equilibration of water using vigorous mixing and agitation with stripping columns is an effective method for removing excess CO_2. The addition of bases (i.e. $Ca(OH)_2$, $NaHCO_3$ or $CaCO_3$) may help control dissolved CO_2 levels, increase pH, and shift the carbonate system. In stagnant systems (e.g., transport trucks), vents or blowers can reduce atmospheric pCO_2 above the tank. A recommended maximum dissolved CO_2 concentration range is 15–20 mg/L, though it is not strongly supported by research (Smart, 1981; Timmons et al., 2002). Higher dissolved CO_2 concentrations, 60–80 mg/L, are used as an anesthetic for brief periods (e.g., for fish weight and length measurements; Summerfelt and Smith 1990), but should be avoided for longer time periods due to possible tissue hypoxia and loss of physiological function(s).

Alkalinity

Alkalinity is the buffering capacity of the carbonate system in water (Wetzel, 2001). Chemically, alkalinity is the total amount of titratable bases in water expressed as milliequivalents per liter (meq/L) as calcium carbonate ($CaCO_3$; Timmons et al., 2002). Alkaline lakes with pH between 9 and 10, show higher concentrations of bicarbonate

(HCO_3^{1-}; 13–40 mM) and carbonate (CO_3^{2-}; 5 -133 mM). Alkalinity ranges from 5 to 500 mg/L as $CaCO_3$ for freshwater systems and 116–120 mg/L as $CaCO_3$ for saltwater systems (Stumm and Morgan, 1996; Timmons et al., 2002), and is affected by H^+, the carbonate cycle, temperature, and TDS. For example, if pH = 8.0 at 24 ºC in typical seawater, an estimated 8 percent of the alkalinity is in the CO_3^{2-} . Yet, in freshwater at the same pH and temperature, only 0.5 percent of the alkalinity is CO_3^{2-} (Spotte, 1970; Stickney, 1991, Boyd, 1997).

The pH directly affects the quantities of H_2CO_3, CO_3^- and CO_3^{2-} in alkaline water. This relationship is beneficial to prevent large pH-related effects on fish respiration or aquatic plant photosynthesis; but it can be deleterious during long-term holding of fishes (e.g., in aquaculture). In particular, for high-density systems and for determining flow rates through holding containers, the monitoring and adjustment of alkalinity and dissolved CO_2 concentrations is employed as a method for maintaining an optimal pH (Timmons et al., 2002).

Recommendation for Short-Term Holding

For short-term holding, some alkalinity is essential for maintaining optimal pH and supporting biological filters (see ammonia section). This is an issue for fish transportation when there is no water flow or attempt to improve water quality. Alkalinity is also used as an indicator of photosynthesis. Low alkalinity levels indicate low dissolved CO_2 and a weak carbonate buffering system, which are essential for photosynthesis. However, in the majority of short-term holding situations, photosynthesis is not important for maintaining DO.

Hardness

Water hardness, often confused with alkalinity because they are both reported as mg/L as $CaCO_3$, was originally based on the water’s ability to precipitate soap. “Hard” water required a larger soap amount to get the same cleaning action compared to “soft” water. Here, hardness is defined as the total concentration of divalent ions, typically calcium (Ca^{2+}, or magnesium [Mg^{2+}], iron [Fe^{2+}], or manganese [Mn^{2+}]) in terms of mg/L as $CaCO_3$.

In natural systems, total water hardness may range from 5 to 10,000 mg/L as $CaCO_3$, with soft water generally ranging over 0–75 mg/L, moderate over 75–150 mg/L, hard over 150–300 mg/L and very hard > 300 mg/L as $CaCO_3$ (Stumm and Morgan, 1996). Seawater has an estimated hardness of 6,600 mg/L as $CaCO_3$ (Timmons et al., 2002). Because hardness is dependent upon the mineral content of the watershed geology, hardness is sometimes correlated with alkalinity, especially in water derived from limestone basins. These waters can have similar hardness and alkalinity concentrations (Stumm and Morgan, 1996). However, many coastal-plain groundwaters or acidic waters have high hardness and low alkalinity concentrations (Timmons et al., 2002).

Effects of Water Hardness

Water hardness can ameliorate the effects for non-optimal levels of the pH, and dissolved metals and carbonates. Soft water, which is low in Ca^{2+} and other minerals, forces fish to increase the osmotic workload to replace electrolytes continuously lost. However, the fish will tolerate low calcium in water if it is introduced through the diet (Wedemeyer, 1996). Dissolved Ca^{2+} protects against ion loses by limiting gill membrane permeability, specifically the channels that are permeable to OH^- (Howells et al., 1983). Water hardness > 150 mg/L as $CaCO_3$ minimizes the toxicity of trace elements. With increasing water hardness, fish can tolerate high doses of copper. For example, with a water hardness of 10 mg/L as $CaCO_3$ fish can tolerate 0.001 mg Cu/L, whereas at a water hardness of 300 mg Cu/L as $CaCO_3$ the tolerated level increased to 0.28 mg Cu/L (Alabaster and Lloyd, 1982).

Water hardness affects osmoregulation and reduces disease incidence and/or severity (Fryer and Lannan, 1993, Wedemeyer, 1996). In freshwater systems, hard water can be beneficial to fish because it provides the necessary Ca^{2+} and reduces energetic expenditures to replace lost electrolytes. Dissolved Ca^{2+} is important to support newly fertilized freshwater eggs, and for the calcification of larval skeleton structures (Alabaster and Lloyd, 1982). For example, red drum, *Sciaenops ocellatus*, kept in a low hardness water experienced reduced survivability (Pursely and Wolters, 1994), possibly due to the inability of fish to osmoregulate effectively in waters with low divalent cation concentrations. Conversely, high water hardness can be detrimental to salmonid eggs and larvae (Ketola et al., 1988).

Recommendation for Short-Term Holding

Because water hardness is important for development and osmoregulation, water hardness, particularly Ca^{2+} and mg^{2+} concentrations should be monitored in freshwater, short-term holding systems.

SECTION 2: STOCKING DENSITY AND CONFINEMENT

Holding fishes at high densities is known to adversely affect many biological functions including metabolism (Vijayan et al., 1990; Christiansen et al., 1991; Jørgensen et al., 1993; Montero et al., 1999; Barton et al., 2002), growth (Refstie, 1977; Trzebiatowski et al., 1981; Vijayan and Leatherland, 1988; Soderberg et al., 1993; Procarione et al., 1999), health and immune function (Pickering and Pottinger, 1987; Yin et al., 1995; Demers and Bayne, 1997; Rotllant et al., 1997; Ortuño et al., 2001), corticosteroid responses (Leatherland and Cho, 1985; Schreck et al., 1985; Kebus et al., 1992; Mazur and Iwama, 1993; Ruane and Komen, 2003), agonistic behaviors (Fenderson and Carpenter, 1971, Li and Brocksen, 1977; Fagerlund et al., 1981; Fleming and Johansen, 1984; Brown et al., 1992), and survival (Soderberg and Krise, 1986; Soderberg and Meade, 1987; Plumb et al., 1988; Holm et al., 1990; Kwak and Henry, 1995). Despite numerous studies on the effects of stocking density and confinement on various physiological aspects of fishes, there is a lack of consensus in the literature as to how these processes are affected in fishes held in unnatural settings.

It is important to note the difference between loading and density when addressing carrying capacity for certain system. Loading is defined as the weight of fish per unit of flow (kg/L/min), while density refers to the weight of fish per unit space (kg/m^3). Density can be multiplied by rearing volume to determine fish biomass. Flow rate is also related to biomass and loading. Each of these relationships provides parameters for designing aquaculture production systems.

Confinement can refer to either the entire volume of a small tank (Pankhurst and Sharples, 1992; Clearwater and Pankhurst, 1997; Carey and McCormick, 1998; Hobby et al., 2000; Fevolden et al., 2003) or to a restricting net placed within the larger volume of a tank (Carmichael et al., 1984b; Haux and Sjöbeck, 1985; Strange and Cech, 1992; Ruane et al., 1999). In either case, confinement causes fish to be in close proximity to one another where the number of fish or biomass per volume (density) may be the same. For example, fish confined in a, 20-L net within a 75-L tank experience the same density as fish simply confined to a, 20-L tank. However, if the system is a static (non-flowing) one, the fish confined to the, 20-L tank have a decreased volume for water exchange, potentially affecting water quality and related stress responses. Confinement stress results when space requirements are not met, stimulating a physiological response. Confinement stress is often associated with high stocking density and leads to crowding stress. Acute stress is of short duration allowing the fish to respond to the stressor(s) and recover (i.e., return to homeostasis), whereas chronic stress is long-term with more severe effects (Pickering, 1981; Barton et al., 2002). Physiological responses in affected fishes reflect the duration and intensity of the confinement (or water-quality-associated stressors). Intense, short-term crowding stress that commonly occurs in aquaculture, commercial and recreational fishing, stocking, and salvage practices, possesses characteristics of chronic as well as acute stress, including compromised immune systems resulting in disease or death. Therefore, it is important not to exceed optimal densities for held fishes, regardless of profitability or convenience (see Ellis et al., 2002 for review with published stocking densities of rainbow trout).

High densities contribute to deteriorating water quality when being held in systems with inadequate filtration or water flow (see Water Quality section; Pickering and Stewart, 1984; Wedemeyer et al., 1990; Kebus et al., 1992). High fish densities can lead to hypoxia and accumulation of ammonia, which can be detrimental to fish health. Relationships among fish biomass (kg), temperature, and oxygen levels have been determined for rainbow trout, channel catfish, black basses, *Micropterus* spp., and walleye, *Sander vitreus* (Piper et al., 1982; Schramm and Heidinger, 1988; Goeman, 1991; Hartley and Morning, 1993). However, fish biomass may be just one measure of fish density for predicting water quality changes or stress effects. For example, does one large fish have the same effects as multiple smaller fish of the same total biomass? Piper et al. (1982) suggest that the maximum permissible biomass of rainbow trout that can be held is directly proportional to length. Presumably because of the allometric relationship between body mass and metabolism, a smaller mass of small fish can be held per volume water compared to the same mass of large fish (Piper et al., 1982; Wedemeyer, 1996). Because maximum and optimal stocking densities vary with species, body size, life stage, and holding conditions, more investigation is needed in determining optimal fish density capacities.

Metabolism and Growth

Metabolism and growth are mediated by underlying physiological substances and mechanisms. Corticosteroids (e.g., cortisol) affect growth and other functions through the hypothalamic-pituitary-interrenal (HPI) axis in teleost fish (Vijayan and Leatherland, 1990; Barton and Iwama, 1991; Barton et al., 2002). Cortisol increases, typifying a primary stress response in teleosts, promote gluconeogenesis. This mobilization of energy reserves, in response to possible demands of overcoming stressors, may deprive energy that would otherwise be invested in growth, reproductive capacity, and performance (Vijayan et al., 1990; Barton et al., 2002). High stocking density impacts metabolism and growth, most often attributed to decreased food consumption and conversion (Refstie, 1977; Vijayan et al., 1990; Alanärä and Brännäs, 1996), agonistic social interactions (see Behavioral and Predatory Impacts section; Fenderson and Carpenter, 1971; Refstie and Kittelsen, 1976; Fleming and Johansen, 1984; Brown et al., 1992; Wedemeyer, 1996; 1997), or diminished water quality (see Water Quality section; Pickering and Stewart, 1984; Kwak and Henry, 1995; Plumb et al., 1988). This expenditure of a fish’s energy reserves is exacerbated by reduced food consumption (Refstie, 1977; Vijayan et al., 1990; Alanärä and Brännäs, 1996). Vijayan et al. (1990) suggest that food consumption decreases, as a response to a stressor (e.g., high stocking density) may be an adaptation by which stored body reserves are directed for utilization in maintenance functions. (See figure 1.)

High stocking density affects lipid and fatty acid metabolic pathways. Crowded fishes have been shown to increase mobilization of triglycerides to meet metabolic demand by improving the gluconeogenic capacity from glycerol (Vijayan et al., 1990; Montero et al., 1999). Liver weight and the hepatosomatic index are thus significantly reduced due to higher hepatic lipid utilization (Leatherland and Cho, 1985; Papoutsoglou et al., 1987; Vijayan et al., 1990; Montero et al., 1999; Barton et al., 2002). At the same time, liver 3-hydroxylacyl CoA dehydrogenase, an enzyme implicated in ß-oxidation, is elevated (Vijayan et al., 1990). Fatty acid composition of the liver is altered due to high stocking density, which can be observed by the reduction in oleic acid. Oleic acid is one of the principal lipid energy sources when fishes are under high energy demand (Montero et al., 1999). Another principle energy source is glycerol, which is mainly metabolized in the liver. Elevations of glycerol metabolizing enzymes (i.e., glycerol kinase, glycerol-3-phosphate dehydrogenase) of fishes held at high density suggest that this condition enhances the gluconeogenic process from glycerol (Vijayan et al., 1990). These precursors are utilized to make glycogen for storage in the liver; however the increased maintenance requirements of a fish under stress exceeds the rate of glycogen synthesis, resulting in a glycogen debt. Thyroid hormones, which promote protein synthesis (i.e., anabolic processes), are at reduced levels in the plasma of fishes held at high densities (i.e., thyroxin [T4]; Vijayan et al., 1990). This suggests a density-dependent inhibition to thyroxin production which may result from decreased food consumption.

The influence of fish-holding densities on growth can be mediated by other variables (e.g., experimental conditions, water quality, agonistic behavior, fish size). High densities can decrease rainbow trout growth (Trzebiatowski et al., 1981; Procarione et al., 1999), although Kebus et al. (1992) and Li and Brocksen (1977) found that confinement of rainbow trout at high densities did not affect their growth. However, Kebus et al. (1992) conducted their experiments at 5–10 °C less than that conducted by Procarione et al. (1999), possibly influencing their results. High stocking densities reduced feeding activity and food conversion rates in Atlantic salmon, coho salmon, brook charr (*Salvelinus fontinalis*), and lake charr (*Salvelinus namaycush*), where stress was the primary contributing factor (Refstie and Kittelsen, 1976; Fagerlund et al., 1981; Vijayan and Leatherland, 1988; Elrod et al., 1989; Vijayan et al., 1990). Jørgensen et al. (1993) found that Arctic charr (*Salvelinus alpinus*) held at low densities (<25 kg/m^3) had lower growth rates but similar cortisol levels than those fish reared at high densities. Peak growth rates for Arctic charr occurred at approximately 100 kg/m^3, while growth rates ranged between 10–25 kg/m^3 for other salmonid species (Trzebiatowski et al., 1981; Wallace et al., 1988; Brown et al., 1992; Jørgensen et al., 1993). Increased growth rate at increased densities for Arctic charr may be strongly influenced by behavior (see Behavioral and Predatory Impacts section; Wallace et al., 1988; Brown et al., 1992).

Investigations of metabolic rates assessed by cardiac responses during live-well retention under different stocking densities have revealed that as density increased, cardiac output and heart rate also increased while stroke volume remained the same (Cooke et al., 2002). When smallmouth bass (*Micropterus dolomieu*) were alone, recovery from handling stress was found to take only an hour for cardiac parameters to return to basal levels while in live-wells with continuous flow-through water conditions. However, when fish density was greater than one fish, angling/handling-associated metabolic rate increases and variable cardiac activity failed to return to prehandling levels during 6 hours of live-well confinement (Cooke et al., 2002). Parker (1973) noted that *Micropterus*, a documented (and cannibalistic) predator was the only fish that did not display a conspecific group-associated decrease in metabolic rate. Another interesting finding from the Cooke et al. (2002) study is that the addition of salt and water conditioners more than doubled the time required for cardiac parameters to normalize. These findings contradict others that have found stress to be minimized by the addition of salt, water conditioners, and antibacterial agents (Carmichael et al., 1984b; Plumb et al., 1988; Swanson et al., 1996).

Corticosteroid Response

Studies examining stress-related effects of high fish densities within a holding container have shown conflicting results. Observed differences in the stress response can most likely be attributed to different species, life stage, size, behavior, nutritional status, amount of handling, sampling techniques and time of sampling. In addition, direct comparisons of absolute plasma cortisol concentrations, as a measure of the primary stress response between species, are complicated by different handling protocols, husbandry, and tameness of fish that can generate substantial plasma cortisol concentration differences (Pankhurst and Sharples, 1992). Woodward and Strange (1987) found that confinement of wild rainbow trout for 6 hours resulted in plasma cortisol concentrations nearly three times higher than hatchery stock that were under the same conditions. However, cultured rainbow trout (>2 years old) can acclimate to a confined space within 2 weeks, expressed by the return of cortisol to basal levels (Pottinger and Pickering, 1992). Many authors have reported a temporary increase in blood glucose and/or plasma cortisol levels during crowding under high densities (Schreck, 1981; Carmichael et al., 1984a; Woodward and Strange, 1987; Barcellos et al., 1999; Ruane et al., 2002), while others have observed no effect (Vijayan et al., 1990; Kebus et al., 1992; Procarione et al., 1999). These inconsistencies may reflect sampling differences due to handling, because elevations in plasma cortisol associated with crowding stress are much less than those due to handling (Robertson et al., 1988; Ruane and Komen, 2003). For example, rainbow trout show either an increase (Pickering and Stewart, 1984; Pottinger and Pickering, 1992), a reduction (Leatherland and Cho, 1985), or no response (Kebus et al., 1992; Procarione et al., 1999) in plasma cortisol levels due to high densities or confined space. Therefore, the return of plasma cortisol concentrations to basal levels in a chronically stressed fish may not indicate a return to unstressed homeostasis. Such a return may reflect the effects of a negative feedback mechanism due to a prior cortisol spike on the HPI axis (Rotllant et al., 2000). Vijayan and Leatherland (1990) found that this phenomenon was not due to a reduction in cortisol secretion rate, but may reflect changes in cortisol metabolism. They found no effect of density on the metabolic clearance rate of cortisol in brook charr, but observed an elevated uptake of cortisol by the liver, where it is metabolized and excreted in the bile. Chronic crowding under high densities of young coho salmon appears eventually to lead to increased cortisol clearance rates (Schreck et al., 1985). Ruane and Komen (2003) found common carp (*Cyprinus carpio*) plasma cortisol levels were highest when initially introduced to high densities, and then returned to basal levels in a few days. Pankhurst and Sharples (1992) also discovered that cortisol levels of snapper (*Pagrus auratus*) were initially elevated and remained high until after 60 min of confinement. Due to its relatively fast transient response as a primary stress indicator, plasma cortisol levels may be an unreliable chronic stress indicator for overcrowding.

Plasma cortisol affects carbohydrate metabolism by stimulating glucose production through gluconeogenesis resulting in an elevation of plasma glucose (Barton and Iwama, 1991). Measuring fluctuations in blood glucose in addition to cortisol levels has become one of the most widely used techniques to monitor stress in fish (Pickering and Pottinger, 1989; Barton and Iwama, 1991), especially for acute stress because they return to basal levels within 24 hours (Pickering and Pottinger, 1989; Carmichael et al., 1984b). Fish held at high stocking densities are more likely to show increased levels of plasma cortisol and plasma glucose than those held at lower densities and may be incapable of acclimating to the crowded conditions (Clearwater and Pankhurst, 1997; Vazzana et al., 2002), although other findings suggest that brown trout (*Salmo trutta*) and rainbow trout can acclimate to high densities (Pickering and Stewart, 1984; Pottinger and Pickering, 1992).

Only a few studies have investigated the role of life stage development on cortisol and stress responses of fish. Larval rainbow trout respond to acute stress with elevated levels of cortisol at only 2 weeks after hatching, demonstrating that the HPI axis is fully developed by this stage (Barry et al., 1995). Atlantic salmon parr are less responsive to confinement than smolts (Carey and McCormick, 1998). Naturally occurring plasma cortisol increases during the parr-smolt transformation phase are associated with lipid metabolism, increase in gill Na^+, K^+–ATPase activity, activation of saltwater-type gill chloride cells, and osmoregulation in marine environments. These factors may increase the responsiveness of the HPI axis on their ocean migration. Because of already heightened cortisol levels and increased responsiveness to environmental stressors, care should be taken when handling, holding, and transporting salmonid smolts to minimize negative effects and mortality.

The mechanisms through which reproduction is affected by stress are not fully understood; however, there is evidence that reproduction is mediated by cortisol (Carragher et al., 1989; Campbell et al., 1992; 1994; Foo and Lam, 1993; Hobby et al., 2000). Increased levels of plasma cortisol result in lower levels of plasma androgens and estrogens in stressed fishes (Pickering et al., 1987; Pankhurst and Dedual, 1994; Clearwater and Pankhurst, 1997). There may be an effect of stress on metabolism and clearance of steroid hormones from the plasma. Whereas sex steroid binding protein protects androgens and estrogens from metabolism and aids in transport to target tissues, cortisol has been identified as a chief component of stress that changes the concentration of sex steroid binding protein and its binding characteristics (Hobby et al., 2000). Estradiol bound to sex steroid binding protein is not normally displaced by physiological levels of cortisol; however, it can be under extraordinary circumstances, such as, when the cortisol concentration is two orders of magnitude greater than that of estradiol (Hobby et al., 2000). Both rainbow and brown trout subjected to acute and chronic stressors before spawning exhibited reduced egg sizes, reduced sperm counts, and decreased survival rates of progeny (Campbell et al., 1992; 1994). Tank confinement (1–96 hours) initially increased plasma cortisol levels and decreased estradiol and testosterone levels. The sex hormones remained low, indicating no recovery of steroidogenesis in confined fish (Clearwater and Pankhurst, 1997; Hobby et al., 2000).

Health and Immune Function

Fish immune function responses to stress indicate that the type, intensity, and duration of the stressor are major determinants of the immune response. Improved fish immune function (i.e., increased concentrations of lysozymes, cytotoxic cells, and phagocytes; Demers and Bayne, 1997; Ruis and Bayne, 1997; Ortuño et al., 2001) has been observed following an acute stress. In these cases, the fish's body mobilizes the immune system after acute stress, presumably protecting itself from potential subsequent trauma. Most often, deleterious effects associated with immune system dysfunctions result from both severe acute and chronic stress (Yin et al., 1995; Ortuño et al., 2001; Vazzana et al., 2002). Elevated (especially, prolonged) plasma cortisol levels act as an immunosuppressant in fish, reducing the number of leukocytes in the circulating blood and phagocytic activity (Pickering and Pottinger, 1989; Barton and Iwama, 1991; Montero et al., 1999; Vazzana et al., 2002).

Cellular immune responses to stress can also be affected by stress. Crowding stress can elicit a decrease in the chemiluminescent response of pronephros (kidney) cells in fish, depressing the phagocytic function of leukocytes (Yin et al., 1995; Vazzana et al., 2002). Monocyte and granulocyte concentrations are mobilized to the circulating blood from the head-kidney for 48 hours after exposure to a stressor (Ortuño et al., 2001). Despite their significant increase in number, the phagocytic ability of these leukocytes is significantly reduced immediately after stress (apparently due to incomplete development), and normal immunocompetence may not recover for more than 48 hours (Ortuño et al., 2001; Vazzana et al., 2002). Short-term crowding stress also depressed serum hemolytic activity, an important humoral immune parameter (Ortuño et al., 2001). Increases in hematocrit, hemoglobin, and erythrocyte count have been also observed and may suggest a strategy for increasing the blood's oxygen carrying ability during metabolically challenging periods (Montero et al., 1999). Data suggest that even short duration (i.e., a few hours) confinement exposure under high fish densities elicits an immune response and might result in a reduced immunocompetence (Yin et al., 1995; Ortuño et al., 2001).

Survival

There is a lack of consensus in the literature whether survival is density-dependent when holding fishes. In most studies survival decreased with increasing density (Refstie, 1977; Trzebiatowski et al., 1981; Soderberg and Krise, 1986; Kindschi et al., 1991b; Pickering et al., 1991), some showed no effect (Kilambi et al., 1977; Kwak and Henry, 1995; Miller et al., 1995; Soderberg et al., 1983, 1993), while a few others have reported survival increasing with increasing density (Trzebiatowski et al., 1981; Papoutsoglou et al., 1987; Kjartansson et al., 1988; Bagley et al., 1994).

Mortality at high-densities has been commonly ascribed to poor water quality, predation/cannibalism, and disease (see respective sections: Water Quality, Behavioral and Predatory Impacts, and the health and immune function subsection above). Poor water quality can place an extra burden on an already physiologically compromised fish under high densities. Dissolved oxygen concentration may be low or toxic compound (e.g., ammonia) concentrations may be high in the water. The risk of pathogen transmission in high stocking-density systems is elevated because of the closer proximity of fish (Bosakowski and Wagner, 1994a; Wedemeyer, 1996). Conversely, mortality at low densities may be attributed to increased (and often severe agonistic) behaviors, discussed above, that may alter the fish's feeding behavior making them more susceptible to disease.

Fish survival may differ due to species, origin and holding conditions. Domestic and wild strains of fish may not respond similarly to crowding. Soderberg et al. (1993) observed that Atlantic salmon could be reared at 14 kg/m^3 without detrimental effects to growth and survival and that density should not exceed 26 kg/m^3. The higher permissible holding densities are achieved with lower water temperatures, although other factors may be important also (Soderberg and Meade, 1987; Soderberg et al., 1993). Their holding density capacity is much less than that determined for other salmonids, such as, rainbow trout (Buss et al., 1970). Jørgensen et al. (1993) reared Arctic charr at more than 100 kg/m^3 without mortalities, while a few mortalities were observed at lower densities.

High stocking densities increase the demand for oxygen, which may affect the activity level of confined fishes. Increased activity during confinement may lead to additional physiological stress and physical harm that may be detrimental to a fish's survival. Cooke et al. (2002) discovered that smallmouth bass when held alone in a 75-L live-well had high swimming activity only when first introduced. When more than one fish was held, fish expressed variable and increased swimming activity. The increased metabolic cost of heightened locomotor activity coupled with other stressors can lead to reduced survival rates (Goeman, 1991; Cooke et al., 2000; 2002). We speculate, that this may not be the case for more social, shoaling fishes (e.g., shad, mullet, herring, tuna) and these fishes may react differently as conspecifics are added to the holding container. Socially complex fishes may prefer to be with other members of their species, possibly resulting a calming effect while under stress. More research is needed to define the relationships between social behavior of fishes and their physiology.

Most often, mortality of fishes held for relatively short periods is not the result of a single stressor. The cumulative and physiologically interactive effects of sublethal stresses that occur during capture, handling, confinement, and transport may be lethal, even if each independently does not exceed a physiological threshold (Carmichael et al., 1984b; Barton et al., 1986).

SECTION 3: HOLDING CONTAINER DESIGN

Successful holding of fishes requires creation of a favorable environment. The basic principles of fish holding structures include minimal stagnant regions, adequate removal of solids, and an even distribution of dissolved oxygen, metabolites, and/or food. Most fish holding containers (e.g., tanks, raceways, ponds, silos, live-wells) have been designed for efficiency, profitability, and maximum carrying capacity, with less attention to container-related effects on the fish. Container design directly and indirectly affects the functionality (e.g., metabolic rates) and health of fishes (Burrows and Chenoweth, 1955; Kindschi et al., 1991a; Barnes et al., 1996; Cooke et al., 2002). Ideally, a fish holding system for mixed species or size groups might include areas with characteristics that meet species or life stage requirements. However, there is little documentation of short-term holding effects on fishes, especially from wild habitats, and the types of structures used to keep them.

It is useful to define different holding container designs. Tanks refer to smaller, portable holding containers (which are usually < 4 m diameter, but may be many meters in diameter), while ponds refer to larger, permanently installed basins usually constructed of concrete or dirt (Wheaton, 1977; Klapsis and Burley, 1984). Most modern tanks are constructed from fiberglass, plastic, acrylic, or aluminum. Tanks may also be constructed from glass, wood, concrete, stainless steel, galvanized iron, and sheet metal (Piper et al., 1982). Fiberglass is a superior building material because it can be shaped into any configuration and is strong, easy to repair, simple to clean, corrosion-free, nontoxic to fish, and chemically unreactive with water. An additional criterion for a building material is that it can be made smooth, so that the interior of the tank will not damage fins or flesh upon contact. Rough, porous surfaces (e.g., concrete or wood) can also harbor disease and make it very hard to treat with antibiotics or fungicides (Wheaton, 1977; Piper et al., 1982). An epoxy or rubberized coating can correct this problem in concrete fish holding structures. Metals (e.g., iron, steel, and aluminum alloys) tend to corrode with time, leaching metals into the water, especially in saltwater applications. Examples of the more common configurations are discussed below, along with possible affects on fishes. (See table 3).

TABLE 3.—Advantages and disadvantages of different tank designs

Tank design	Flow	Distribution	Floor space	Fish removal	Risk of injury to fish	Water quality	Self cleaning
Circular	Uniform, high velocity	Homogenous, orient upstream	Poor	Difficult	Low	Dead spaces	Yes
Square	Uniform flow	Crowding in corners	Good	Moderate	Low	Improved, few dead spaces	Yes
Raceway-type	Continuous low velocity	Aggregations, orient downstream	Good	Moderate	High	Gradient downstream	No
Raceway with baffles	Continuous higher velocity, flow along bottom	Large fish aggregate in top end , fish size decreases downstream	Good	Moderate	Higher	Improved	Yes
Rectangular cross-flow and rectangular mixed-cell	Mixing flow, higher velocity	More uniform, orient laterally	Good	Moderate	High	Uniform	Yes
Oval	Non-uniform	Species and size distribution	Poor	Difficult	Low	Non-uniform	No
Foster-Lucas	Poor circulation	Aggregations	Good	Moderate	High	Poor, many dead spaces	No
Rectangular Circulating	Uniform	homogenous	Poor	Moderate	Low	Improved	Yes
Silo and Upwelling	Upwelling from bottom	Randomly	Poor	Difficult	Low	Improved	Yes

Circular Tanks

Circular tanks are generally constructed with influent water creating a vortex circulation to a bottom center drain by way of a standpipe (figure 5). As early as, 1904, circular shaped salmon rearing tanks had been designed with perforated water injection pipes to stimulate spiral flow to a center outlet (Cobb and Titcomb, 1930). Circular tanks were not popular for many years because they provided relatively poor water conditions for holding fish (e.g., due to poor water mixing patterns in early designs), and the shape made it difficult to remove fish (Larmoyeux et al., 1973). The hydraulic characteristics of circular tanks have been well studied and reviewed by Cobb and Titcomb (1930); Burrows and Chenoweth (1955); Larmoyeux et al. (1973); Timmons et al. (1998).

Flow patterns in circular tanks are a function of depth, diameter, and the type of influent flow. Burrows and Chenoweth (1955) reported poor mixing patterns in circular tanks caused by relatively short circulating currents. These flow patterns were beneficial for self-cleaning, where the brief vortex water pattern sweeps across the bottom of the tank to the center drain screen. However, this type of flow can lead to dead zones within the water column, where there is little or no mixing, resulting in regionally poor water quality (figure 4). An increase in depth-diameter ratios causes an increase in dead zone area (Larmoyeux et al., 1973). Burrows and Chenoweth (1955) also reported similar findings for Foster Lucas and raceway type ponds (figures 9 and 7, respectively). In tanks with dead zones, fish distribution can be sporadic, however, if dead zones in circular tanks are minimized, fish distribution is quite uniform (Burrows and Chenoweth, 1955; Larmoyeux et al., 1973). Circular tanks can be superior to most other fish holding vessels by optimizing the design of the water inlet structure with sufficient water pressure for mixing and reaeration, and also creating water exchange rates that do not lead to the accumulation of nitrogenous wastes (Larmoyeux et al., 1973; Timmons et al., 1998).

It has been speculated that pelagic fishes should be kept in circular structures, where they can constantly swim and are not impeded by walls (Nicholson et al., 1992). Ross and Watten (1998) observed that circular tanks had a dramatic effect on orientation and most fish tended to swim directly into the current (upstream). They also exhibited a significantly reduced pivot or turning frequency, which probably reflects homogeneity of current direction and velocity (Ross and Watten, 1998). Furthermore, pelagic fishes tend to perform poorly in structures with corners (e.g., raceways and square tanks) where they can aggregate (Burrows and Combs, 1968).

Circular tanks tend to have relatively high circulating flows providing conditioning for fish that will benefit them upon release in the wild (Wheaton, 1977). Unfortunately, high flows may cause stress for small or weak fish. If the influent water is reduced, resulting in decreased flows, dead zone area will increase, leading to decreased efficiency of the flow’s self-cleaning action. Fish that are exercised have a greater metabolic demand. However, fingerling chinook salmon (*Oncorhynchus tshawytscha*) held in circular tanks grew at the same rate as those fish held in large ponds, and higher than those held in

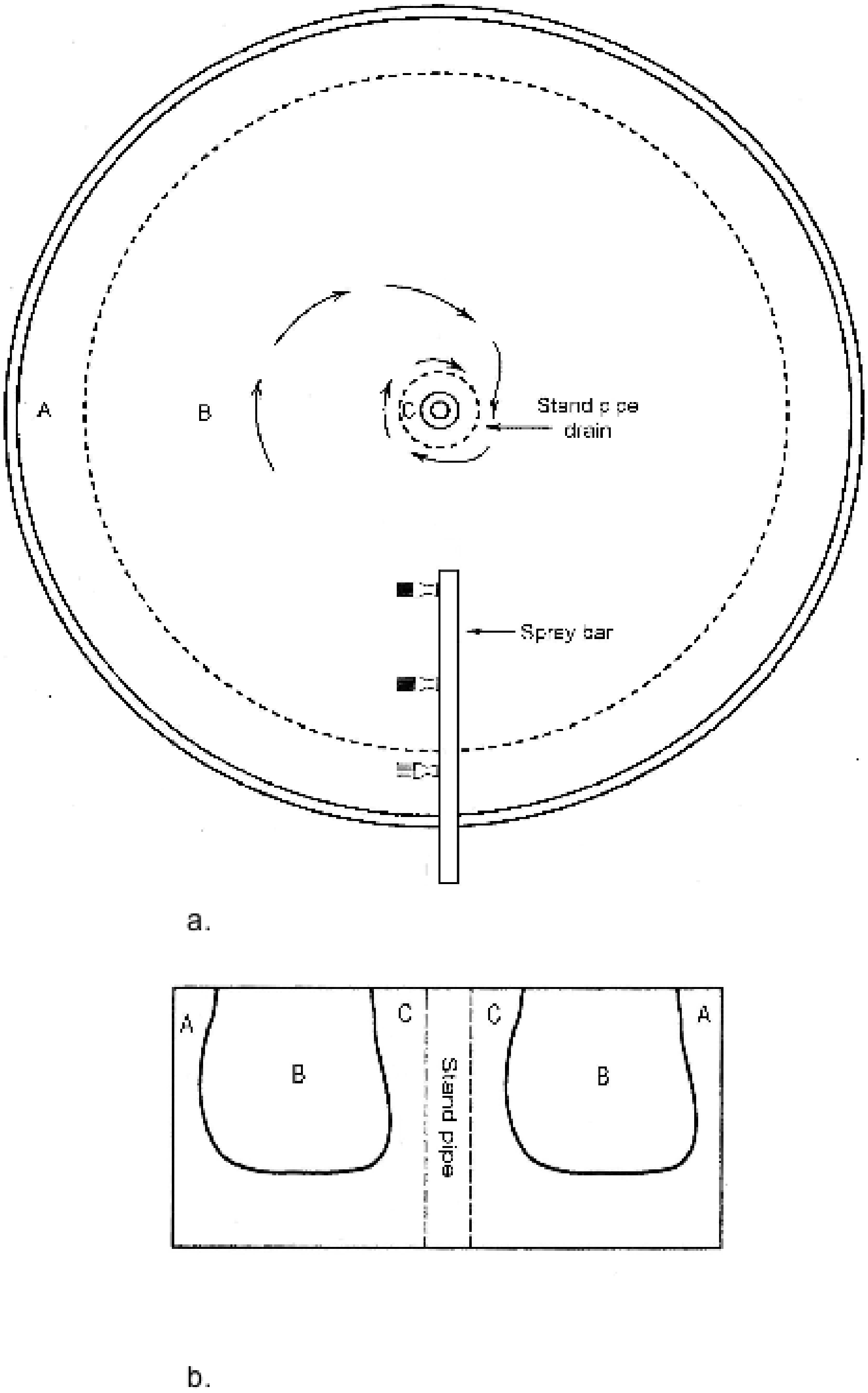


FIGURE 5.—(a) Circular tank design and (b) resulting dead zones, cross-section view (modified from Wheaton, 1977; Klapsis and Burley, 1984).

raceways (Johnson and Gastineau, 1952). Disparately, Palmer et al.(1952) found no difference, and Ross et al. (1995) observed that rainbow trout in circular tanks had the least amount of growth in terms of biomass gain. In addition, Kelly and Kohler (1996) reported no differences in survival, growth rate, or food conversion of striped bass (*Morone saxatilis*), sunshine bass (♀ *M. chrysops* x ♂ *M. saxatilis*), and palmetto bass (♀ *M. saxatilis* x ♂ *M. chrysops*) reared in circular versus rectangular tanks. Furthermore, Ross and Watten (1998) found no difference in biomass gain among different tank designs for lake charr, but did reveal at high velocities, circular tanks were the least likely to produce more robust fish.

Although circular tanks are not as efficient at conserving floor space and are more difficult to remove fish because of the lack of corners to crowd them, this design provides many important advantages including relatively low building costs, a self-cleaning action, and ease in creating desirable water velocities.

Square Tanks

Square tanks are not as common as circular designs, but they tend to fit better in smaller facilities (figure 6). Burley and Klapsis (1985) analyzed the hydraulic performance of a 1-m square tank. They concluded that a square tank with four symmetrical jets of water entering from each corner and exiting after tank rotation through a center drain could provide a uniform flow of water with less dead zone than a circular tank. Elvers (i.e., young eels) that were placed into the square tank were found to distribute themselves evenly throughout the tank. It is important to note that elvers are fairly tolerant of hypoxia, decreasing their value as a rectangular tank test species for fish distributional non-uniformity due to dead zones (Cruz-Neto and Steffensen, 1997). Quadrangular tanks may also be poor for holding wild fishes, they tend to crowd into corners of the tank where they may deplete the local oxygen causing stress and possibly death. By trying to swim into the corner to get out, they risk physical injury or may exhaust themselves (Wheaton, 1977).

Raceway-Type Ponds/Tanks

Raceways, sometimes referred to as plug-flow tanks, are shallow rectangular ponds or tanks. They are commonly made from concrete and operate under a continuous flow of water (Losordo and Westers, 1994; Ross et al., 1995) (figure 7). They are normally much longer than they are wide and have relatively shallow depths (1 to 2 m maximum, Wheaton, 1977). Because the water is continuously flowing, a large volume of water is required. High fish densities can be maintained because of this flow-through water system (Wheaton, 1977; Klapsis and Burley, 1984; Ross et al., 1995). However, if raceways are designed to run in series to conserve water, the outflow from one becomes the inflow of the next. This accumulates wastes and decreases dissolved oxygen

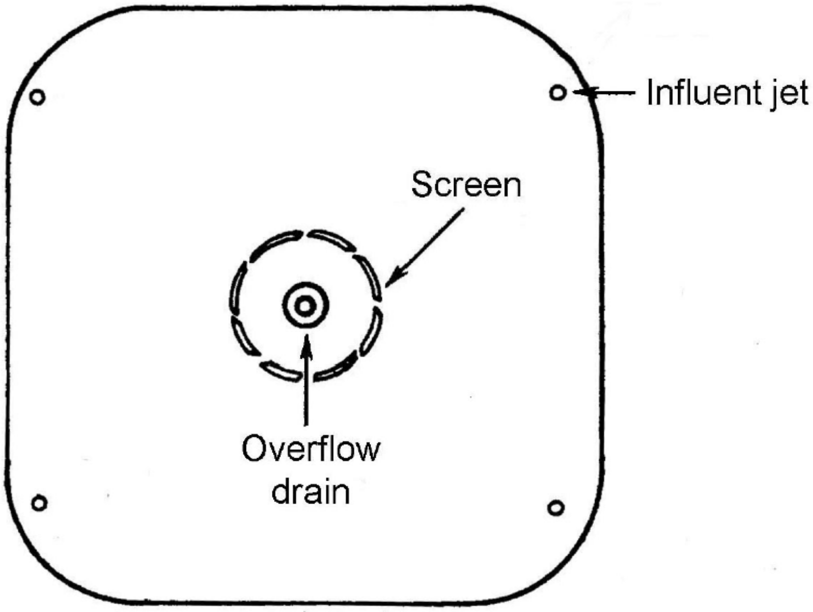


FIGURE 6.—Square tank design (modified from Burley and Klapsis, 1985).

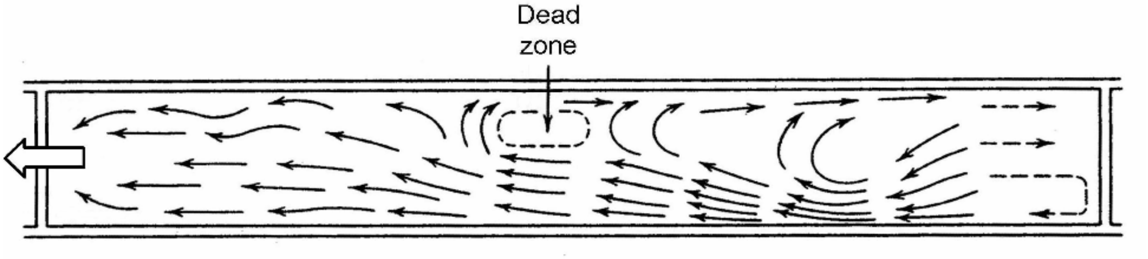


FIGURE 7.—Raceway design (modified from Wheaton, 1977; Klapsis and Burley, 1984).

concentrations. Poor water conditions in the series can limit growth and influence survival, especially if densities are high and the species are sensitive to less than optimal water quality. Raceways are often configured in a parallel manner to alleviate this problem, if water is not limited (Wheaton, 1977). Even so, the design of raceways produces a distinct gradient in water quality from the inflow downstream to the outflow (Lorsodo and Westers, 1994). Generally, dissolved oxygen levels decrease, while ammonia and carbon dioxide increase.

Fin abrasion is a common problem when fish are held at high densities in tanks, concrete ponds, and raceways (Kindschi et al., 1991a; Bosakowski and Wagner, 1995). Worn fins can make the fish susceptible to microbial infection and hemorrhaging, which may lead to fin loss (Schneider and Nicholson, 1980; Goede and Barton, 1990; Bosakowski and Wagner, 1995; Barton et al., 2002). Infection and fin loss would likely reduce swimming performance, hence survival in the natural ecosystems (Nicola and Cordone, 1973; Bosakowski and Wagner, 1995; Wagner et al., 1996). Fishes held in raceways with concrete bottoms showed significantly reduced relative fin length compared to those with earthen bottoms. Bosakowski and Wagner (1994a, 1994b, and, 1995) found that fin condition improved in fishes reared in raceways with natural bottom substrates (gravel or dirt). However, coble and earthen bottoms present potential drawbacks in inefficient collection of fishes by providing escape routes and hiding places from nets or screens. Also, during longer holding times, sinking foods are easily lost in the substrate and not eaten by fish, decreasing food conversion and growth (Bosakowski and Wagner, 1995; Wagner et al., 1996). Furthermore, this uneaten food typically accumulates in substrate niches increasing bacteria growth and system oxygen demand (Wagner et al., 1996).

Cleaning tanks and raceways may not only cause physical injury to fishes, resuspended waste reduces water quality which may increase stress (Wood, 1979; Post, 1983). A major drawback of raceways is that overall they are not self cleaning. Water velocities are generally very low, 1–3 cm/s, which cause feces and excess feed to settle and accumulate on the bottom (Losordo and Westers, 1994). Fish swimming activity can exacerbate this problem by resuspending this material taking longer for it to settle. To facilitate the self cleaning of fish-holding structures, there must be at least a 6 cm/s (0.2 ft/s) flow velocity (Burrows and Chenoweth, 1970). Raceway baffles have been developed to maintain water flow along the bottom of the raceway and facilitate the movement of solid fish wastes and uneaten food to the effluent end of the raceway (Boersen and Westers, 1986). Baffles affect fish size distribution within raceways; larger fish tend to aggregate in the top section at the influent end, and fish size decreases toward the downstream, effluent end (Kindschi et al., 1991c). But even with the improved water quality as a result of installing baffles, some cultured (e.g. lake charr) and wild fishes do not survive well in raceways with baffles. They tend to aggregate in certain areas and suffocate due to localized hypoxia (Boersen and Westers, 1986; Kindschi et al., 1991c). On the other hand, the hydraulic action from baffles may create a more natural environment than that in standard raceways for some salmonids (Tipping, 1998). Without baffles rainbow trout tend to orient themselves downstream in raceways (Ross and Watten, 1998). Barnes et al. (1996) also found that while baffles improved water quality and maintenance within concrete raceways, they also increased pectoral and pelvic fin erosion in rainbow trout compared to raceways without baffles. It has been speculated that reduction in pectoral and pelvic fin length occurred because of the abrasion during fish movement under the baffles and along the bottom because of the resulting water flow (Barnes et al., 1996). However, Ross and Watten (1998) discovered that salmonids had contact with the sides of rectangular tanks more often than other tank types. Furthermore, Kindschi et al. (1991b) found poor fin quality a result of daily dewatering and cleaning of raceways without baffles.

Rectangular Cross-Flow Tanks and Rectangular Mixed-Cell Tanks

Both rectangular cross-flow tanks and rectangular mixed-cell tank designs provide means to convert a rectangular raceway into a more thoroughly circulated tank (Watten and Beck, 1987; Watten and Johnson, 1990; Watten et al., 2000). The rectangular mixed-cell design establishes a mixing flow that eliminates water quality gradients and promotes self cleaning (Watten et al., 2000). Six counter-rotating mixing cells are positioned equidistant on the raceway floor. Cells receive water from vertical pipes extending to the tank floor that are positioned in the corner of the cells. Vertical pipes direct water tangentially to establish rotary circulation. Water exits through a floor drain in the center of each cell, producing similar hydraulic conditions to that of circular tanks and the rectangular cross-flow unit (Watten et al., 2000).

Standard raceways feature little circulation and reaeration, unless supplemental air is provided or structures such as baffles are installed. In a rectangular cross-flow tank, a raceway is retrofitted with a PVC manifold, distributing water down the length of one side and is collected in a drain gutter system spanning the length of the other side (Watten and Beck, 1987; Watten and Johnson, 1990). Influent water is forced across the tank floor to the effluent side, creating rotary circulation about the longitudinal axis (Watten and Johnson, 1990). This method eliminates the gradient of water that would otherwise flow the length of a raceway and increases self cleaning properties and mixing of the water column. Watten and Beck (1987) found that mixing performance in cross-flow tanks was similar to that of circular tanks. The unusual flow pattern created by a cross-flow design appears to affect fish behavior. Fish must swim more aggressively because of the 15-fold increase in velocity. They typically orient laterally in the tank with the flow, and exhibit many more agonistic behaviors (i.e., flight and flee responses) than those of fish in a standard raceway (Ross and Watten, 1988). However, there appears to be no difference in survival, body composition, or growth between fish held in plain raceways versus the cross-flow system (Watten and Beck, 1987; Watten and Johnson, 1990).

Oval, Foster-Lucas, and Rectangular Circulating Tanks

Oval tanks are formed by connecting two parallel channels with 180 degree turning sections at the ends to create a continuous track (figure 8). Water currents are created by delivering influent water in the direction of the intended circulation (Burrows and Chenoweth, 1970). Oval tanks have water velocity gradients due to their non-uniform shape. This velocity gradient is believed to be desirable to fishes, since it provides velocities that may be more suitable to species preferences, size, or physical condition (Burrows and Chenoweth, 1970).

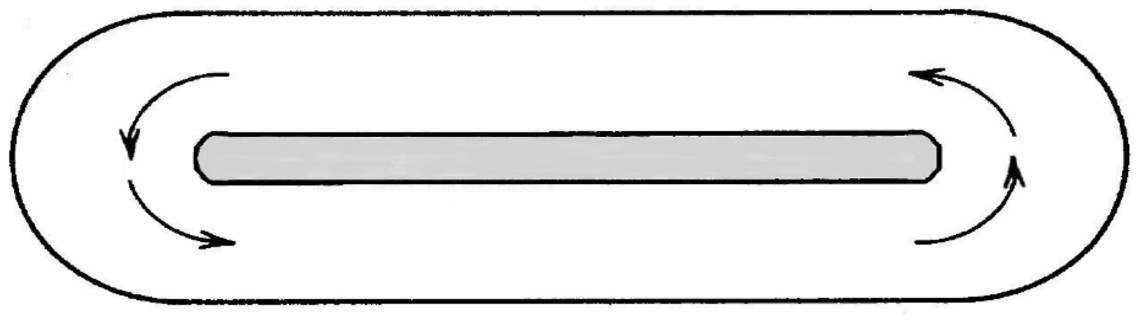


FIGURE 8.—Oval tank design (modified from Wheaton, 1977; Klapsis and Burley, 1984).

Another type of oval tank is the Foster-Lucas tank (Burrows and Chenoweth, 1955) (figure 9). This tank is designed with influent water jets located at the midpoint of the major axis on the two parallel sides. The center wall that divides the parallel channels is offset with a drain in the center. Studies revealed that this design caused poor water circulation, with short circulating problems and dead zones (Cripps and Poxton, 1992).

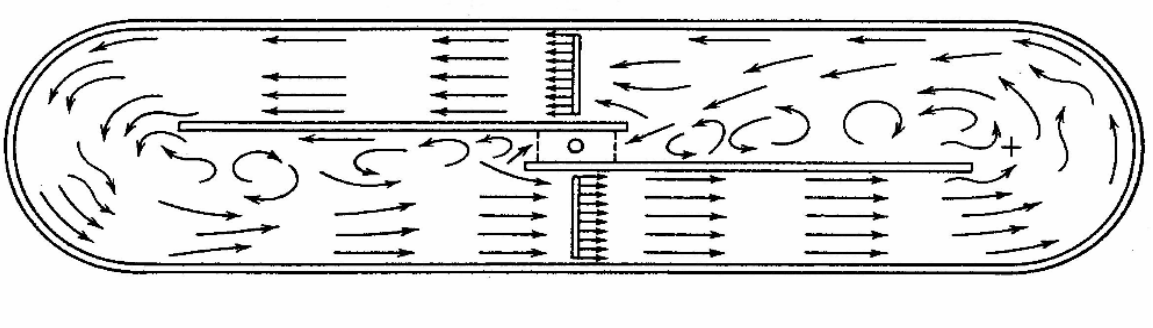


FIGURE 9.—Foster-Lucas design (Klapsis and Burley, 1984).

Burrows and Chenoweth (1970) amalgamated the fundamentals of a rectangular raceway and a Foster-Lucas tank to formulate a rectangular circulating tank (pond). This design is simple to build or to retrofit preexisting rectangular raceways. The rectangular circulating tank is similar to the other mentioned oval tanks, but the corners are not rounded and the turns are performed with the insertion of flow guide vanes at each of the four corners (Burrows and Chenoweth, 1970) (figure 9). The rectangular circulating tank has one straight wall dividing the two parallel channels with two center drains and drains at opposite corners. This design improves the removal of fish wastes; however the turning vanes need periodic cleaning and may increase physical injury and fin erosion (Burrows and Chenoweth, 1970; Wheaton, 1977). Advantages of this design are that the fish are well distributed in the tank and the flow delivers food to them. Burrows and Chenoweth (1970) speculated that this tank design produces fish of high stamina and survival potential compared to other tank/pond designs.

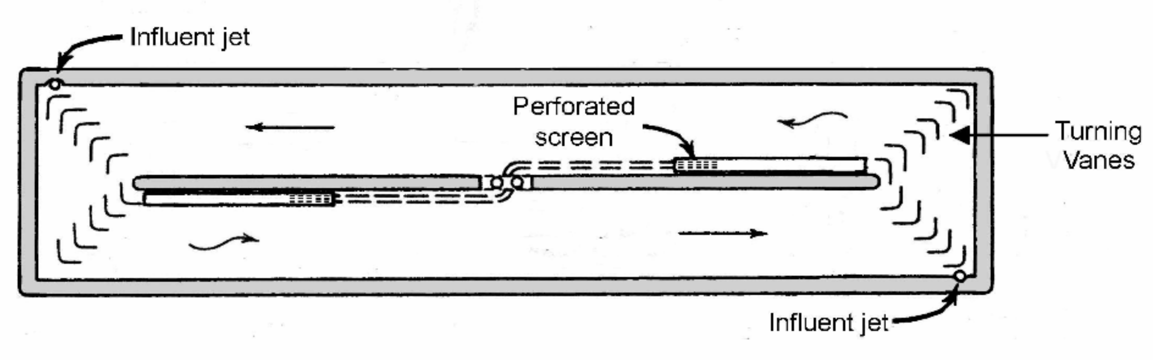


FIGURE 10.—Rectangular circulating tank design (modified from Burrows and Chenoweth, 1970).

The semicircular ends of oval tanks cause turbulence in the more laminar flow of the parallel sections (Burrows and Chenoweth, 1970). Action of the influent water jets corrects most of the turbulence and returns the flow to a more laminar quality. Burrows and Chenoweth (1970) utilized the hydrodynamic properties of the turbulent zones at each end of the rectangular circulating tank to increase self cleaning and force particles toward two drains on the center wall. Particles tend to settle out in these slower, but turbulent areas as opposed to being continually carried in the laminar flow. These flows eliminate large dead zone areas with sufficient dissolved oxygen for high fish densities. The combination of good flow patterns with adequate velocities and efficient waste water discharge rates lowers the fishes' disease susceptibility (Burrows and Chenoweth, 1970).

Silo and Upwelling Tanks

Deep cylindrical tanks (i.e., silo tanks, figure 11) were developed for fish holding and rearing under high densities by Buss et al. (1970). Hydraulic characteristics of silos are quite simple. Water and air is pumped directly to the bottom of a large cylindrical tank where it flows upward, carrying with it fish wastes and uneaten food that spill over the edge into a drain gutter encircling the top of the tank (Buss et al., 1970). There are no obvious dead zones or eddies with this design. Buss et al. (1970) observed that water quality was a much greater factor than crowding when holding rainbow trout. These fish were found to be randomly distributed in the tank with no size stratification.

Pedersen and Amble (2001) developed a similar arrangement for water and oxygen distribution in live-wells to improve live holding conditions aboard commercial fishing vessels. Seawater is supplied evenly through a perforated grid arrangement in the bottom of the tank. Deep water fishes with swim bladders that have been damaged during capture or stressed have a tendency to lie on the bottom of the tank, where dissolved oxygen levels can reach 2 ppm in tradition commercial live-well designs (Pedersen and Amble, 2001). Influent water through a perforated grid system offers upwelling forces

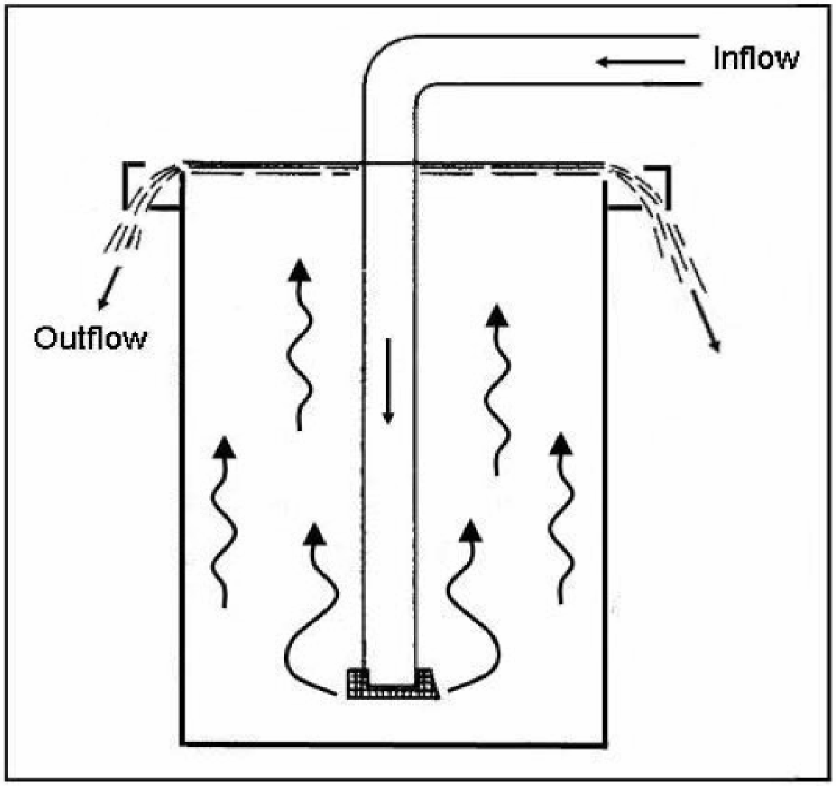


FIGURE 11.—Silo tank design (modified from Buss et al., 1970; Wheaton, 1977; Klapsis and Burley, 1984).

that lift these fishes, which have completely or partially lost their neutral buoyancy, off the bottom. Survival of fishes was nearly 100 percent in tanks with this water delivery system, compared with 50–90 percent in those without it (Pedersen and Amble, 2001).

Whether live-wells are designed for commercial or sport fishing applications, holding fish for several hours to days is thought to be detrimental to health and survival; mortality was as much as 25 percent (Kwak and Henry, 1995; Plumb et al., 1988; Wilde, 1998). The harm caused to these fishes is a direct result of physical injury, density affects to water quality (e.g., decreased dissolved oxygen), and cumulative sublethal stressors. It may seem counter-intuitive, but larger capacity live-wells can have greater proportions of weak or physiologically exhausted fish (Kwak and Henry, 1995). This may be explained by lower water exchange rates in larger volume live-wells which results in degrading water conditions. Larger live-wells also make it more difficult to catch and remove held fishes, resulting in additional stress to fish where survival is important (i.e., catch-and-release angling tournaments, fish salvage, and stocking programs). Hence, it has been speculated that intermediate live-well sizes (80–100 L) for catch-and-release anglers are optimal (Kwak and Henry, 1995; Cooke et al., 2002).

SECTION 4: BEHAVIORAL AND PREDATORY IMPACTS

Fish behaviors associated with spawning, optimal foraging, habitat selection, and anti-predator defenses directly affect population and community dynamics. Stress from environmental or anthropogenic sources decreases the ability of fish to perform daily activities through physiological and/or behavioral impairments (deviations from normal activity), potentially resulting in mortality. Until recently, few studies have considered the consequences of capture, holding, transportation, and subsequent release on fish behavior and performance. For instance, these physical stressors elicit behavioral impairments that detract from the prey fish's ability to avoid predation. This section's goal is to highlight short-term holding impacts on fish behavior, and their ability to avoid predation, or conversely, predators' ability to forage.

Sub-optimal or lethal environmental conditions (e.g., poor water quality) are factors that cause stress and behavioral impairments. For example, thermal stress affects the ability of fish to behaviorally thermoregulate, suppresses feeding, prevents spawning, and alters parental care patterns (De Staso and Rahel, 1994; Dockray et al., 1996; Cooke et al., 2003a). Poor swimming performance at sub-optimal temperatures has been documented in several species (Koumoundouros et al., 2002; Ward et al., 2002). Temperatures also affect social dominance between species. At, 20 °C neither brook charr nor rainbow trout were able to exhibit dominant behavior, however, at cooler temperatures (8 and 13 °C) brook charr were dominant (De Staso and Rahel, 1994). Dissolved oxygen content is another environmental stressor that results in erratic swimming, side-lying, reduced spawning activity, foraging suppression, avoidance of low oxygenated areas and movement to cooler areas (Hughes, 1981; Kramer, 1987; Schreck, 1981, Lutnesky and Szyper, 1990; Szyper and Lutnesky, 1991). Similarly, water pollution at sub-lethal levels (below the EPA standards) can have varying effects on fish behavior. For example, fish exhibit suppressed appetite, reduced growth and fecundity, impaired coordination and sensory responses, and erratic swimming (Weis et al., 1999, Little, 2002) when exposed to low levels of pollutants. Although mortality is often not the direct result of sub-optimal water quality, the reduced behavioral and physiological performance of fishes exposes them to increased predation.

Fish also display altered and agonistic behaviors as a result of stocking density and confinement. Behaviors to indicate social rank and aggressive intent include visual clues, such as, darkened body coloration, raised fins, increased swimming activity, and also physical threats, biting, nipping, lateral display, and charging (Abbott and Dill, 1985; Brown et al., 1992; Pottinger and Pickering, 1992; Ellis et al., 2002). If the threats are not acknowledged, then the attacker will proceed to nip and bite until the submissive fish is displaced or signals its subordinate status. Signals include visual cues, such as, depressed fins, color change, lack of activity, unresponsive to attacks, and/or position in tank (Abbott and Dill, 1985; Ellis et al., 2002). Fin nipping can lead to fin erosion and act as a vector for bacterial infection and disease, and may be worsened under conditions of poor water quality, which may be severe enough to cause death (Kindschi et al., 1991b). Fin erosion may be caused by several factors: aggressive nipping, abrasion with holding environment, abrasion with other fish under high stocking densities, and poor water quality. Rainbow trout held individually showed less fin damage, compared to those held with conspecifics at different densities (Abbott and Dill, 1985; Kindschi et al., 1991b), while there was no difference among stocking densities with respect to bodily harm (bite marks) in channel catfish (Lochmann et al., 1998). However, Lochmann et al. (1988) used a narrow range of stocking densities which may have contributed to the absence of observable differences in the number of bites.

Generally, aggressive behaviors tend to increase with increased fish densities to a maximum at intermediate densities, and decrease as densities increase further. Aggressive social interactions cause physiological stress responses (e.g., elevated levels of cortisol or other corticosteroids) in subordinate fish, however, dominant fish show no stress response (Laidley and Leatherland, 1988; Vijayan and Leatherland, 1988; Pottinger and Pickering, 1992). Densities and social hierarchies can markedly affect the growth, health, and stress of fish of different social status. Dominance hierarchies develop quickly in most salmonids, and fish of lower status usually have impaired feeding and poor growth as a result (Jørgensen et al., 1993). Because stress (i.e., with plasma cortisol increases) can reduce appetite, aggressive behavior can result in cascading effects on fish growth and health. Aggressive interactions may also inhibit foraging time and activity, reducing food intake (Brown et al., 1992; Ellis et al., 2002).

Elevated activity levels associated with agonistic behaviors increase metabolic rates in juvenile sockeye salmon (Brett, 1964) rainbow trout (Li and Brocksen, 1977), and Arctic charr (Christiansen et al., 1991). Christiansen et al. (1991) found that Arctic charr under social stress consumed oxygen at rates similar to those when they swam at intermediate speeds. Arctic charr growth increased at high stocking densities (60–120 kg/m^3) because of decreased aggressive behaviors and increased shoaling time (Jobling, 1985; Wallace et al., 1988; Brown et al., 1992; Jørgensen et al., 1993). A reduction in physiological stress as a consequence of reduced aggressive behaviors and conserved energy is most likely the means for increased growth rates in Arctic charr at high densities (Brown et al., 1992). This seems to be unique to a few fish species. Although some investigators found no indication that aggressive behaviors decrease as stocking density increases in other species (Li and Brocksen, 1977, Lochmann et al., 1998; Keeley, 2000), those experiments were not conducted at stocking densities typical of hatcheries, aquaculture operations, and salvage facilities. At the lower densities, Alanärä and Brännäs (1996) found that the number of dominant Arctic charr increased with density, but dominance hierarchies remained intact. Nonetheless, their growth rates were proportional to density at the higher ranges (Alanärä and Brännäs, 1996). Differences in behavior between Arctic charr and other salmonids, notably rainbow trout, at higher densities may be directly associated with their responses to stress. Whereas stocking density was directly correlated with oxygen consumption and ammonia excretion rates in rainbow trout, it was not in Arctic charr (Alanärä and Brännäs, 1996), presumably due to increased activity and physiological stress in rainbow trout. However, it is difficult to evaluate whether aggressive behavior or lower food intake is directly responsible for the rate of oxygen consumption (Brett, 1964; Christiansen et al., 1991; Jørgensen et al., 1993)

Brook charr, a congener of Arctic charr, alters its aggression type as stocking density increases (McNicol and Noakes, 1984). Brook charr exhibit more threat display behaviors at higher densities, compared with increased biting, nipping, and chasing activities at lower densities. Decreased physical attacks apparently decrease the energetic costs associated with social encounters under high densities where fish may be experiencing reduced caloric intake as a result of stress, competition, and lower food conversion efficiencies (McNicol and Noakes, 1984).

Species-specific holding densities that provide maximum growth, overall good health, and/or increased survival are needed for aquaculture, fisheries (e.g., in boat live-wells), and fish salvage. Some of the stress caused by aggressive social interactions may be alleviated by sorting fish by size and species (Wedemeyer, 1996; Chang and Liao, 2003a).

Predation and/or predation threat affects prey fishes behavior by forcing them to make assessments on the predator avoidance costs and the daily activities benefits (Lima and Dill, 1990). If predation or threat influences the fish's decision making process, the results are costly behaviors that divert metabolic energy from non-vital processes (i.e., growth, fecundity) and/or increases metabolic expenditures (Lima and Dill, 1990; Fraser and Gilliam, 1992; Cooke et al., 2003b; Woodley and Peterson, 2003). For example, predator-derived stress can have population and community costs like delayed-age-of-maturity, reduced growth and fecundity, and poorer progeny quality (Fraser and Gilliam, 1992; Belk, 1998; McCormick, 1998; Woodley and Peterson, 2003). Physiological stress responses are well studied, but not as well understood when applied to predator-derived stress and subsequent behaviors. Documented immediate physiological responses include an increase in metabolic expenditure, respiration rate, heart rate, and plasma cortisol, in addition to bradycardia and hyperactivity (Huuskonen and Karjalainen, 1997; Kelsey et al., 2002; Woodley and Peterson, 2003). The prey's ability to recover from lost foraging opportunities and increased energetic costs is partially dependent upon the overall fitness and health of the prey, predator attack frequency, and structural habitat (Cooke et al., 2003b; Masuda and Ziemann, 2003; Woodley and Peterson, 2003).

Structural refugia and the degree of habitat complexity can provide complete or partial refuge for prey, reduce predator efficiency, and mollify the amount or intensity of predator-prey interactions (Savino and Stein, 1989; Buekers and Jones, 1997; Woodley and Peterson, 2003). Predators exhibit behavioral alterations in response to habitat and its degree of complexity (Savino and Stein, 1989). Because of this, structural refugia alone will not protect prey; the prey must use the structure to avoid predators (Savino and Stein, 1989; Jordan et al., 1996) inferring that the prey too must alter their behavior. In situations of limited or declining structural habitat, inhabitants are forced to spend time searching for refuge, thus increasing their exposure to predation (McIvor and Odum, 1988). In addition, fish that are less protected or are more exposed while they compete for refuge increase their risk to predation (Holbrook and Schmitt, 2002; Woodley and

Peterson, 2003). Consequently, the increased predation vulnerability and interference competition for refuge results in physiological stress (e.g., increased respiration rates and plasma cortisol levels) and behavioral alterations (e.g., suppressed foraging, anti-predatory responses; Cooke et al., 2003b; Woodley and Peterson, 2003).

Holding containers often offer little structural refugia for fishes to escape predation or aggressive attacks. The literature on the effects of holding container design on fish behavior is scant and needs to receive more research attention. Knowledge of captive fish behavior improves fish husbandry and survival. Fish have complex behaviors that are species and life-stage specific. Fish in a holding container may establish dominance hierarchies and be aggressive, as mentioned previously. Ross et al. (1995) observed that under high flows rainbow trout were less likely to flee aggressive fish, especially in raceway type tanks, since rainbow trout were "preoccupied" with swimming and maintaining position. At lower flows, there was significantly more nipping, especially in circular tanks and at the influent areas, with associated good water mixing and reliable oxygen levels. Raceway designs may promote territoriality, because an end can be defended more efficiently (i.e., with less nips and chases) than the continuous nature of a circular tank. Territoriality increases to a limit related to fish density and then falls at relatively high densities in some species (Ross et al., 1995). Agonistic behaviors among fishes can stress fish, causing them to stop feeding and to become disease susceptible, reducing survival. Solutions to decrease aggressive (including predatory) behaviors within holding containers may include lowering ambient light levels (Stringer and Hoar, 1955; Baras et al., 2000), separating fish by size classes or species (Chang and Liao, 2003a, 2003b), adjusting fish densities, increasing water velocities, manipulating water clarity, and increasing food amounts (Liao and Chang, 2002). Size disparity is the most important factor affecting predation (cannibalism), whereas other factors, such as water turbidity and fish stocking density had less of an effect (Liao and Chang, 2002; Chang and Liao, 2003a). For example, red drum of the same size would not prey on each other (Chang and Liao, 2003b).

Capture, handling and transportation of fishes are known factors that elicit behavioral and physiological stress responses. Many species suffer increased mortality rates due to predation after handling, holding and/or transportation release (Olla and Davis, 1989; Masuda and Ziemann, 2003). For example, stressed juvenile Pacific threadfin (*Polydactylus sexfilis*) remained still for 30–60 seconds after release and did not regain "normal" swimming capacity for 5 minutes (Masuda and Ziemann, 2003). Coho salmon exhibit a similar response to handling and their ability to avoid predation, but the recovery time was 90 minutes (Olla and Davis, 1989). Behavioral impairment also occurs after capture events and includes responses like poor anti-predator performance, nest abandonment and less ability to defend nests (Suski et al., 2003). Fish captured, held and transported are also subjected to inter-specific stress that manifests in both behavioral and physiological responses (Kelsey et al., 2002). Thus, the stress from capture and handling activities can have pertinent effects on the survivability of fish stocks and populations.

For short-term holding, behavioral impairment will occur from sub-optimal water quality, stocking density and confinement stress, handling stress, species involved, and tank design. In most holding containers, each stressor is controllable to some degree. If the prior recommendations for each water quality, confinement and tank design are met (within reason), one can assume that the physiological stress and behavioral impairments will be effectively minimized. The activities of capturing, holding and transferring fishes will undoubtedly be stressful for fishes, and consequently, behavioral impairment will occur. The capture of various fish species and sizes into common holding containers (e.g., fish salvage facilities) will evoke some degree of stress and the potential for behavioral alterations. These facilities do not offer any type of refuge for small fish or different species. They increase social and competitive interactions, and the perceived predation threat, and thus compound the stress response. Due to the size of these facilities, the large volume of water and fish passage through them, they are unique and further investigations into the stress and impeding behavioral impairments of fishes are needed.

CONCLUSION AND FINAL CONSIDERATIONS

The integrated approach of this review for aquaculturists, biologists, fisheries scientists, and managers points out that the problems associated with short-term holding may be very specific, however the applications are very broad. Stress associated with short-term holding of fishes can have profound effects on overall health and well-being. The goal of this review was to synthesize current knowledge of short-term holding effects of fishes from a wide variety of papers that have examined or incorporated short-term holding and confinement of fishes into their research. Our objective in doing this was to summarize and point out some of the noteworthy findings on four aspects of short-term holding: water quality, density/confinement, holding container design, and agonistic behaviors and predation. These four aspects are major factors contributing to the physiology, behavior, and survival of fishes held for relatively short-term basis.
There are many published studies reporting water quality, density, confinement, and tank design affects of holding fishes in captivity. However, most of these studies take place over a few to several months in duration. There is a need for further studies to test the short-term holding effects, especially of wild fishes. Much of the information in the literature about short-term holding effects of fish comes from relatively few species, most of which are cultured fishes. There are many interesting questions that need to be answered. What are the maximum and optimal densities that different individual species can be held under certain conditions? How do wild fishes adjust to confinement and unnatural densities? What changes occur in their physiologies and behaviors? What then happens to these fishes if they are released back into the wild? These are important questions for biologists, aquaculturists, and fisheries managers.

There is also the need for further application and development of techniques for sampling the physiology of fish, especially when handling and sampling techniques can have greater effects than the holding practice under study. More research is needed to better understand the physiological stress response of fishes and their life stages, and determine better methods for evaluating stress and its significance related to fish performance. Also, more reliable techniques for measuring stress outside of the controlled environment of the laboratory are needed.

Some sources of stress in aquaculture, fish salvage, and commercial and sport fisheries may be unavoidable. Collecting, handling, sorting, holding, and transporting are all part of the routine operations of these practices that contend with successfully holding live fishes. Nevertheless, there are some aspects and approaches of holding fishes that are under the control of aquaculturists, biologists, or fishers that help reduce stress and its detrimental effects.

ACKNOWLEDGEMENTS

We would like to thank Alex Daniels, Skyler Feltman, Rebecca Riley, Julie Roessig, Meredith Rose, Lisa Thompson, and Naomi Yoder for their help in preparing this review. The authors would also like to express their appreciation to Harry Westers, Scott Lankford, Brent Mefford, Barnaby Watten, Doug Craft, and Michele Macias for lending their professional opinions and assistance. Financial support for this review was provided by the Bureau of Reclamation Mid-Pacific Region and the Tracy Field Office. Support services were also provided by the University of California, Davis. This project is associated with the Tracy Fish Facility Improvement Program and is being carried out in partial compliance with the Federal Central Valley Project Improvement Act of 1992.

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