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Physicochemical environments and tolerances of cyprinodontoid fishes found in estuaries and salt marshes of eastern North America

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Abstract Individuals of 28 species of cyprinodontoid fishes have been reported from estuaries/salt marshes of the Atlantic and Gulf coasts of North America. Some species show limited latitudinal distributions and/or occupy a limited range of habitats; others are widely distributed and/or occupy a wide range of habitats.

A literature survey was made of conditions of water temperature, dissolved-oxygen (DO) concentrations, and salinities at sites where individuals of each species had been collected, and of laboratory-determined tolerances or lethal limits and other responses to those abiotic conditions. Individuals of *Cyprinodon variegatus* showed the widest overall range of tolerance of environmental temperatures, –1.9–45.4°C, with *Gambusia rhizophorae* showing the highest lower temperature-tolerance limit, 17°C. The only species highly sensitive to hypoxia was *Floridichthys carpio*, which showed "stress" at DO levels of 6–8 mg kg^{-1}. All showed use of aquatic surface respiration, except for *Kryptolebias marmoratus*, which uses aerial respiration in the presence of H_2S, and/or under hypoxic conditions. Individuals of *C. variegatus* were found to tolerate ambient salinities ranging from <0.5 to 125.2, or higher, and several species of the genus *Fundulus* were found to tolerate concentrations ranging from < 0.5 to ≥100. However, some of the species discussed cannot tolerate salinities beyond those of dilute brackish waters. In most instances, laboratory-determined tolerance limits of temperature and salinity were wider than conditions under which individuals of these species had been found in nature. The majority of available information related to adult individuals, with few studies focused on immature stages; however, existing information permitted a brief review of spawning, incubation, and early development features in *Fundulus heteroclitus*.

Suggestions were made, based on existing information, as to species that would be most likely to show altered population distributions resulting from continued global warming. These included five species that have tropical/subtropical, or subtropical/temperate distributions. Also, a few others were included that show extensive latitudinal distributions, most extending northward into cooler temperate regions of the Atlantic coast. At present, none of these species has shown a range alteration that can be attributed to global warming.

Keywords Cyprinodontoids · Estuaries/salt marshes · Eastern North America · Temperature · Dissolved-oxygen · Salinity tolerances · Global warming

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Introduction

Cyprinodontoid fishes (Order Cyprinodontiformes, Parenti 1981) are widely distributed in fresh and brackish waters of both Old and New Worlds. Some of these species have wide geographical ranges of distribution, and/or show wide ranges in tolerances of physicochemical environmental conditions. Other species within the group are very limited in geographic distributions and/or in characteristics of their environments, especially with respect to water temperature, dissolved-oxygen (DO) concentration, and salinity. This review will focus on influences of those three abiotic environmental conditions on species of families Cyprinodontidae, Fundulidae, Poeciliidae, and Rivulidae, found to enter or permanently inhabit estuaries/salt marshes of eastern North America, from south Texas to Nova Scotia. Several of the species included comprise significant fractions of the species considered to be permanent residents of some estuarine/salt marsh systems (Nordlie 2003).

Identifying natural conditions, whether biotic or abiotic, that determine or limit distributions of fishes seems simple at the outset. However, other than extreme physical or chemical conditions that serve as physiological limiters to distributions, limitations may not be so obvious (Davenport and Sayer 1993). Ambient temperature has often been thought of as the key abiotic condition influencing the distribution and abundance of aquatic organisms, because of its pervasive influence on chemical activity. However, both ambient temperature and salinity have been referred to as ‘ecological master factors’ because of their demonstrated limiting effects on distributions of aquatic organisms (and also because of the ease of measuring and controlling levels of the two in laboratory experiments, Kinne 1964). Ambient temperature and salinity levels interact in determining saturation levels of oxygen dissolved in water.

All three of the chosen environmental characteristics show significant variations in aquatic habitats, both temporal and spatial, under natural as well as some human-altered conditions. The advent of “natural catastrophes”, generally short-term but extreme alterations in one or more of these conditions can result in fish kills, sometimes of massive proportions. Examples include: sudden drops in environmental temperatures accompanying cold fronts (e.g., Gunter 1941, 1947; McEachron et al. 1994); elevated water temperatures (e.g., Bailey 1955; Gallaway and Strawn 1974); hurricanes (e.g., Tabb and Jones 1962) and cyclonic winds (e.g., Cyrus 1988); reductions in DO concentrations falling to, or near to, anoxic levels, (e.g., Seliger et al. 1985; Smith and Able 2003); increases in DO concentrations to supersaturated levels (Renfro 1963; Woodbury 1941); and dramatic increases in salinity following evaporation of water from isolated pools (e.g., Simpson and Gunter 1956; Gilmore et al. 1982). Some of these events occur on a very short time-scale of hours to a few days, while others extend over longer time scales, but appearances of dead fishes may be sudden occurrences. Unfortunately, it is difficult to gain information on causation in unexpected events that can generally be monitored only after the fact. There are also reports in the literature of anthropogenic alterations in estuarine conditions of temperature, DO concentrations, and salinities. For example, the use of water in cooling systems, as in electric-power generation in which the heated water is returned to the system, may alter habitability of the discharge location for resident organisms.

Relatively more anecdotal information is available from field measurements of temperature, DO concentrations, and salinity conditions observed in habitats occupied by populations of the cyprinodontoid fishes of interest here, than from laboratory-determined tolerance patterns of those species. While such field information is of great value in learning about the conditions under which organisms are found in nature, it is also necessary to determine for each species their precise limits of tolerance or lethal limits of these conditions. Some such studies have included comparisons of tolerance patterns among different populations of a species, especially those that have extensive latitudinal distributions, or have been introduced into geographical locations where they did not occur naturally. Arguments continue in the literature as to whether abiotic or biotic interactions are the primary determiners of distributions and abundances of various species of organisms. While much can be said about the potentially limiting actions of both biotic and abiotic influences and some of their interactions on fishes, the purpose of this paper is not to argue that case, but rather to focus on the three selected abiotic conditions that are inevitably encountered in estuarine/salt marsh systems, and affect the occupants. Species chosen for discussion include both estuarine/salt marsh permanent resident species, as well as some that occupy only limited portions of such habitats and/or for limited periods of time.

Questions addressed in this paper

1. What are the conditions of ambient temperature, DO concentration, and salinity at which individuals of each of the 28 species of cyprinodontoid fishes included here have been found in nature?
2. What are the laboratory-determined tolerance limits of these species with respect to the same suite of environmental conditions?
3. How do these ranges of ambient environmental conditions, at which individuals of the various species have been taken from nature, compare with temperature, DO, and salinity tolerance patterns determined in laboratory studies?
4. Are there predictable geographical differences, with respect to lethal limits or tolerance ranges of temperature, DO concentration, and salinity, among populations of a species from different parts of its geographic range?
5. What natural catastrophes or human alterations can result in severe impacts on the estuarine/salt marsh biota with respect to these abiotic environmental conditions?
6. Which of the species discussed seem most likely to show alterations in geographic and habitat distributions as global warming continues?

Approach

The group of fishes chosen for discussion belong to four families within the Order Cyprinodontiformes (after Parenti 1981): Cyprinodontidae; Fundulidae; Poeciliidae; and Rivulidae. The geographical region chosen for discussion includes coastal areas of the Gulf of Mexico from Texas to the Florida Keys, then northward along the Atlantic coast to the Gulf of St. Lawrence. Only those species of cyprinodontoid fishes that have been reported to enter brackish waters of estuaries/salt marshes within that geographical range are included in the analyses. The group totals 28 species (Table 1). Scientific names follow Nelson et al. 2004, except in a case where a newer revision in nomenclature is known (C. R. Gilbert, pers. com.). Patterns of tolerance or lethal limits of a number of other species including some related species, whether from adjacent inland-aquatic habitats, or occupying estuarine/salt marsh habitats outside of the encompassed region, are included for comparisons with the species of primary interest.

To discuss influences on resident organisms of aquatic systems of the three major abiotic environmental conditions, a means of categorizing and/or subdividing the various conditions encountered and the ways in which they exert influences on organisms is needed. General approaches and terminologies used by Brett (1944, 1952, 1956), Doudoroff (1938, 1945), Fry (1947, 1971), Fry et al. (1946), Hart (1952) are followed. That involves considering impacts of environmental conditions as categorized by five environmental "factors" that indicate the level or type of influence being exerted by an environmental condition on individuals under a specific set of circumstances. The five categories (lethal, controlling, limiting, masking, and directive factors), are followed, where useful, to provide a conceptual basis in the review, but, as Fry (1971) pointed out, they are categories of convenience and imperfect as such. The present review, primarily focused on tolerable ranges or lethal limits of temperature, salinity, and DO concentrations, is, thus, of lethal factors, though others are also considered in some situations. However, where lethal limits of any one of these three abiotic factors are discussed, conditions of the other two at the time of measurement are included wherever possible.

Several approaches have been developed to evaluate survival or mortality of organisms as

Table 1 Cyprinodontoid fishes reported to have been collected from estuaries of eastern North America

Family Cyprinodontidae
Cyprinodon variegatus Lacepède—Sheepshead minnow
Floridichthys carpio (Günther)–Goldspotted killifish
Jordanella floridae Goode and Bean—Flagfish
Family Fundulidae
Adinia xenica (Jordan and Gilbert)—Diamond killifish
Fundulus chrysotus (Günther)—Golden topminnow
Fundulus confluentus Goode and Bean—Marsh killifish
Fundulus diaphanus (Lesueur)—Banded killifish
Fundulus grandis Baird and Girard—Gulf killifish
Fundulus heteroclitus (Linnaeus)—Mummichog
Fundulus jenkinsi (Evermann)—Saltmarsh topminnow
Fundulus luciae (Baird)—Spotfin killifish
Fundulus majalis (Walbaum)—Striped killifish
Fundulus notatus (Rafinesque)–Blackstripe topminnow
Fundulus nottii (Agassiz)–Bayou topminnow
Fundulus olivaceus (Storer)–Blackspotted topminnow
Fundulus pulvereus (Evermann)—Bayou killifish
Fundulus seminolis Girard–Seminole killifish
Fundulus similis (Baird and Girard)—Longnose killifish
Fundulus stellifer (Jordan)–Southern studfish
Lucania goodei Jordan—Bluefin killifish
Lucania parva (Baird and Girard)—Rainwater killifish
Family Poeciliidae
Belonesox belizanus Kner—Pike killifish—Introduced species
Gambusia affinis (Baird and Girard)—Western mosquitofish
Gambusia holbrooki Girard—Eastern mosquitofish
Gambusia rhizophorae Rivas—Mangrove gambusia
Heterandria formosa Agassiz—Least killifish
Poecilia latipinna (Lesueur)—Sailfin molly
Family Rivulidae
Kryptolebias marmoratus (Poey)—Mangrove rivulus

they are subjected to various environmental stressors in laboratory experiments. The most extensive set of terms of interest here is related to influences of ambient temperatures. There has been much concern to improve standardization of procedures and techniques for determining lethal-temperature limits or thermal-tolerance ranges, since the basic techniques have been applied to a number of vertebrate groups. Differences among techniques have created problems of interpretation and comparison (reviewed in Lutterschmidt and Hutchison 1997). The laboratory evaluations cited primarily include values of upper and lower lethal temperatures (ULT, LLT) or upper and lower incipient lethal temperatures (UILT and LILT), defined as the temperature level that is lethal to 50% of the individuals being subjected for a defined period of time following a defined acclimation (after Fry et al. 1946; Fry 1947). Also, frequently included are critical thermal maxima and critical thermal minima (CTMax, CTMin), that are defined as the thermal points at which locomotory activity becomes disorganized and the organism loses its ability to escape from conditions that will lead to its death (Cowles and Bogert 1944). The zone of thermal tolerance is the region of ambient temperature bounded by the lower and upper incipient lethal temperatures, within which 50% of the individuals of a particular species can be expected to live for an indefinite period following a defined acclimation sequence (after Fry et al. 1942, 1946; Hart 1947). Thermal preferenda as used here are defined as the range of temperatures in which individuals of a particular species congregate in a thermal gradient when given a free choice, and following a specific acclimation regime (Reynolds 1977). The final thermal preferendum (FTP) differs in that it is the environmental temperature toward which an individual of a particular species gravitates when given free choice, regardless of its previous thermal history. That is the point at which the preferred and acclimation temperatures are equal (after Fry 1947).

The terminology for either DO or salinity limits is less complex than that for temperatures, and terms will be presented in the text when necessary for clarity. A review of DO levels that have been reported as constituting lethal limits or otherwise restrictive to fishes, also indicates a multitude of different techniques being used in determining these limits (Davis 1975). Values representing DO concentrations are presented in mg kg^{-1} (DO concentrations), and tensions (P_{O_2}) in Torr. Where such environmental conditions as ambient water temperature, air pressure, salinity, and relative humidity were not available, conversions represent the best approximations possible. Salinities are expressed as dimensionless numbers following current practice. Salinities of <0.5 are generally indicated as fresh water (FW), while numerical values of salinities indicated as sea water (SW) are generally indicated. However, if a specific value is not given it is assumed to be ca. 34.5. In discussions where experimentally determined limits of any one of these three conditions is given, tolerance ranges are taken as the differences between upper and lower lethal limits.

Abbreviations of states in the USA are found on the internet at http://www.com/ncsc/lookups/abbreviations.html.

Findings

Temperature: lethal limits, and tolerance ranges

It has been suggested that despite the eurythermal capabilities of many fishes and of other poikilothermic animals, they are still vulnerable to rapid changes in temperature. While water buffers temperature changes compared with aerial environments (Blaxter 1992), rates of change in water temperatures can be more rapid than resident fishes and other organisms are able to accommodate to them, despite longer-term acclimation capabilities. Anecdotal information on environmental temperatures at which collections of fishes were made, or were found to survive in nature, is used here to provide an environmental context. Generally, information on laboratory-determined thermal response patterns was available only for species with the widest geographical ranges, of greatest interest as laboratory models, or with greatest economic value (e.g., sold as live-bait, or used in mosquito control).

Ambient temperatures ranges for cyprinodontoids in the field

Individuals of the species collected over the widest reported range of ambient temperatures were of *Cyprinodon variegatus*, found in waters as cold as 2°C (DE, Warlen 1964); –1.9°C (TX, tide pools of unspecified location, Bennett and Beitinger 1997); to a high temperature of 43°C (FL, Harrington and Harrington 1961) (Table 2). Individuals of *Kryptolebias marmoratus*, a more tropical species were also taken at 43°C in that Florida collection (Harrington and Harrington 1961), while the coldest temperatures at which live individuals of *K. marmoratus* have been recorded were 5–7.5°C (FL, Taylor 1993). Other species reported taken at low environmental temperatures were *Fundulus heteroclitus*, from –1.5°C (overall, –1.5–25°C, NJ, Smith and Able 1994); –1.0°C (overall, –1.0–28°C, DE, Meredith and Lotrich 1979); and *Fundulus diaphanus menona*, –0.5°C (overall, –0.5–25°C, ND, Fivizzani et al. 1984), a different subspecies from that taken in estuarine systems of the Atlantic coast (*F. d. diaphanus*). Individuals of *Gambusia affinis* from populations established in Illinois and Michigan were reported to survive the winter in waters with an ice cover, therefore at temperatures likely to have been between 0°C and 4°C (Krumholz 1944). Individuals of *C. variegatus* and *F. heteroclitus* and, apparently, *F. diaphanus* were reported to burrow into the substratum in the late fall in some habitats, but were observed to become active under an ice cover on sunny days (NJ, Chidester 1916, 1920; MA, Raposa 2003). While there are few published reports of any of the other species being observed alive at ambient temperatures approaching that of freezing waters of any salinity, that may reflect a lack of winter observations or winter collections of such widely

Table 2 Temperature tolerances of cyprinodontoid fishes found in estuaries of eastern North America

Family & Species	Location	Experimental lower temperature limit C	Location	Experimental upper temperature limit C	Location	Encountered range of temperatures C
Family Cyprinodontidae						
Cyprinodon variegatus	?	–1.9, static; 0.6, dynamic Bennett and Beitinger 1997	?	41.5, static; 45.4, dynamic Bennett and Beitinger 1997	TX	8.8–34.9 Gunter 1945
					FL	43 Harrington and Harrington 1961
					DE	2–33 Warlen 1964
					?	–1.9 Bennett and Beitinger 1997
					TX	Spawning, at 17.4–27.5 Renfro 1960
Floridichthys carpio					FL	13 Reid 1954
					FL-Keys	19.9–33.6 Springer and McErlean 1962
					FL-Keys	37.8 Kaill 1967
Jordanella floridae					FL	11–30 Dickinson 1948
					FL	20.9–31.8 Brockmann 1974
					FL	Adults, 12.8–37.0, sal. 0.3–17.7; spawning, 26.2–32.0, sal. 0.3–9.9 Hale in St. Mary et al. 2004
Family Fundulidae						
Adinia xenica					TX	12.2–28.5 Gunter 1945
					FL	38 Hastings and Yerger 1971
					MS	5.0–24.9 Christmas and Waller 1973
					FL	7–38 Nordlie 1987
					FL	Spawning, at ≥22 Koenig and Livingston 1976

Table 2 continued

Family & Species	Location	Experimental lower temperature limit C	Location	Experimental upper temperature limit C	Location	Encountered range of temperatures C
Fundulus chrysotus					FL	20.9–28.3 Brockmann 1974
Fundulus confluentus					FL	12–34 Tabb and Manning 1961
					GA	7.8–29.3 Dahlberg 1972
					FL	7–38 Nordlie and Haney 1998
Fundulus diaphanus	PA	6 Melisky et al. 1980	Nova Scotia	27.5 (sals., 0, 32), 33.5 (sal., 14) Garside and Jordan 1968	ND	–0.5–25 (water temp. range of collection localities) Fivizzani et al. 1984
			PA	36 Melisky et al. 1980		
Fundulus grandis	FL	4 (sals. 27 and 33) Umminger 1971a			TX	13.0–34.0 Gunter 1945
					FL	14.5–30.0 Reid 1954
					TX	17.0–35.0 Simpson and Gunter 1956
					TX?	Spawning at 4–33 Hubbs and Drewery, in Pattillo et al. 1997
					FL	4 Umminger 1971a
					MS	5.0–34.9 Christmas and Waller 1973
					FL	26.5–39.2 Carr and Giesel 1975
Fundulus heteroclitus	CN	–1.5 Umminger 1971b	Nova Scotia	31.5 at sal. 32, 34 at sal. 14 Garside and Jordan 1968	DE	3.5–32.0 Shuster 1959
					GA	7.8–32.2 Dahlberg 1972
			Nova Scotia	35.39 at sal. 32, 36.31 at sal. 14, accl. temp. 25 Garside and Chin-Yuen-Kee 1972	FL	26.5–39.2 Carr and Giesel 1975
			NC?	38.1 ± 0.42, accl. temp. 10; 38.9 ± 0.39, accl. temp. 20; 41.7 ± 0.55, accl. temp. 30 Burnside 1977	DE	–1.0–28.0 Meredith and Lotrich 1979

Table 2 continued

Family & Species	Location	Experimental lower temperature limit C	Location	Experimental upper temperature limit C	Location	Encountered range of temperatures C
			VA	CTM 42.45 ± 0.40; 1200 h., accl. temp. 27, sal. 7–22; 44.1 ± 0.14, 1200 h.accl. accl. temp. 36 Bulger 1984	NJ	–1.5–25 Smith and Able 1994
Fundulus jenkinsi					TX	18.0–27.0 Simpson and Gunter 1956
					MS	5.0–24.9 Christmas and Waller 1973
Fundulus luciae					VA	4.0–36 (adults) Byrne 1978
					NC	16.0–31.0 Schwartz et al. 1981
					NJ	15.0–33 (larval fish) Talbot and Able 1984
Fundulus majalis			NC?	37.2 ± 0.63, accl. temp. 10; 38.5 ± 0.61, accl. temp. 20, 40.9 ± 0.36, accl. temp. 30 Burnside 1977	DE	3.5–36.0 Shuster 1959
					GA	7.0–32.2 Dahlberg 1972
					FL	26.5–39.2 Carr and Giesel 1975
					NC	9.0–29.1 Schwartz et al. 1981
Fundulus nottii					MS	10–34 Peterson and Ross 1991
Fundulus olivaceus			MO	38.3 ± 0.59 Smale and Rabeni 1995	MS	8.9–30.0 Christmas and Waller 1973
					MS	10–34 Peterson and Ross 1991
Fundulus pulvereus					TX	17–34.5 Simpson and Gunter 1956
Fundulus seminolis					FL	26.0–27.5-Surface Phillips and Springer 1960

Table 2 continued

Family & Species	Location	Experimental lower temperature limit C	Location	Experimental upper temperature limit C	Location	Encountered range of temperatures C
Fundulus similis					TX	8.8–34.9 Gunter 1945
					FL	9.6–33.3 Martin and Finucane 1968
					MS	5.0–34.9 Christmas and Waller 1973
					FL	7–38 Nordlie 2000b
Lucania goodei					FL	13.5–33.0 Reid 1954
					FL	18.5–37.5 Arndt 1971
Lucania parva			FL	37–38 Hard water, accl. temp. 23 Dunson and Travis 1991	TX	8.8–33 Gunter 1945
					FL	18.5–37.5 Arndt 1971
					FL	12–36 Subrahmanyam and Drake 1975
Family Poeciliidae						
Belonesox belizanus	FL	9.7 Shafland and Pestrak 1982				
Gambusia affinis	AZ	2.7	TN	37.3, accl. temp. 30 Hart 1952	MS	10–33 Brown-Peterson and Peterson 1990 Tabb and Manning 1961
	UT	0.5 accl. temp. 5–10;	AZ	CTM 42.3–43.7, accl. temp. 35; 43.7 ± 0.4, 34–41.5 temp. diel cycle; 33.7, accl. temp. 5 Otto 1974	GA	7.3–30.7 Dahlberg 1972
	AZ	ca. 11.2			MS	5.0–34.9 Christmas and Waller 1973
	UT	ca. 11.2 accl. temp. 35 Otto 1973			FL	26.5–39.2 Carr and Giesel 1975

Table 2 continued

Family & Species	Location	Experimental lower temperature limit C	Location	Experimental upper temperature limit C	Location	Encountered range of temperatures C
Gambusia holbrooki	FL	1.5, accl. temp. 15, 5.5, accl. temp. 20, 14.5, accl. temp. 35 Hart 1952	FL	35.4, accl. temp. 15, 37.3, accl. temps. 20–35 Hart 1952	SC	38 Meffe 1991; 1992
			SC	CTM 39.8 ± 0.39–40.1 ± 0.38, accl. temp. 25 Meffe et al. 1995	FL	7–38 Nordlie and Mirandi 1996
Gambusia rhizophorae	FL	17 Baumgarten, in Getter 1982				
Heterandria formosa	FL	CTMin 10	FL, SC	CTM 41–42 Baer and Travis 2000	GA	3.5–30.5 Dahlberg 1972
	SC	CTMin 8.5 Baer and Travis 2000			FL	≤8–≥30 Baer and Travis 2000
Poecilia latipinna			MD?	Preferred temps., means over range 20–35, 2–4 wk. juv., 30.6; adult males, 27.6; adult females, 30.8 Stauffer et al. 1985	FL	13–37 Tabb and Manning 1961
					FL	36, saltwater pond Trexler et al. 1990
					GA	7.3–32.2 Dahlberg 1972
					FL	27.6–39.2 Carr and Giesel 1975
					FL	12–36 Subrahmanyam and Drake 1975
Family Rivulidae						
Kryptolebias marmoratus					FL	43 Harrington and Harrington 1961
						5–7.7 Taylor 1993

distributed species as *F. confluentus*, *F. luciae*, *F. majalis*, or *Lucania parva*.

While no reports were found of species other than *C. variegatus* and *K. marmoratus* being taken from waters at ambient temperatures as high or higher than 40°C, species reported taken at ambient temperatures near 40°C included *Floridichthys carpio*, 37.8°C (Kaill 1967); *Adinia xenica*, 38°C (Hastings and Yerger 1971; Nordlie 1987); *Fundulus confluentus*, 38°C (Nordlie and Haney 1998); *F. grandis*, 39.2°C (Carr and Giesel 1975); *F. heteroclitus*, 39.2°C (Carr and Giesel 1975); *F. majalis*, 39.2°C (Carr and Giesel 1975); *F. similis*, 38°C (Nordlie 2000b); *Lucania goodei*, 37.5°C (Arndt 1971); *L. parva*, 37.5°C (Arndt 1971); *Gambusia affinis*, 39.2°C (Carr and Giesel 1975); *G. holbrooki*, 38°C (Meffe 1991, 1992; Nordlie and Mirandi 1996); and *Poecilia latipinna*, 39.2°C (Carr and Giesel 1975) (Table 2).

Thermal acclimation

It was discovered in early attempts to determine thermal limits of fishes that the ambient temperature at which individuals being tested had been living could alter the responses to experimental temperatures. Alterations in resistance or tolerance limits to both raised and lowered ambient temperatures at various salinities were shown in individuals of "*Fundulus*" (most likely *F. heteroclitus*, since they were said to have been collected from waters of Long Island Sound). Individuals of that species placed in a thermal gradient chose temperatures that were influenced, within limits, by the previous thermal history of the individuals (acclimation) (Loeb and Wasteneys 1912). Later studies confirmed those phenomena (Hathaway 1927; Wells 1935; Sumner and Wells 1935; Doudoroff 1938, 1942, 1945; Sumner and Doudoroff 1938; and Brett 1941, 1944, 1946). Thermal acclimation was found to play a greater role in tolerance of low temperatures than of elevated temperatures. Individuals of *C. variegatus* were the most affected by acclimation temperature among a heterogeneous group of 21 species of fishes evaluated (Beitinger and Bennett 2000).

Individuals of *C. variegatus* showed a CTMin of 11.3°C and a CTMax of 44.2°C following acclimation to a constant temperature of 30°C. However, the CTMax reached 45.1°C after a 30-day acclimation with the temperature cycling between 37°C and 42°C (Bennett and Beitinger 1997). In a similar study, individuals of *Cyprinodon nevadensis amargosae* that inhabit thermally unstable desert waters, were acclimated to a series of constant temperatures (15, 25, and 35°C). A range or scope of thermal tolerance of 39°C (between CTMin and CTMax) was found for this population. Upon acclimating to a symmetrical fluctuating temperature regime (15–35°C), that range of thermal tolerance increased significantly to ca. 41°C (Feldmeth et al. 1974). It appeared that there was simultaneous physiological compensation for both warm and cold temperatures when the individuals were subjected to such cycling temperature fluctuations, but not when subjected to a single acclimation temperature. A CTMax value of 45.5°C was found for individuals of *Cyprinodon artifrons* from Belize that had been acclimated to a daily cycling temperature of ≈26–40°C, while acclimation to a constant 30°C reduced the CTMax value to 43.7°C (Heath et al. 1993). Individuals of *Floridichthys polyommus*, and of *Gambusia yucatana*, also from Belize, were found to attain CTMax levels of 43.9°C, and 43.3°C, respectively, when acclimated to a cycling temperature range of ≈26–41°C, compared with levels of 42.5°C, and 42.6°C, respectively, when acclimated to a single constant temperature of 30°C, roughly the mean of their daily temperature cycle (Heath et al. 1993). Rates of acclimation to changes in ambient temperature were evaluated using determinations of CTMax in *Cyprinodon dearborni* from Laguna Los Patos, Cumana, Venezuela. An initial acclimation response to increased temperature (24–31°C) was seen after three hours, and individuals were fully acclimated after three days. The reversed acclimation required 12 days before initial responses were seen and 39 days for completion (Chung 1981). Those individuals had been captured from water of a temperature of 31°C, salinity of 15, and DO >4 mg kg^{-1}. The physiological phenomena demonstrated in these experiments are of special interest, as well as of general application. The species involved that are not residents in the estuaries/salt marshes of interest, are all closely related to species being evaluated here:

C. artifrons, *C. dearborni*, and *C. n. amargosae* to *C. variegatus*; *F. polyommus* to *F. carpio*; and *G. yucatana* to *G. affinis*, *G. holbrooki*, and *G. rhizophorae*.

Thermal limits determined in laboratory studies

The widest tolerable temperature limits found experimentally for any of these species (Table 2), among the limited number of laboratory studies, were again for *C. variegatus*, with a range of –1.9–41.5°C, using a static technique, and 0.6–45.4°C, using a dynamic technique (suggested to be more ecologically relevant limits), for which locations of collection were not given (Bennett and Beitinger 1997). *Fundulus heteroclitus* was found to have a tolerance range extending from a low of –1.5°C (CN, Umminger 1971b), to a high of 44.1 ± 0.14°C (CTMax conditions at 1200 h, acclimation temperature, 36°C, salinity, 17–22, VA, Bulger 1984). The CTMax of individuals of *G. affinis*, from an introduced population in Arizona, was found to be 43.7 ± 0.4°C (acclimated to a diel cycle of 34–41.5°C, Otto 1974). Other species showing low lower thermal limits included *G. holbrooki* with +1.5°C (acclimation temperature, 15°C, FL, Hart 1952), and 4°C for *F. grandis* (salinities, 27 and 33, FL, Umminger 1971a). Among other species with high upper thermal limits, a CTMax of 41–42°C was determined in *Heterandria formosa* (FL, SC, Baer and Travis 2000); 40.9 ± 0.36°C in *F. majalis* acclimated to 30°C (NC?, Burnside 1977); and 40.1 ± 0.38°C in *G. holbrooki* (acclimation temperature, 25, SC, Meffe et al. 1995).

Female individuals of *G. affinis* were found to be more tolerant of elevated temperatures than were males. No significant difference was found between mean ULTs of gravid and non-gravid females. Daily rhythms in mean ULTs were shown in individuals of *G. affinis*, with that for males ranging from a low of 31.9°C (0200–0359 h) to 37.4°C (1000–1159 h). For females the daily excursion in ULTs ranged from a low of 33.8°C (2200–2359 h) to a high of 38.0°C (1200–1359 h). While there were some differences between males and females in specific times of lows and highs in ULTs, the lows were during night-time hours and the highs were in mid-day for both sexes (Johnson 1976).

Within the limited information available on laboratory determinations of lower temperature limits in cyprinodontoid fishes included here (Table 2), the highest reported LLT was in Florida individuals of *Gambusia rhizophorae*, a species limited to south Florida and Cuba (Robins and Ray 1986), with a lower limit of 17°C (Baumgarten, cited in Getter 1982). Next was among individuals of *H. formosa* with a CTMin of 10°C (FL), and a CTMin of 8.5°C (SC) (Baer and Travis 2000). Also among those species showing least tolerance to low temperatures was *Belonesox belizanus*, a species introduced from Central America, with a reported LLT of 9.7°C (FL, Shafland and Pestrak 1982). Another tropical/subtropical species found in Florida, *K. marmoratus*, was reported to become moribund when subjected to prolonged exposure at water temperatures < 9°C (FL, Taylor et al. 1992).

Comparisons of laboratory thermal limits with field measurements

Ranges of tolerated temperatures determined in laboratory studies were compared with ranges of temperatures at which individuals of a species had been collected from nature (Fig. 1). Unfortunately, there were complete sets of data for only six of the species. All six fell above the line of equality between laboratory-determined limits and field observations, indicating that the overall ranges of thermal limits determined in the laboratory exceed the ranges of temperature at which these fishes have been encountered in the field. Two values each were included for *C. variegatus* and for *G. affinis*. The case for two values for *C. variegatus* was based on differences in results from static and dynamic techniques used in laboratory studies (Bennett and Beitinger 1997), while that for *G. affinis* was based on differences in results from laboratory determinations of temperature limits from two introduced populations (Otto 1973; 1974).

Evaluations were also made in the set of data in which information on laboratory determinations and field observations were only available for either lower or upper thermal limits.

Comparisons again showed that laboratory-determined thermal limits were almost always higher and lower than extremes of environmental temperatures at which individuals of the species had been found in nature (Table 2). Overall, *C. variegatus* and *F. heteroclitus* were found to have the widest ranges of thermal limits (combining laboratory and field observations) among this group of species. Both are species with wide latitudinal distribution ranges. However, some species with more limited latitudinal distributions (e.g., *G. affinis*, *G. holbrooki*) also show relatively wide thermal limits. Species limited to lower latitudes were found to tolerate greater ranges of elevated than lowered temperatures (e.g., *G. rhizophorae*, *K. marmoratus*). There were no species in this group that were limited to higher latitudes. It appears that among all species of fishes whose thermal limits are known, *C. variegatus* is certainly among those with the widest limits (Bennett and Beitinger 1997; Beitinger and Bennett 2000; Beitinger et al. 2000).

Overall thermal limits are broader than thermal ranges within which a species generally functions (general activity, reproduction, feeding, thermal preferences, Fry 1971). The present results are consistent for upper temperature limits of fishes with those of Cech et al. (1990), who found a close match between laboratory-determined upper temperature-tolerance limits and upper temperature limits suggested by field observations. However, their laboratory data did not predict fish distributions well for low temperatures.

Thermal preferences

Most species of fishes are largely dependent on behavioral control of their body temperatures, but this means of regulating body temperature is limited by the range of accessible water temperatures

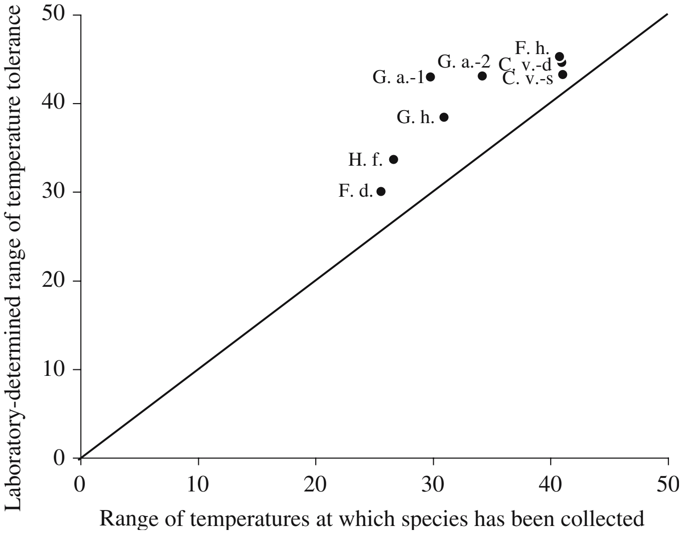

Fig. 1 Temperature limits (°C) of cyprinodontoid fishes. Values along the *x*-axis represent maximal ranges of ambient temperatures (differences between highest and lowest temperatures) at which individuals of a species have been collected. Values along the *y*-axis represent experimentally determined tolerable temperature ranges (differences between highest and lowest tolerated or lethal temperature) of a species. Abbreviations used to identify species in graph and sources of information follow. C. v.-s, *C. variegatus* (static technique)—Warlen 1964; Harrington and Harrington 1961; Bennett and Beitinger 1997. C. v.-d, *C. variegatus* (dynamic technique)—Bennett and Beitinger 1997. F. d., *F. diaphanus*—Fivizzani et al. 1984; Melisky et al. 1980. F. h., *F. heteroclitus*—Carr and Giesel 1975; Smith and Able 1994; Umminger 1971b; Bulger 1984. G. a.-1, *G. affinis*—Christmas and Waller 1973; Otto 1973; Otto 1974. G. a.-2, *G. affinis*—Carr and Giesel 1975; Otto 1973; Otto 1974. G. h., *G. holbrooki*—Nordlie and Mirandi 1996; Hart 1952; Meffe et al. 1995. H. f., *H. formosa*—Dahlberg 1972; Baer and Travis 2000. Note: A temperature of 2°C was the lowest temperature at which individuals of *C. variegatus* have been reported collected at a specific location. The two upper experimentally determined limits represent values obtained by a static, and a dynamic technique, respectively. Two different values from different populations were used for the highest temperature at which individuals of *G. affinis* have been collected

Table 3 Dissolved-oxygen relationships of cyprinodontoid fishes found in estuaries of eastern North America

Family and Species	Location	Lower lethal DO limit, mg kg^{-1}	Location	Hypoxic conditions DO, mg kg^{-1}	Location	Observed ranges of DO, mg kg^{-1}
Family Cyprinodontidae						
Cyprinodon variegates	NJ	LD50, 0.33 ± 0.03, 24°C, no ASR, 40 min Smith and Able 2003	FL	Sal. : Pc, torr.	FL	4–7, no discomfort 1, present but uncommon Kaill 1967
	?	24-h larvae, LC50, 7- day, 0.53, sal. 31–32, temp. 20–21, Poucher and Coiro, in USEPA, 2000		FW 57.0±6.9	VA	Summer, daily range < 0.1–21, 27–38°C, sal. 20–35 Layman et al. 2000
	?	Larvae, 7-day, 2.0, 38% growth red.; 1.7, 40% growth red.; 1.2, 67% growth red.; 0.8, 76% growth red., sal. 32, temp. 21 Larvae, 14-day, 1.5, 58% growth red., sal. 32, temp. 21 USEPA, 2000	2	51.5±5.9	TX	< 5 Gelwick et al. 2001
			15	53.7±4.9	NJ	Surface range 0–20; bottom range 0–17.3 Smith and Able 2003
			30	52.2±5.1		
			40	52.1±2.7		
			50	61.8±4.9		
			60	63.4±6.1		
			70	66.3±5.6		
			80	79.5±5.6		
			90	74.9±8.0		
			100	73.9±8.8		
			Temp.	20 ± 1 Haney and Nordlie 1997		
			FL	39.6 ± 1.2 Torr., 24 h. survival, sal., 30 ± 1, temp. 30 ± 1 Peterson 1990		
			NJ	Responded to decreasing DO by resting on bottom; ASR begun at 1.0 ± 0.01, 24°C Smith and Able 2003		

Table 3 continued

Family and Species	Location	Lower lethal DO limit, mg kg^{-1}	Location	Hypoxic conditions DO, mg kg^{-1}	Location	Observed ranges of DO, mg kg^{-1}
Floridichthys carpio			FL	ASR begun at 4–5 temp. not given Kaill 1967	FL	6–8, showed stress, 4–5, nearly incapacitated Kaill 1967
Jordanella floridae					FL	Adults, 0.5–12.1, sal. 0.3–17.7, temp., 12.8–37.0; spawning, 5.0–12.1, sal., 0.3–9.9, temp., 26.2–32 Hale in St. Mary et al., 2004
Family Fundulidae						
Adinia xenica					TX	4.5, FW wetland 2.85–5.40, brackish water Gelwick et al. 2001
Fundulus chrysotus					FL	8.7–10.2, temp., 15–24, FW, pH, 4.2–5.65 Dickinson 1948
Fundulus grandis			LA	Pc 34 Torr., temp. 25 ± 0.5, sal., 10–13 Virani and Rees 2000	LA	fall, 3.7–10.0, Temp., 12.2–25.2, sal., 3.1–9.9 winter, 7.3–12.3, temp., 18.6–21.9, sal., 1.9–3.4 spring, 2.7–10.9, temp., 21.2–28.4, sal., 2.6–6.3 summer, 1.4–9.7, temp. 24.0–33.0, sal., 0.6–6.9 Love and Rees 2002
			LA	with ASR 50%, fall, 0.81 ± 0.11, winter, 0.65 ± 0.09, spring, 0.78 ± 0.13, summer, 0.48 ± 0.10 P_{O_2}, fall 15 ± 2, winter, 12 ± 2, spring, 14 ± 2 summer, 9 ± 2 sal., 9–12, temp., 20–23 Love and Rees 2002		
Fundulus heteroclitus	DE	No hypoxia-related mortality in 9 days, DO 1, temp. 25, with or without access to water surface Stierhoff et al. 2003	NC	Did not avoid DO of 1, showed proportionally more ASR at lower DO, temp. 25–26, sal., 28–35 Wannamaker and Rice 2000	NC	7.2–10.3 Schwartz et al. 1981
	NJ	LD50 at 0.23 ± 0.02, 24.5°C, no ASR, 240 min Smith and Able 2003 Embryo, 24-h., 4.5, 10% mort.; 24-h., 2.4, 23.3% mort., 14-day, 2.4, 26.7% mort., sal., 30, temp. 20. Voyer and Hennekey, 1972	DE	ASR, DO ≤ 3, 25°C, sal., 25, L:D 14:10, hemoglobin elevated at DO 1.0, 25°C. No hypoxia-related mortality at DO 1, 25°C, with or without ASR Stierhoff et al. 2003	RI	Highly reduced respiratory oxygen uptake in air, temp., 15 Halpin and Martin 1999

Table 3 continued

Family and Species	Location	Lower lethal DO limit, mg kg^{-1}	Location	Hypoxic conditions DO, mg kg^{-1}	Location	Observed ranges of DO, mg kg^{-1}
					VA	Summer daily range < 0.1–21, 27–38 C, sal. 20–35 Layman et al. 2000
					NJ	Surface range 0–20, bottom range 0–17.3 Smith and Able 2003
Fundulus luciae					VA	< 1.0–6.8, temp., 4–36, sal., 0.2–12.7 Byrne 1978
Fundulus pulvereus	MO	0.88 ± 0.23, 26°C, FW Smale and Rabeni 1995			TX	< 5 Gelwick et al. 2001
Lucania goodei					FL	1.0–16.0, temp., 18.5–35.0, FW Arndt 1971
Lucania parva	NJ	LD50 at 0.23 ± 0.04, 23°C, no ASR, 60 min Smith and Able 2003			FL	1.8–23.0, temp., 22.0–37.5, sal., 0.3–36.5 Arndt 1971
					NJ	Surface range 0–20; bottom range 0–17.3 Smith and Able 2003
Family Poeciliidae						
Gambusia affinis	India	Survived at 0.23–1.54, sal., ca. 60 Ahuja 1964	CA	ASR 20–65 Torr, obligatory, 20 Torr, temp., 20, FW males more sensitive to hypoxia than females Cech et al. 1985	MS	1.0–10.0, temp., 10–33, sal., FW-8.1 Brown-Peterson and Peterson 1990
	CA	25 Torr., temp., 15–35, FW Cech et al. 1985				
Gambusia holbrooki	FL	0.28, temp., 22–23, FW, lethal to all when prevented from ASR no mortality at 1.3 when submerged Odum and Caldwell 1955	FL	ASR and gulping Odum and Caldwell 1955 ASR at spring boil site, DO 0.20 ± 0.06 McKinsey and Chap-man, 1998	FL	0.2–0.3, temp., 22–23, FW Odum and Caldwell 1955
					FL	0.2–3.3, temp., 21.1–22.0, FW McKinsey and Chapman 1998
Heterandria formosa					FL	0.3, temp., 21–22, FW Odum and Caldwell 1955
					FL	0.2–3.3, temp., 21–22, FW McKinsey and Chapman 1998
Poecilia latipinna	FL	0.28, temp., 22–23, FW, lethal to all, no mortality at 1.3 when submerged Odum and Caldwell 1955	FL	ASR, at DO 1, temp., 25, sal., 10; for females (greater % of gestating females showed ASR than nongestating) Timmerman and Chapman 2003	FL	0.2–0.3, temp., 22–23, FW Odum and Caldwell 1955 < 2.0 Timmerman and Chapman 2003

Table 3 continued

Family and Species	Location	Lower lethal DO limit, mg kg^{-1}	Location	Hypoxic conditions DO, mg kg^{-1}	Location	Observed ranges of DO, mg kg^{-1}
Family Rivulidae						
Kryptolebias marmoratus			Curaçao	Emersion Kristensen 1970	Grand Cayman,	Emersion at 19–20°C Huehner et al., 1985
			FL	Emersion, H2S Abel et al., 1987	FL	0.6–3.8 Taylor 1990
			FL	Aerial respiration Grizzle and Thiyagarajah 1987	FL	0.3–2.5 Dunson and Dunson 1999
			Belize, FL	Semi-terrestrial Davis et al. 1990		
			FL	Episodic hypoxia Dunson and Dunson 1999		

(Beitinger and Fitzpatrick 1979). Some species have been found to be able to discern temperature differences as small as 0.03°C, making adjustments easily possible where temperature gradients are present. In some cases individuals of a species show a laboratory FTP outside the normal range of temperatures encountered in nature, suggesting that temperature selection may be ‘‘overridden or masked’’ by other conditions (Beitinger and Fitzpatrick 1979).

Thermal preferences (Table 2) were evaluated in individuals of *F. diaphanus*, taken from a Nova Scotia lake population, and acclimated to four ambient temperatures in FW and in SW (Garside and Morrison 1977). Mean thermal preference values ranged from 15.5°C in SW and 23.9°C in FW for individuals acclimated to 5°C, to 22.6°C in SW and 27.3°C in FW when acclimated to 30°C. Those thermal preference values decreased at increased acclimation temperatures from 5°C to 25°C, with lowest values of 13.1°C in SW and 19.9°C in FW at 25°C, then increased at 30°C. Results were compared with thermal preference values of *F. heteroclitus* from a marine water in Nova Scotia, over a set of acclimation temperatures from 5°C to 35°C. Mean thermal preferences ranged from 23.6°C in SW and 16.0°C in FW at 5°C, to 30.9°C in SW and 24.8°C in FW at 35°C, first increasing at 15°C, dropping at 25°C, then rising at 30°C and peaking at 35°C. The FW species, *F. diaphanus*, showed consistently higher thermal preferences in FW than in SW, and *F. heteroclitus*, a SW species, showed the opposite pattern. Estimated values of the FTPs of these two species were: *F. diaphanus*, SW 14°C, FW 21°C; *F. heteroclitus*, SW 24°C, FW 22°C (Garside and Morrison 1977).

Preferred temperatures of pregnant females and juveniles of *P. latipinna* showed no significant differences from one another, but were significantly higher than preferred temperatures of mature males of the species. It was speculated that higher preferred temperatures may direct juveniles to areas where the threat of intra- and interspecific predation is reduced and/or where higher temperatures increase their metabolic rates and result in higher growth rates (Stauffer et al. 1985). Upper avoidance temperatures and

FTP for *G. affinis* (Bacon et al. cited by Coutant 1977) were as follows: adults showed an upper avoidance temperature of 29.5°C and a FTP of 27°C; individuals of 15–19 mm showed an upper avoidance temperature of 32°C; and individuals of <15 mm showed an upper avoidance temperature of 35°C. Those results indicated that smaller individuals were more tolerant of elevated temperatures. Final thermal preference values were not given for the two smaller size groups, nor were sources given for the individuals used.

Geographic variations in thermal response patterns

A growing interest has been taken regarding possible local differences in thermal response patterns among populations of a fish species. Some species have shown significant variation in lethal limits, thermal tolerances and preferenda among populations, especially with respect to latitudinal ranges, while others have not. Among cyprinodontoid species, a population of *F. diaphanus* from Nova Scotia showed a FTP of 21.0°C (Garside and Morrison 1977), while a Pennsylvania population had a higher FTP, 28.6°C, though determined using a different technique (Melisky et al. 1980). Similarly, individuals of *F. heteroclitus* from Nova Scotia showed ULT levels of 34.0°C (sal., 14), and in a later study 36.31°C (25°C, sal., 14) (Garside and Jordan 1968; Garside and Chin-Yuen-Kee 1972), while individuals from North Carolina (?) showed an ULT of 41.7 ± 0.55°C (30°C acclimation) (Burnside 1977), and from Virginia, a CTM value of 44.1 ± 0.14°C (36°C acclimation, 1200 h) (Bulger 1984).

Individuals of *G. affinis* have been widely introduced into nonnative locations, not only in North America, but also among continents and oceanic islands (Alberta, Canada, McAllister 1969; AZ, Otto 1973; HI, Scribner et al. 1992; India, Ahuja 1964; Iraq, Al-Daham and Bhatti 1977; Israel, Chervinski 1983; MT, Brown and Fox 1966). Several of the locations where populations have been successfully introduced are colder areas than areas within the original North American distribution of the species. Thermal limits, measured following laboratory acclimations, were compared between individuals of *G. affinis* taken from a warm spring population introduced in the Sonoran Desert of Arizona and individuals from a cold-adapted, introduced population in northern Utah. The non-genetic scope for adaptation was identical for both populations, though offset, with the cold-adapted population doing better at lower temperatures and the warm-adapted population doing better at high temperatures. The LLT and ULT for cold-adapted individuals were (ca.) 0.6°C and 36.2°C, respectively; and for the warm-adapted population the LLT and ULT were (ca.) 2.6°C, and 37.8°C, respectively (Otto 1973). In other studies, individuals of two populations of *G. holbrooki*, one from an ambient-temperature pond, the other from a pond whose water was heated to near the ULT for 60–90 mosquitofish generations, were compared for CTMax values. Individuals from the thermal pond had higher CTMax values. Also, in comparing individuals of the two populations to thermal LD_{50} stress, the survivors were found to have higher levels of heterozygosity, suggesting that genetic diversity may be contributing to thermal tolerance. In a third set of experiments, it was found that selection for thermal tolerance had not depleted the population of genetic variation associated with thermal tolerance (Meffe et al. 1995).

Thermal limits were compared between populations of desert pupfishes (genus *Cyprinodon*) that had been isolated for varying periods of time in thermally constant environments, with individuals of populations inhabiting environments showing dramatic fluctuations in water temperatures (Brown and Feldmeth 1971). Results suggested that acclimation, rather than genetic differences, accounted for some or all of the differences in thermal limits among those populations inhabiting springs of different temperatures. It was concluded that the populations have been isolated in their present habitats for sufficient time to undergo evolutionary changes, but that their thermal limits did not seem to have been altered. It was further suggested that the homeostatic systems involved in thermal responses must be highly resistant to evolutionary change. The predicted correspondence between the range of an environmental parameter encountered and the range that can be tolerated does not hold in this case. The overall range of thermal tolerance in that group of species and subspecies of *Cyprinodon* was roughly from 0° to 40°C. The conclusions that the differences represented physiological acclimations rather than genetic differences varied from those of a study comparing individuals of *C. nevadensis mionectes* from Big Spring, NV, a constant temperature desert spring (27.3°C) with individuals of *C. n. amargosae* from the more variable Amargosa River, CA (≈0–40°C). The *C. n. mionectes* fish had a narrower range of temperature and DO tolerances than individuals of *C. n. amargosae*. Those results suggested genetic divergence between the two populations that have been isolated from one another for 400–4000 years (Soltz and Naiman 1978) or 400–5000 years (Hirshfield and Feldmeth 1980). It appears that thermal responses to altered environmental conditions vary among species and among populations of various species of cyprinodontoids as well as among other taxa of fishes (e.g., Garside et al. 1977; Røed 1979; Winkler 1979; Feminella and Matthews 1984 and Matthews 1986). The bases of that variation may also vary among species and populations.

Cold fronts

There are numerous reports of winter fish kills produced by weather patterns that rapidly reduce water temperatures in marine shallows and estuaries along the lower Atlantic and Gulf coasts. All of the reports included here are for estuaries/salt marshes located between 26° and 32° N latitude. Unfortunately, laboratory thermal limits have been determined for only a few of these species (Table 2). Most of those values ignore possible geographical variations in thermal-response patterns. If individuals of the most cold-hardy cyprinodontoid species are killed by sudden drops in temperature it would be expected that other less cold-hardy cyprinodontoids in the affected areas would also be killed under the same circumstances. Observations of extensive fish kills made during the winter (1939–1940) along the shores of Copano, Aransas, and Rattlesnake Bays, TX, included individuals of a number of species of fishes, crabs, and shrimp. The only cyprinodontoid fish mentioned as being found dead was *F. carpio*. The lowest temperature noted in open bay waters was 4°C though there was ice along the shores (Gunter 1941). An analysis of sizes of individuals of marine fishes found dead following such cold fronts suggested higher survival of the smaller/younger ones (Gunter 1947). Local populations of *C. variegatus*, one of the normally cold-tolerant species of cyprinodontoids, were said to have been “wiped out” in some shallow ponds in the vicinity of St. Charles Bay, TX in the winter of 1951. Again, there was said to be ice along the shoreline (Gunter and Hildebrand 1951). Another cold front in the area of Redfish Bay, TX on the night of Jan. 11, 1973 dropped the water temperature to the range of 0.5–4.5°C. Dead individuals of *C. variegatus*, *F. grandis*, and *F. similis*, were found the following day along with other species of fishes (Moore 1976).

Individuals of 56 species of fishes were found dead in the Indian River Lagoon, FL following a cold front in the winter of 1977 during which water temperatures dropped as low as 6°C. Individuals of *F. carpio* and *F. similis* were collected alive there and appeared to suffer no ill effects of the severe cold in those waters (Gilmore et al. 1978). However, a distinct reduction in numbers of *K. marmoratus* was noted in the year following a cold front along the southeast coast of Florida (region of Titusville and Ft. Pierce) in Dec., 1989, when water temperatures dropped as low as 7.7°C, and remained at < 10°C for five to seven days. There was no evidence of any impact on other cyprinodontoids at that time (Taylor 1993). Three cold fronts along the Texas coast (Dec. 1983, Feb. 1989, and Dec. 1989) killed massive numbers of a total of 103 species of fishes. The most severe of the three events was the Dec. 1983 cold front during which the water temperature dropped ca. 15°C in 10 days to near 0°C, and remained between 0°C and 5°C for ca. seven days. Species of interest that were identified as being killed were: *C. variegatus*, *A. xenica*, *F. grandis*, *F. similis*, *L. parva*, *P. latipinna*, and unidentified killifish (likely *F. pulvereus* and/or *F. jenkinsi*) (McEachron et al. 1994).

Other recent cold-induced fish kills along the coast of the Gulf of Mexico and lower Atlantic coast of the U. S. in which no individuals of cyprinodontoid fishes were among species reported to have been killed included: January, 1970, water temperatures to ≈0°C in shallows over marshes, and 4.5°C in estuarine waters of Jekyll, Saint Simons, and Sapelo Islands, GA (Dahlberg and Smith 1970); January, 1970, Sanibel Island and Tampa Bay, FL estuaries (Gilmore et al. 1978); 1977, Indian River Lagoon, FL 1977 water temperatures as low as 4–6°C, salinity 20–32 (Snelson and Bradley 1978); December, 1983, and January, 1985, temperatures in the Indian River Lagoon of 4.0°C and 2.8°C, salinity 17, at which time individuals of 23 species were found dead (Provancha et al. 1986).

The paucity of reports of cyprinodontoids being killed by cold fronts (noted by Snelson and Bradley 1978) may stem from one or more of several circumstances:

1. All of these species are cold-hardly for the ranges of temperatures experienced at locations throughout their distributions.
2. All of these cyprinodontoids are relatively small fishes, and while most of the individuals making up the noted kill are larger and of game species, the small individuals are rarely seen or collected when such fish kills are studied (suggested by Gilmore et al. 1978).
3. Small fishes (small individuals of a species or small species) generally move offshore as temperatures decrease, while some of the species that are most affected are the less mobile ones (Gilmore et al. 1978).
4. Individuals of some of these species burrow into the substratum at low environmental temperatures in areas where that is possible (e.g., Chidester 1920; Frederick and Loftus 1993).
5. Smaller individuals are less influenced by rapid changes in temperature than are larger individuals of the same or other species (Gunter 1947; Snelson and Bradley 1978). However, there is evidence that overall winter mortality is size specific, with greater loss of smaller individuals of a species than of larger individuals (e.g., Conover 1984; Henderson et al. 1988; Conover and Present 1990).

The likelihood is that all of these circumstances play a part in the relative rarity of cyprinodontoid fishes being reported in cold-induced fish kills. It is to be expected that the effects of a rapid reduction in water temperature will exert influences on the fish fauna as functions of: the lowest temperature reached; the rate of change of temperature in reaching the lowest level; the length of time that the temperature remains at the extreme level (very important), or other critical low levels; existing salinity levels; and possibly DO concentrations in the particular environment. It also seems likely that the stage of the tide, enhancing or reducing the opportunity for escape from shallows at the time that the water temperature is showing maximal change or reaching a critical level, would affect the potential mortality. Smaller individuals are less restricted by lower water levels than larger ones.

Results of evaluations of temperature sensitivity of various of these fishes seem consistent with information presented by Brett (1970), demonstrating that the breadth of thermal limits among various species of adult fishes that had been evaluated in laboratory studies were broadest among those from middle latitudes, ca. 30–50° North or South. However, embryos/larvae did not show the same latitudinal relationship, but this was due, at least in part, to the paucity of information on developmental stages of many species for which information existed for adults.

Oxygen: lethal dissolved-oxygen limits and tolerances

Dissolved-oxygen (DO) concentrations can determine presence/absence/abundance of aerobically respiring estuarine inhabitants including fishes. Limitations may be for short or long periods of time, and in limited or relatively large areas. The short-term dynamics of DO concentrations in shallow regions of an estuary can be keyed to diel cycles of the primary production to respiration relationship of the estuarine system, as well as to tidal cycles, ambient temperature and salinity. DO concentrations can range from supersaturated, generally in afternoons on bright, still days, to anoxic levels during warmer periods and at low tide, usually late at night or in early morning hours. Longer term, and generally wider scale hypoxic to anoxic conditions are generally related to circulation patterns and density stratification in larger and deeper estuarine areas, e.g., Chesapeake Bay (Newcombe and Horne 1938).

Influences of both reduced and elevated oxygen concentrations were evaluated, first considering ambient conditions at collection locations. Information on ambient temperatures and salinities are included where reported. Information is also presented giving low DO concentration limits determined in controlled experiments, along with other relevant environmental conditions of the experiments. The use of aquatic surface respiration (ASR) by individuals of these species, and of critical oxygen tensions (P_c values—the P_{O_2} level at which DO consumption, at standard level of metabolism, becomes dependent on DO concentration, Fry 1947; McNab 2002) was included when reported. As was the case for thermal relationships, extensive laboratory determinations of tolerable and lethal low (or high) DO concentration limits have been made for relatively few of the species of interest.

The only species among those represented here (Table 3) that seems not to tolerate low ambient DO concentrations, even for short periods of time, is *F. carpio*. Individuals showed ‘‘stress’’ at 6–8 mg kg^{-1}, and were ‘‘nearly incapacitated’’ at ambient DO levels of 4–5 mg kg^{-1}, under which conditions they showed ASR (Kaill 1967). However, individuals of *F. carpio* were among the most abundant fishes in a restored area of mangrove on Key Biscayne, FL. DO concentrations there were found to range from a high of 10.62 mg kg^{-1} (32.3°C, 32.5 sal.) to a low of 2.76 mg kg^{-1} (29.3°C, 32.6 sal.) during wet seasons, and 12.35 mg kg^{-1} (28.8°C, 33.4 sal.) to a low of 1.36 mg kg^{-1} (23.9°C, 31.2 sal.) during dry seasons (Barimo and Serafy 2003). DO saturation levels ranged from ca. 178% to 44% during wet seasons and from ca. 197% to 20% for dry seasons. The lower ranges of DO during both wet and dry seasons were well into the ranges found to be extremely stressful to *F. carpio* (Kaill 1967). The only other species for which it appeared from published field information that suitable habitat was limited to areas with high DO was *F. chrysotus* (Dickinson 1948); however, individuals of the species have been observed in locations with lower levels of DO (Nordlie, unpublished data).

Hypoxia

Fish kill reports in North America resulting from declining DO concentrations historically have been largely from fresh waters. Many lakes at higher latitudes experience a lack of photosynthetic activity in winter under heavy ice and snow covers resulting in oxygen depletions. Swamps and canals in Florida and other Southeastern states are reduced in volume during dry seasons, concentrating fishes and other aquatic organisms in small volumes of water in which DO concentrations are gradually depleted, killing the captive inhabitants (Kushlan 1974). However, increasing rates of reduction in DO concentrations in estuarine systems in many areas of the world have gained attention in recent years, including Chesapeake Bay (e.g., Newcombe and Horn 1938; Seliger et al. 1985; Breitburg 1992; Breitburg et al. 1997, 2003). Other estuarine areas reported to show hypoxic conditions include: Charlotte Harbor, FL (Taylor 1974); Tampa Bay, FL (Simon 1974); Louisiana coastal waters and continental shelf waters of the Gulf of Mexico (Renaud 1986; Rabalais et al. 2001); Mobile Bay (May 1973; Turner et al. 1987); the Rappahannock River, a tributary of Chesapeake Bay (Kuo and Neilson 1987; Kuo et al. 1991); Herring River, Cape Cod, MA (Portnoy 1991); and Waquoit Bay, Cape Cod, MA (D'Avanzo and Kremer 1994); Belgium (Maes et al. 1998); Japan (Karim et al. 2003); Norway (Johannessen and Dahl 1996); Sweden (Rosenberg and Loo 1988); noted as a global phenomenon (Diaz 2001; Breitburg 2002); and tidal salt marshes in general (Smith and Able 2003). Stratigraphic analyses of sediment cores taken in a transect across Chesapeake Bay revealed that even anoxic conditions were not a new phenomenon there, but the rate of production of such conditions has been increasing since the time of European settlements in the area in the 17th and early 18th centuries

(Cooper and Brush 1991). This is likely true of other areas as well.

There have been numerous laboratory demonstrations of responses in various species of teleost fishes to decreasing DO concentrations, and while there are reports of ‘‘fish kills’’ in estuarine and coastal waters that were shown to follow reduced DO concentrations (hypoxic conditions) in a particular system, (e.g., Portnoy 1991; D’Avanzo and Kremer 1994), few of the fish kill events have supporting data. A few studies have combined field and laboratory analysis of responses of fishes to hypoxic conditions (e.g., Pihl et al. 1991), but most information on responses of fishes of coastal, estuarine, and salt marsh fishes to reduced DO concentrations is based on laboratory studies.

Experimental studies of hypoxic conditions on cyprinodontoids, including influences of aquatic surface respiration

Lewis (1970) provided an early demonstration of morphological adaptation for, and behavioral utilization of higher DO concentrations in the layer of water at the air-water interface, the phenomenon later called aquatic surface respiration (ASR). Included in that study among test species were *F. notatus*, *G. affinis*, and *Poecilia reticulata*, all of which exhibited ASR. That work has been greatly expanded by examination of a wide variety of temperate and tropical fishes (e.g., Kramer and Mehegen 1981; Kramer and McClure 1982; Kramer 1983, 1987; Stierhoff et al. 2003; Smith and Able 2003). Several examples are presented showing abilities of cyprinodontoid fishes to survive under hypoxic conditions, in some cases using ASR. Individuals of *F. heteroclitus* did not avoid DO levels as low as 1 mg kg^{-1} (NC, Wannamaker and Rice 2000). In a later study (Smith and Able 2003) individuals of that species showed 50% mortality in 240 min when the DO concentration decreased to 0.23 ± 0.02 mg kg^{-1} in a closed system. When possible, individuals began ASR at a DO concentration of 1.09 ± 0.02 mg kg^{-1}. Individuals of *L. parva* showed 50% survival for 60 min without ASR down to a DO concentration of 0.23 ± 0.04 mg kg^{-1} (23°C), beginning ASR, when possible, at 0.91 ± 0.02 mg kg^{-1}. Individuals of *C. variegatus* survived 40 min to 50% mortality at a DO concentration of 0.33 ± 0.03 mg kg^{-1}, and began ASR, when possible, at an ambient DO concentration of 1.00 ± 0.01 mg kg^{-1} (24.0°C). The ambient salinity for all three sets of experiments was 30 (Smith and Able 2003) (Table 3).

In another study, individuals of *F. heteroclitus* were found to maintain high rates of growth at DO concentrations as low as 3 mg kg^{-1} (Stierhoff et al. 2003). When the DO concentration was reduced to 1 mg kg^{-1} growth rate decreased by ca. 60% if individuals were allowed access to the water surface. If denied access to the water surface the growth rate decreased by 90% at an ambient DO concentration of 1 mg kg^{-1}. Decreased rate of feeding at this low DO concentration appeared to be primarily responsible for the reduced rate of growth. Diel cycling of DO (1–11 mg kg^{-1}) had no effect on those results. That study found ASR to be initiated at DO concentrations of <3 mg kg^{-1}. No hypoxia-related mortality was noted under any of those experimental conditions over a period of nine days. Individuals of *F. heteroclitus* have also been found to be capable of carrying on limited respiratory gas exchange in an aerial environment, both taking up O_2 and releasing CO_2. Aquatic respiration did not increase following re-immersion of the individuals that had been respiring aerially, so it was assumed that anaerobic metabolism was not used during such emergences (RI, Halpin and Martin 1999).

Individuals of *P. latipinna* from a periodically hypoxic salt marsh at Cedar Key, FL, acclimated for six weeks to hypoxic conditions (DO 1 mg kg^{-1}, ca. 20 Torr), spent less time conducting ASR and had lower gill-ventilation rates than hypoxia-acclimated individuals from a Santa Fe River, FL population where normoxic conditions prevailed (Timmerman and Chapman 2004b, c). Ventilation frequency increased by a factor of two in the Cedar Key individuals when introduced into the hypoxia acclimation, and did not decrease with time. However, the immediate increase in use of ASR did decrease with time, and within five weeks showed no difference in frequency from individuals in normoxic water (Timmerman and Chapman 2004a). Individuals from both populations showed lowered P_c values following acclimation to hypoxic conditions. However, individuals from the salt marsh population showed lower P_c values than did those from the Santa Fe River population, assumed to be the result of living in a chronically hypoxic environment. Also, salt marsh individuals had 14% greater gill surface areas than did individuals from the normoxic river population, potentially related to the hypoxic conditions in the salt marsh (Timmerman and Chapman 2004b).

Seasonal variations in the frequency of ASR were demonstrated in individuals of *F. grandis* taken from Lake Pontchartrain, LA (Love and Rees 2002). Fish collected during the summer did not initiate ASR until the DO concentration had dropped to lower values than for any other season, and laboratory acclimation to low DO concentrations did not alter that response. Fish collected during the summer and winter had significantly longer survival times at severe hypoxic conditions than did individuals collected during the fall. It was also demonstrated that condition of the individual fish was positively associated with survival time, and that there were seasonal variations in condition. Anaerobic metabolism was found in individuals of *F. grandis* by monitoring blood-lactate levels under hypoxic conditions (P_{O_2} levels below the P_c, <34 Torr, 25 ± 0.5°C). It was also found that there was significant, repeatable variation among individual fishes in metabolic levels (Virani and Rees 2000).

Routine metabolic rates (RMR) of individuals of *G. affinis* were evaluated at ambient temperatures of 10, 15, 20, 25, 30 and 35°C, under extremely hypoxic ($P_{O_2} = 25$ Torr), hypoxic ($P_{O_2} = 40$ Torr), normoxic, and hyperoxic ($P_{O_2} = 300$ Torr) conditions. Under normoxic conditions RMR increased with increasing temperature ($Q_{10} = 2.11$). Males exhibited higher mortalities than did females under hypoxic conditions, especially at 25°C. The RMR values were elevated under hyperoxic conditions at 25°C and 30°C, but not at 35°C. It was found that ASR was initiated at a P_{O_2} of 20–65 Torr in *G. affinis*, and was obligatory below 20 Torr at 20°C, a DO concentration of ca. 1.14 mg kg^{-1} (Cech et al. 1985). Responses in CTM were compared among groups of individuals of *Fundulus notatus*, and two cyprinids, *Notropis lutrensis* and *Pimephales vigilax*, all from freshwater habitats, acclimated to hypoxic, normoxic, or hyperoxic conditions, 30°C, 12:L:12D photoperiod (Rutledge and Beitinger 1989). Half of the members of each group were allowed to carry on ASR, the other half prevented from doing so. Critical thermal maximum values were higher among individuals of all three groups in hypoxic waters when allowed to carry on ASR than when prevented from doing so. No such difference was noted at normoxic or hyperoxic DO concentrations. Among those three species, *F. notatus* had the highest CTMax at all three DO levels. The mean CTMax values under hypoxic conditions were significantly lower than those for normoxic or hyperoxic conditions, the latter two of which were not significantly different from one another.

Individuals of *G. affinis* (introduced population) were found to show >50% survival at ambient DO concentrations as low as 0.23–1.54 mg kg^{-1}, temperature 19.0–20.5°C, salinity of ca. 30 (India, Ahuja 1964). In another introduced population of *G. affinis*, prolonged exposure in FW at a P_{O_2} of 25 Torr without access to ASR resulted in deaths of 22% of males, but only 3% of females, in the temperature range 15–35°C (DO concentrations ca. 1.5 mg kg^{-1}at 15°C, and 1.1 mg kg^{-1} at 35°C) (CA, Cech et al. 1985). The closely related species, *G. holbrooki* was found to have 100% mortality at a DO concentration of 0.28 mg kg^{-1}, temperature of 22–23°C, FW, when prevented from ASR, but survived under those circumstances when ASR was possible in a field experiment (FL, Odum and Caldwell 1955). There was no mortality in the absence of ASR at a DO concentration of 1.3 mg kg^{-1} in that spring system. The identical results were obtained for *P. latipinna* in the same spring (Odum and Caldwell 1955).

A number of physiological conditions were compared among individuals of *C. variegatus* and *P. latipinna* collected from a Florida mangrove swamp and held in the laboratory at normoxic conditions ($P_{O_2} = 150$ Torr, DO, ca. 5.94 mg kg^{-1}) or hypoxic conditions ($P_{O_2} = 40$ Torr, DO, ca.1.58 mg kg^{-1}), all at 30°C and a salinity of 30 (Peterson 1990). Significant reductions in respiratory-oxygen consumption were noted in individuals of both species subjected to hypoxic conditions. Field experiments also suggested that individuals of *C. variegatus* and *F. heteroclitus* survived in environments subjected to sporadic depletion of DO, even at summer temperatures, in waters ranging in salinity from 20 to that of SW (Layman et al. 2000; Smith and Able 2003). It may be that individuals seek out areas of highest available DO concentration at such times, as well as relying on ASR.

Males of *G. affinis* were found to be more sensitive to hypoxia than were females (Cech et al. 1985), while a greater percentage of gestating females of *P. latipinna* used ASR at a particular DO level than did non gestating females (Timmerman and Chapman 2003). Females of *P. latipinna* in late stages of gestation had higher weight-specific routine metabolic rates than males or other females. The gestating females spent ca. 27% more time in ASR than did non-gestating females exposed to chronic hypoxic conditions (DO of 1 mg kg^{-1}) (Timmerman and Chapman 2003). Acclimation to hypoxic conditions produced no significant reduction in reproductive activity of *P. latipinna* females (Timmerman and Chapman 2004a). However, females of *F. grandis* kept under hypoxic conditions showed significantly lower numbers of ovulated and spawned eggs than did controls (Landry et al. 2003).

Critical oxygen tension

Perhaps the least frequently evaluated response of fishes to decreased levels of DO is that of the critical oxygen tension (P_c), generally determined in the process of measuring aerobic rates of metabolism. Values of P_c increased over salinity for *C. variegatus* in the salinity range from FW to 100. However, the values at salinities between FW and 40 were not significantly different from one another (Table 3). Highest levels of P_c were found at salinities of 80 and greater (Haney and Nordlie 1997). Individuals of *F. grandis* had a P_c of 34 Torr (ca. 1.6 mg kg^{-1}) at an ambient temperature of 25 ± 0.5°C, and a salinity of 10–13 (Virani and Rees 2000), a value somewhat lower and at a higher ambient temperature than any of those for *C. variegatus*. Values of P_c fell by 17–19% in individuals of *P. latipinna* taken from a chronically hypoxic salt marsh at Cedar Key, FL and acclimated for a period of six weeks at a DO concentration of 1 mg kg^{-1} (sal. 10, 25°C). Values dropped to 16.1 and 18.1 Torr, compared with 19.9 Torr and 21.9 Torr in two trials comparing hypoxic and normoxic conditions, respectively (Timmerman and Chapman 2004a).

Emersion

A response that seemed unique to *K. marmoratus* was that of ‘‘emersion’’, leaving the aquatic environment under unfavorable ambient conditions. Individuals of that species have been found to survive in a moist aerial environment for days to months (Abel et al. 1987; Huehner et al. 1985). It was suggested that emersion was an adaptation to avoiding unfavorable concentrations of hydrogen sulfide (H_2S) (Florida, Abel et al. 1987), as well as episodic hypoxic conditions (Curaçao, Kristensen 1970; FL, Brockmann 1975; Grand Cayman, Huehner et al. 1985; FL, Grizzle and Thiyagarajah, 1987; Belize, Davis et al. 1990; FL, Dunson and Dunson 1999). Individuals were unable to survive when confined to very hypoxic or anoxic waters (Davis et al. 1990; Taylor 1988). Oxygen consumption was significantly reduced in the aerial environment (27% in juveniles and 25% in adults), and individuals were said to often show torpor when in an aerial environment. The skin of that species has extensive cutaneous vascularity, an apparent adaptation to aerial respiration (Grizzle and Thiyagarajah 1987).

Hyperoxia and gas-bubble (disease) trauma

A review of earlier literature on dissolved-gas supersaturation in natural waters is found in Weitkamp and Katz (1980). Photosynthetic production of oxygen greatly exceeding respiratory demands of phytoplankton or macrophytes, in areas where there is no significant circulation in the water column, is the process by which exclusively hyperoxic conditions are produced. There have been observations of potential lethality and avoidance by fishes of areas of high DO concentrations. A fish kill in Lake Waubesa, WI in April of 1940 was thought to have been caused by supersaturation of DO, produced by a dense bloom of *Chlamydomonas* sp. Concentrations of

DO ranged from 16.8 mg kg^{-1} at a depth of 3.7 m, to 32.1 mg kg^{-1} at the surface, at a distance of 45 m from shore, and of 30.0 mg kg^{-1} at the surface, 6 m from shore (Woodbury 1941). Those DO values represented a range from 171% to 327% of aerial saturation (water temperatures estimated from the DO values were ca. 15–16°C). A fish kill reported from Galveston Bay, TX may have been caused by gas-bubble trauma. DO concentrations throughout the bay reached levels near 250% of air saturation, a condition produced by a dense phytoplankton bloom. Dead fish examined showed symptoms of gas-bubble trauma. Most of the dead and dying fish encountered were mature adults, but small individuals of some species also died. No cyprinodontoid fishes were reported killed (Renfro 1963).

Hyperoxic conditions in an estuarine situation in a tidal FW region of Chesapeake Bay were accompanied by elevated pHs, both produced in the photosynthetic process. Field observations made in dense beds of *Hydrilla verticillata*, or *H. verticillata* and *Vallisneria americana*, were followed by laboratory experiments roughly approximating field conditions (Serafy and Harrell 1993). Individuals of *F. diaphanus*, *Lepomis macrochirus*, and *Morone saxatilis* were used in experiments involving increasing levels of DO concentrations, pH, and combinations of the two. The results suggested that in areas of high DO concentrations (200–260% air saturation levels) fishes did not avoid high pHs (9.5–10.0) (ambient temperature range of 19–23°C), but at lower levels of DO did avoid pHs exceeding 9.5. No mortality was observed in either the field observations or the laboratory experiments.

DO standards for marine animals

Agencies responsible for the protection of fisheries have engaged in establishing minimum-acceptable DO levels for various waters, both FW (e.g., USEPA 1986) and marine (e.g., USEPA 2000), to enhance chances of survival through all life stages of populations of resident animals. Recommendations for coastal and estuarine waters were "... If the DO exceeds the chronic protective value for growth (4.8 mg/l), the site meets objectives for protections. If the DO is below the limit for juvenile and adult survival (2.3 mg/l), the site does not meet objectives for protection. When the DO is between these values, the site requires evaluation of duration and intensity of hypoxia to determine suitability of habitat for the larval recruitment objective. ..." It was noted that those limits were based on laboratory studies, but were supported by field observations (USEPA 2000). The Commonwealth of Virginia adopted DO standards for estuarine waters of a 5 mg/l daily average, with no observations below 4 mg/l. The lower value approximated 50% saturation levels for summer periods (Kuo and Neilson 1987). These DO levels appear adequate for adult individuals of estuarine cyprinodontoids, with the exception of *F. carpio* (not present in the Virginia area), which would be stressed at even the highest levels recommended here (Kaill 1967). However, the lower limit of 2.3 mg/l, is lower than those considered adequate for development of eggs of *F. heteroclitus* (Voyer and Hennekey 1972; Taylor and DiMichele 1983).

Salinity: salinity lethal limits and tolerances

Environmental salinities can show dramatic fluctuations in estuarine systems, following tidal cycles and variation in amplitudes influenced by FW inflows, precipitation, evaporation, and rates of water exchange in semi-isolated pools and lagoons. Several mechanisms have evolved by which fishes are able to inhabit such systems where they may encounter predictable as well as unpredictable variations in salinities (Kinne 1964, 1966, 1967). Much of the information available on salinity relationships of fishes is based on anecdotal observations of salinities at locations where various species have been collected.

Ambient salinities at which cyprinodontoids have been collected from nature

Individuals of *C. variegatus*, have been taken from waters ranging in concentration from FW to salinities as high as 167 (FL, Gilmore et al. 1982) the highest salinity at which any of these species has been reported (Table 4). Those individuals were living in a tide pond in central Florida, reached only by the highest of tides (Gilmore et al. 1982). No information was given as to how long this situation had existed, nor how long individuals in this pond survived. Freshwater populations of that species were reported from the St. Johns River, FL (McLane 1955), and from the Big Cypress Swamp and FW areas of the Florida Everglades (Loftus and Kushlan 1987). An endemic subspecies, *C. v. hubbsi*, inhabits a series of FW lakes in the upper Oklawaha River drainage, a tributary of the St. Johns River (FL, Guillory and Johnson 1986). Other species among the group that have been found surviving in nature over wide ranges of salinity included: *P. latipinna*, FW (FL, Kilby 1955) to ca. 87 (introduced population, Manila Bay, Philippines, Herre 1929); *K. marmoratus*, found in salinities over the range from FW to 70 (Curaçao, Kristensen 1970); *F. grandis*, 1.8–76.1 (TX, Simpson and Gunter 1956), and also with FW populations (LA, Douglas 1974; TX, Hillis et al. 1980); *F. similis*, 13.1–76.1 (TX, Simpson and Gunter 1956), and at salinities as low as 0.09 (FL, Martin and Finucane 1968); *F. pulvereus*, 11.9–53.6 (TX, Simpson and Gunter 1956, and at salinities as low as 0.4 (TX, Gunter 1950); *A. xenica*, 13.1–53.9 (TX, Simpson and Gunter 1956), and reported from FW (FL, Tabb and Manning 1961; Brockmann 1974); *G. rhizophorae*, 13–53.0 (FL, Getter 1982; FW (Cuba, Getter 1982; FL-Everglades, Loftus and Kushlan 1987); and *L. parva*, 0.05–47.6 (TX, Renfro 1960). Individuals of *G. affinis*, a FW species, were found to survive for a least a week at a salinity of 41 (overall range of salinity, 13–41; temperature, 22–23°C; ammonia >10 ppm; nitrates, >100 ppm; DO <1 ppm) in the Diamond/Y drainage of TX (Hubbs 2000).

Individuals of a close relative of *C. variegatus*, *C. rubrofluviatilis*, have been reported taken from waters ranging in salinity from 0.4 to 150 (Echelle et al. 1972a); also from upper reaches of the Brazos and Red Rivers (TX, OK) where salinities ranged from <0.5 to 0.714, depending on stream discharge (Hill and Holland 1971). Individuals of *P. sphenops vandepolli* from Curaçao, a close relative of *P. latipinna*, have been taken from waters of salinities ranging upward to 135 (Kristensen 1970; Feltkamp and Kristensen 1970).

Experimentally determined salinity-tolerance ranges

Among species considered here for which there were experimentally determined lower salinity tolerance limits (20 species), only *F. carpio* was not successfully acclimated to FW (though taken in collections from FW in south Florida, Odum 1971; Loftus and Kushlan 1987). The lower extreme for laboratory survival over long periods of time was found to be at a salinity of 0.5 (FL, Nordlie and Walsh 1989). Also, Nordlie (FL, 2000b) reported difficulties in acclimating individuals of *F. similis* to salinities lower than 1.0, while Griffith (FL, 1974) reported success in acclimating individuals of the species to FW, though with 25% mortality over a period of a month (Table 4). Upper salinity-tolerance limits varied considerably among the group of cyprinodontoid fishes reported from estuarine (at least brackish) waters of eastern North America. The species with the highest reported tolerance of elevated salinities was *C. variegatus*. Individuals of that species were maintained in the laboratory at a salinity of 125.2 (TX, Renfro 1960), and 125 (FL, Nordlie 1985). Fertilized eggs of the species were reported to hatch and the young to develop in salinities as high as 110 (TX, Renfro 1960). Also in this high salinity-tolerance group was *F. heteroclitus*, individuals of which were maintained at salinities ranging from FW to 120.3 (mean of 113.0 ± 2.55, CN, Griffith 1974). Moreover, a number of the cyprinodontoid species included here, all *Fundulus* spp., have upper salinity tolerances of ≥100, including: *F. confluentus* (FL, Nordlie 2000b); *F. grandis* (FL, Nordlie 2000b); *F. luciae* (CN, Griffith 1974); *F. majalis* (CN, Griffith 1974); *F. similis* (FL, Nordlie 2000b); and *F. pulvereus*, (AL, Griffith 1974). Another member of the Fundulidae found to have an upper salinity tolerance near to, but not at, 100 was *A. xenica*, at 95 (FL, Nordlie 1987). *Aphanius dispar*, a cyprinodontoid from the Mediterranean region, was shown in laboratory experiments to survive in 3.5× SW (salinity ca. 122.5) (Skadhauge and Lotan 1974). Also, individuals of that species have been acclimated in the laboratory to ambient salinities ranging from <1 to 140 for periods of at least four weeks (25 ± 1°C) (Plaut 2000).

Among the group of cyprinodontoids, species with more modest upper salinity-tolerance limits included: *F. chrysotus*, 25.6 (96-h LC_{50}, MS, Crego and Peterson 1997); *F. d. menona*, 34 (FW population, ND, artificial SW, 20 ± 1°C, Ahokas and Duerr 1975); *Lucania goodei*, 20–30 (FL, Dunson and Travis 1991); and *G. holbrooki*, 25 (FL, Nordlie and Mirandi 1996). All of those were found to have upper tolerance limits at levels slightly below the concentration of normal SW, though high enough to permit occupation of or movement through most regions of brackish estuaries.

Comparisons of laboratory salinity limits with field measurements

As with temperature relationships, salinity limits determined in laboratory evaluations were compared with ranges of salinities at which individuals of those species have been collected in nature (Fig. 2). Fourteen of the total of 18 species represented fell above the line of equality, indicating that laboratory-determined limits were wider than ranges of salinities at which the species had been taken in the field. One species, *F. chrysotus*, fell on the line of equality, and three species, *G. holbrooki*, *P. latipinna*, and *C. variegatus*, fell below the line. Only *C. variegatus* showed an appreciable departure below the line of equality. The other three species collected over a range of salinities equal to or greater than laboratory-determined salinity tolerance ranges can likely be explained by limits being for 50% survival or mortality.

The range of salinities normally inhabited by individuals of a species is generally more limited than the ranges of physiological limits found following extensive laboratory acclimations. Most individuals of these species rarely or never encounter a range of salinities in nature as wide as those to which they are subjected in laboratory studies. It is unlikely that individuals of any of these species can fulfill all of their normal functions over the full range of salinities tolerated in laboratory acclimations.

Acclimation to altered salinities

Acclimation studies have varied in lengths of time that individuals were subjected to test salinities, in rates of change of salinities, in experimental temperatures, etc. One aspect of salinity relationships, serving to illustrate the importance of reporting information on conditions and circumstances of the acclimation, was shown in a freshwater-pulse experiment. That experiment tested responses to a cycled alteration in salinity in individuals of several estuarine species including *C. variegatus* and *L. parva*, both of which can be acclimated to FW, have FW populations, and are tolerant of salinities well above those of SW. In challenge experiments salinity levels were reduced from 32 to FW, and then returned to 32 (salinity was 31 for *L. parva*) in a period of two hours (ambient temperature of 28–30°C). In that sequence *C. variegatus* showed 100% mortality and *L. parva* showed 50% mortality (Biscayne Bay, FL, Serafy et al. 1997). Among a group of eight other estuarine fish species tested (*Opsanus beta*, *Lutjanus griseus*, *Eucinostomus gula*, *Haemulon parra*, *H. plumieri*, *H. sciurus*, *Lagodon rhomboides*, and *Cynoscion nebulosus*), two others (*H. plumieri* and *C. nebulosus*) showed 100% mortality, and one (*L. rhomboides*), showed 12.5% mortality. The other five all showed 100% survival. While all of those species show some euryhaline characteristics, especially of tolerating lowered salinities, none compares with overall salinity tolerances of *C. variegatus* (Renfro 1960; Nordlie 1985). It appears that the rate of reduction or increase of salinity, particularly at salinities below that of SW is likely important in such situations.

Interactions of temperature and salinity

Salinity selection was tested in groups of individuals of *F. grandis* acclimated to either 20°C or 28°C, and at salinities ranging from FW to 35, and tested at 23°C, in three seasons of the year, fall (October), spring (March and April), and summer (July). Fish acclimated to 28°C selected lower salinities in fall and spring than did those acclimated to 20°C. No effect of acclimation temperature was noted on fish in summer. In spring (April) individuals acclimated to 20°C or 28°C selected lowest salinities when tested at 28°C (Miller et al. 1983).

Table 4 Salinity relationships of cyprinodontoid fishes found in estuaries of eastern North America

Family and Species	Location	Experimental lower salinity limit	Location	Experimental upper salinity limit	Location	Encountered salinity range
Family Cyprinodontidae						
Cyprinodon variegatus	FL	FW Nordlie 1985; 2000a	FL	125 Nordlie 1985; 2000a 125.2 Hatching, SW-110 Renfro 1960	FL	FW to 167 Gilmore et al. 1982
	FL	FW-pulse experiment, 100% mortality, 32-0-32, 2 h, 28–30°C, 30–41 mm TL Serafy et al. 1997			TX	1.8–142 Simpson and Gunter 1956
					FL-Everglades	FW-35 Tabb and Manning 1961
					FL	FW populations, St. Johns river McLane 1955; Tagatz 1967; Guillory and Johnson 1986
					MS	FW-29.9 Christmas and Waller 1973
					FL-Everglades	FW populations Loftus and Kushlan 1987
Cyprinodon variegatus hubbsi	FL	FW Jordan et al. 1993	FL	70 Jordan et al. 1993	FL	FW Carr 1936; McLane 1955; Guillory and Johnson 1986
Floridichthys carpio	FL	0.5 Nordlie and Walsh 1989	FL	90 Nordlie and Walsh 1989	FL	26.4–27.8 Reid 1954
					FL	2.0–37.6 Kilby 1955
					FL	21.0–30.8 Springer and Woodburn 1960
					FL-Keys	34.5–37.8 Springer and McErlean 1962
					FL	>50 Kaill 1967
					FL	<1.0–26.5 Odum 1971
					FL	0–39.3 Brockmann 1974
					FL-Everglades	FW populations Loftus and Kushlan 1987
Jordanella floridae	FL	FW Nordlie and Walsh 1989	FL	80 Nordlie and Walsh 1989	FL	1.1–26.1 Kilby 1955
					FL	FW-9 Tabb and Manning 1961
					FL	FW-39.3 Brockmann 1974
					FL	Adults, 0.3–17.7; spawning, 0.3–9.9 Hale in St. Mary et al., 2004

Table 4 continued

Family and Species	Location	Experimental lower salinity limit	Location	Experimental upper salinity limit	Location	Encountered salinity range
Family Fundulidae						
Adinia xenica	FL	FW Nordlie 1987	FL	95 Nordlie 1987	TX	8.4–35.7 Gunter 1945
					FL	0.8–37.6 Kilby 1955
					TX	13.1–53.9 Simpson and Gunter 1956
					FL	FW-32 Tabb and Manning 1961
					FL	FW-4.9 Brockmann 1974
Fundulus chrysotus	FL	FW Griffith 1974	FL	Mean 20.1 ± 15 Range 19.5–20.5 Griffith 1974	FL	1.8–24.7 Kilby 1955
			MS	Mean 25.6 96-h LC50 Crego and Peterson 1997	FL	FW-3 Tabb and Manning 1961
					FL	0.12–0.22 Gunter and Hall 1965
					FL	FW-8.9 Brockmann 1974
Fundulus confluentus	FL	FW Nordlie 2000b	FL	100 Nordlie 2000b	FL	FW-35.6 Kilby 1955
					FL	FW-20.4
					GA	FW-24.4 Dahlberg 1972
					FL	FW-39.3 Brockmann 1974
Fundulus diaphanus	CN	FW Griffith 1974	CN	Mean 69.6 ± 2.80 Range 56.5–73.4 Griffith 1974	CN	FW-14.10 Griffith 1974
					NC	5.0 Schwartz 1998
Fundulus grandis	FL	FW Griffith 1974;	FL	110 Nordlie 2000b	FL	0.8–29.8 Kilby 1955
	LA	Kolok and Sharkey 1997;			TX	1.8–76.1 Simpson and Gunter 1956
	FL	Nordlie 2000b			TX	0.05–58.6 Renfro 1960
					MS	FW-29.9 Christmas and Waller 1973
					TX	FW Hillis et al. 1980
Fundulus heteroclitus	CN	FW Griffith 1974	CN	Mean 113.9 ± 2.55 Range 106–120.3 Griffith 1974	DE	1.0–35 deSylva et al. 1962
	Nova Scotia	FW Marshall et al. 1999			FL	0–22.7 Tagatz 1967
					GA	0–34 Dahlberg 1972
					PA	FW population Denoncourt et al. 1978
					NC	0.0–30.0 Schwartz et al. 1981
					NY	FW population Samaritan and Schmidt 1982

Table 4 continued

Family and Species	Location	Experimental lower salinity limit	Location	Experimental upper salinity limit	Location	Encountered salinity range
Fundulus jenkinsi	FL	FW Griffith 1974	FL	Mean 73.6 ± 3.75 Range 67.2–80.2 Griffith 1974	FL	4.5–24.0 Bailey et al. 1954
					TX	3.4–20.6 Simpson and Gunter 1956
					LA	27.4 Forman 1968
					MS	FW-16.7 Christmas and Waller 1973
Fundulus luciae	CN	FW Griffith 1974	CN	Mean 101.3 ± 4.31 Range 73.4–106.0 Griffith 1974	DE	41 deSylva et al. 1962
					VA	0.2–12.7 Byrne 1978
					NC	28.1–35.6 Kneib 1978
					NC	3.4–32.0 Schwartz et al. 1981
					NJ	11.0–33.5 Talbot and Able 1984
Fundulus majalis	CN	FW Griffith 1974	CN	Mean 98.8 ± 9.70 Range 73.4–106.0 Griffith 1974	NC	1.0–37.0 Tagatz and Dudley 1961
					GA	6.8–34.0 Dahlberg 1972
					MD	4–5 - 9–10 Baker-Dittus 1978
					NC	4.0–29.6 Schwartz et al. 1981
Fundulus notatus					?	“Brackish waters” Thomerson 1966
Fundulus nottii					?	FW species, enters brackish waters, and reportedly, SW Miller 1955
					NC	5 Schwartz et al. 1981[a]
					MS	“Oligohaline waters”-0.0–10.0 Peterson and Ross 1991
Fundulus olivaceus					?	Penetrates brackish waters and may occur in SW Miller 1955
					MS	FW-5.0 Christmas and Waller 1973
					MS	“Tidal FW” 0.0–4.0 Peterson and Ross 1991

Table 4 continued

Family and Species	Location	Experimental lower salinity limit	Location	Experimental upper salinity limit	Location	Encountered salinity range
Fundulus pulvereus	AL	FW Griffith 1974	AL	Mean 100.8 ± 3.00 Range 95.6–106.4 Griffith 1974	TX	0.4–16.0 Gunter 1950
					TX	11.9–53.6 Simpson and Gunter 1956
					LA	1.1–32.3 Forman 1968
Fundulus seminolis					FL	1.3–13.5 (surface) Phillips and Springer 1960
					FL	0.26–2.4 Gunter and Hall 1963
					FL	0.13–7.3 Gunter and Hall 1965
Fundulus similis	FL	FW Griffith 1974 1 Nordlie 2000b	FL	100 Nordlie 2000b	FL	0.8–37.6 Kilby 1955
					TX	13.1–76.1 Simpson and Gunter 1956
					TX, Laguna Madre	25–75 Simmons 1957
					FL	0.09–35.35 Martin and Finucane 1968
					MS	0.3–35.5 Christmas and Waller 1973
Fundulus stellifer					NC	10.0 Schwartz 1998
Lucania goodei			FL	20–30 Dunson and Travis, 1991	FL, Silver Springs	FW Hubbs and Allen 1943
					FL	FW-10.3 Kilby 1955
					FL	FW-12.5 Loftus and Kushlan 1987
Lucania parva	FL	FW-pulse experiment, 50% mortality, 32–0-32, 2 h, 28–30°C, 9–55 mm TL Serafy et al. 1997	FL	ca. 80 for 50% survival, slow accl. Dunson and Travis 1991	FL, Silver Springs	FW Hubbs and Allen 1943
					FL	0.1–28.2 Kilby 1955
					TX	<1.0–44.8 Simpson and Gunter 1956
					TX	0.05–47.6 Renfro 1960
					FL	FW-39.3 Brockmann 1974
					NC	15.0 Schwartz 1998
Family Poeciliidae						
Belonesox belizanus					FL	FW–≥35 Robins and Getter, in Robins and Getter, in Robins et al. 1980

Table 4 continued

Family and Species	Location	Experimental lower salinity limit	Location	Experimental upper salinity limit	Location	Encountered salinity range
Gambusia affinis					TX	< 1.0–20.6 Simpson and Gunter 1956
					MS	FW-29.0 Franks 1970
					TX	13–41, 20°C Hubbs, 2000
Gambusia holbrooki	FL	FW Nordlie and Mirandi 1996	FL	25 Nordlie and Mirandi 1996	FL	FW-26.1 Kilby 1955
					FL	FW-30 Tabb and Manning 1961
					GA	FW-34 Dahlberg 1972
					FL	17.7–31.2 Carr and Giesel 1975
					NC	22.0 Schwartz 1998
Gambusia rhizophorae	FL	FW Getter 1982			Cuba	FW Getter in Getter 1982
					FL	13.0–53.0 Getter 1982
					FL-Everglades	FW population Loftus and Kushlan 1987
Heterandria formosa	FL	FW Baer and Travis 2000			FL	FW-15 Kilby 1955
					LA	13.7 Chipman 1959
					FL	0.12–30.2 Gunter and Hall 1965
					FL	FW-23 Odum 1971
					LA	0.2–1.7 Castellanos and Rozas 2001
Poecilia latipinna	FL	FW Nordlie et al. 1992	FL	70, FW pop., 80, salt marsh pop. Nordlie et al. 1992	Philippines, Manila Bay	ca. 87 Herre 1929
					FL	FW-37.6 Kilby 1955
					TX	< 1.0–53.9 Simpson and Gunter 1956
					MS	0.3–29.9 Christmas and Waller 1973
Family Rivulidae						
Kryptolebias marmoratus					Curaçao	FW-70 rarely above 40 Kristensen 1970
					FL	SW, may not be in FW Robins et al. 1980

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[a] Schwartz et al. (1981), suggested that the identification of *F. notti* was incorrect, and likely *F. lineolatus*, but in a later paper (Schwartz 1998) he included F. notti, not F. lineolatus

A study of effects of ambient salinity on ULTs encompassed six species of Fundulidae (*A. xenica*, *F. chrysotus*, *F. grandis*, *F. pulvereus*, *F. similis*, and *L.* parva); two species of Poeciliidae (*G. affinis* and *P. latipinna*); one Cyprinodontidae (*C. variegatus*); and one Centrarchidae (*Lepomis symmetricus*). An ambient salinity range of 11–13, roughly isosmotic with the blood of these fishes, was found to be optimal in producing the highest ULT for all of the species (Strawn and Dunn 1967). Individuals of *C. variegatus* showed the highest ULT across all salinities among the species. The centrarchid, *L. symmetricus*, was found to have the lowest ULT among this group of species, except at salinities of < 2, where it was roughly co-equal to *G. affinis* (180-min tests).

Somewhat similar results were obtained in a comparison of ambient salinity on ULTs in *F. heteroclitus* and *F. diaphanus* (Garside and Jordan 1968). Highest ULTs of both species were found at an ambient salinity of 14, compared to FW (sal., <0.5) and SW (sal., 32). The ULT of *F. diaphanus* was 27.5°C when evaluated in FW and SW (sal., 32), but was higher, 33.5°C, at an ambient salinity of 14, close to the isosmotic point for the species (Garside and Jordan 1968). Similar results were found for *F. heteroclitus*, with an ULT of 28.0°C in FW, of 31.6°C in SW, and of 34°C at an ambient salinity of 14 (Garside and

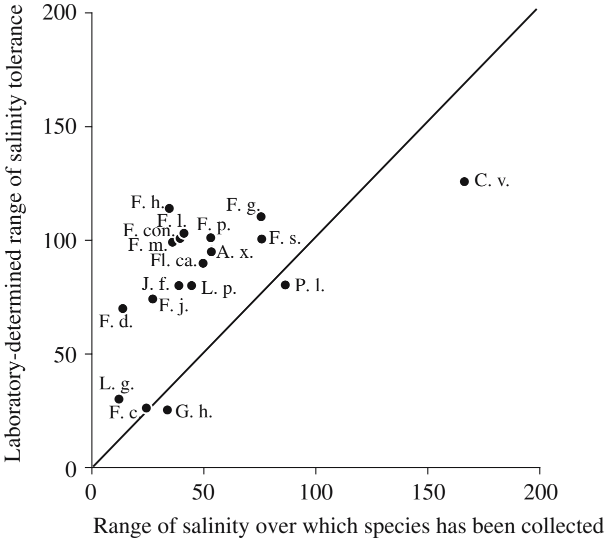

Fig. 2 Salinity limits (dimensionless numbers) of cyprinodontoid fishes. Values along the *x*-axis represent ranges of ambient salinity (differences between the highest and lowest salinities) at which individuals of a species have been collected. Values along the *y*-axis represent ranges of experimentally determined tolerable salinities (differences between highest and lowest tolerated or lethal salinity) of a species. Abbreviations used to identify species in graph and sources of information follow. C. v., *C. variegatus*—Gilmore et al. 1982; Nordlie 1985; Renfro 1960. Fl. ca., *F. carpio*—Brockmann 1974; Kaill 1967; Nordlie and Walsh 1989. J. f., *J. floridae*—Tabb and Manning 1961; Brockmann 1974; Nordlie and Walsh 1989. A. x., *A. xenica*—Tabb and Manning 1961; Brockmann 1974; Simpson and Gunter 1956; Nordlie 1987. F. c., *F. chrysotus*—Tabb and Manning 1961; Griffith 1974; Crego and Peterson 1997. F. con., *F. confluentus*—Kilby 1955; Brockmann 1974; Nordlie 2000b. F. d., *F. diaphanus*—Griffith, 1974. F. g., *F. grandis*—Renfro 1960; Simpson and Gunter 1956; Nordlie 2000b. F. h., *F. heteroclitus*—Tagatz 1967; deSylva et al. 1962; Griffith 1974. F. j., *F. jenkinsi*—Christmas and Waller 1973; Forman 1968; Griffith 1974. F. l., *F. luciae*—Byrne 1978; deSylva et al. 1962; Griffith 1974. F. m., *F. majalis*—Tagatz and Dudley 1961; Griffith 1974. F. p., *F. pulvereus*—Gunter 1950; Simpson and Gunter 1956; Griffith 1974. F. s., *F. similis*—Martin and Finucane 1968; Simpson and Gunter 1956; Griffith 1974; Nordlie 2000b. L. g., *L. goodei*—Hubbs and Allen 1943; Loftus and Kushlan 1987; Dunson and Travis 1991. L. p., *L. parva*—Hubbs and Allen 1943; Renfro 1960; Serafy et al. 1997; Dunson and Travis 1991. G. h., *G. holbrooki*—Kilby 1955; Dahlberg 1972; Nordlie and Mirandi 1996. P. l., *P. latipinna*—Kilby 1955; Herre 1929; Nordlie et al. 1992. Note: No experimentally determined lower lethal salinity limit was reported for *L. goodei*; however, since it is a freshwater species it was assumed that the species tolerates FW, and the higher reported upper limit of 30 was used as the upper experimentally determined lethal salinity limit

Jordan 1968). However, in a later study, ULTs of 35.39 and 35.72°C were found when evaluations were made at a common salinity of 32, following acclimation to salinities of 32 and 14, respectively (Garside and Chin-Yuen-Kee 1972). No difference was found in the LLT of *F. grandis* between ambient salinities of 27 and 33, where the LLT was found to be 4.0°C (Umminger 1971a). Results of a study of thermal preferences of individuals of *F. heteroclitus* and *F. diaphanus* acclimated to FW or SW (32), over a series of ambient temperatures ranging from 5°C to 35°C, showed individuals of each species preferred highest temperatures when acclimated to their normal environmental concentrations, which was FW for individuals of *F. diaphanus*, and SW for individuals of *F. heteroclitus* (Garside and Morrison 1977).

Eggs and larvae: conditions for successful reproduction

Early life stages of most organisms are generally considered to be the most vulnerable to rapid and extreme changes in environmental conditions, circumstances true of fishes (Blaxter 1992). Most experimental studies on environmental relationships of fishes in any life stage have encompassed only a single factor. However, an early laboratory study tested simultaneous involvement of all three abiotic factors considered in this study in development of the cyprinodontoid, *C. macularius* (Kinne and Kinne 1962). General results showed that increasing salinity led to progressive retardation of development, while increasing DO concentrations produced progressive acceleration in development. Both retardation and acceleration were accentuated with increasing temperatures. The reduction in DO saturation with increases in temperatures and salinity was concluded to be primarily responsible for the retarding effects on development.

There is probably more known about the influences of temperature on fish reproduction than of possible influences of DO concentrations or of salinity. In addition to direct lethal or tolerance limits of eggs and larvae of various species, sub-lethal effects may include increases in rates of hormone responses that may affect rate-dependent processes, thus interfering with normal cycles in ectothermic vertebrates. In some species of fishes, sex determination is temperature sensitive (Conover 1984), so an increase in water temperature may alter the sex ratio of offspring. Increased water temperatures during the time of gametogenesis can also influence the developing gametes, either/both in quality or/and quantity, and can alter hatching time (reviewed in Van Der Kraak and Pankhurst 1997).

Sub-lethal effects of temperature on developmental stages and juvenile fishes can have a significant role in determining adult distributions (Brett et al. 1982). The zone of thermal tolerance has been shown to be considerably narrower during embryonic development than for later life in temperate-zone fishes. Fertilization and early cleavage stages are generally the most restrictive ones with respect to thermal tolerances. Also, the center of the zone of thermal tolerance has been shown to shift to increased temperatures as development proceeds. Unlike temperate species, tropical species show little change in width of the zone of tolerance with continued development. Unfortunately, there is little information available on temperature tolerances of eggs and larvae of species at high latitudes (Rombough 1988, 1997).

Despite the extreme importance of environmental relationships associated with reproduction, there are only scattered pieces of information about effects of temperature, DO, or salinity ranges on successful reproduction for most of these cyprinodontoid species. The most extensive work is on *F. heteroclitus* where this discussion will be focused. While all aspects of the annual reproductive cycle of that species could not be covered, several examples of influences of environmental conditions were included to illustrate how they, especially temperature, can be key features in determining latitudinal limits of successful reproduction and maintenance of populations.

Seasonality of reproductive cycles

Both temperature and photoperiod were found to be the primary environmental conditions controlling the seasonal reproductive cycles of

F. heteroclitus, with temperature said to dominate over photoperiod (deVlaming 1972), a conclusion that was called into question by Taylor (1986). The role of temperature in spawning of *F. heteroclitus* was seen to be twofold: warm temperatures were necessary for final oocyte maturations and spawning; but oocytes progressed into early vitellogenesis only after being subjected to low temperatures and a short photoperiod (Day and Taylor 1984). A semi-lunar gonadal cycle was found to be superimposed on the annual reproductive cycle, the resulting interaction synchronized reproductive maturity and spawning with availability of high intertidal sites where most egg laying occurred (Taylor et al. 1979; Taylor 1986). Aerial incubation of eggs has been well documented in *F. heteroclitus* (Taylor et al. 1977; DiMichele and Taylor 1980; Kneib and Stiven 1982; Taylor and DiMichele 1983; Taylor 1986), and has been reported or suggested for several other species belonging to the Fundulidae (*A. xenica*, Cummingham and Balon 1986; *F. confluentus*, Harrington 1959, Harrington and Harrington 1961; suggested for *F. grandis*, (Harrington 1959, Harrington and Harrington 1961); as well as for the rivulid, *K. marmoratus* (Taylor et al. 1992). Among populations of *F. heteroclitus* in the area of Woods Hole, MA (West Falmouth Harbor, Sippiwisett Marsh, Waquoit Bay), ca. 90% of the females of *F. heteroclitus* were found to carry mature eggs continuously from the time that the offshore water temperature rose above 11°C till late June or early July when temperatures in the offshore waters reached 18–19°C (Wallace and Selman 1981). While that seemed to rule out a semi-lunar spawning cycle, Taylor (1986) demonstrated the presence of semi-lunar cycles, though weak ones in those populations. A similar demonstration of a semi-lunar spawning cycle in *F. heteroclitus* was made at Sapelo Island, GA (Kneib 1986). A midsummer spawning interruption was demonstrated in populations of that species in Georgia and Delaware waters (Kneib 1986). However, not all of the northern populations of *F. heteroclitus* show a semi-lunar spawning cycle. Individuals spawning in a Maine creek were found to spawn daily during the two-month spawning period, though daily higher tides were preferred over lower tides. At another site with little tidal influence, spawning became completely decoupled from times of high tide. Also, those Maine populations deposited eggs over a much wider range of habitats (Petersen et al. 2004). Other cyprinodontoid species in which semilunar spawning cycles with spawning on high spring tides has been demonstrated include *F. grandis* (Greeley Jr and MacGregor III 1983), *F. majalis* (Taylor 1984), and *F. similis* (Greeley Jr et al. 1986). There is also evidence of such semilunar spawning cycles in *A. xenica* (Greeley Jr 1984), *F. confluentus* (Harrington 1959), and *F. pulvereus* (Greeley Jr 1984), and semilunar spawning cycles were suggested to occur in *F. luciae* (Kneib 1984). All of these species belong to the Family Fundulidae, suggesting that this is a common spawning pattern in that group.

The more northern populations of *F. heteroclitus* (New Jersey northward) were placed into a separate subspecies (*F. h. macrolepidotus*) from the more southern ones, New Jersey to Florida, (*F. h. heteroclitus*), based on spawning locations and egg characteristics (Powers and Place 1978; Cashon et al. 1981; Morin and Able 1983; Able 1984; Able and Hata 1984; Able and Felley, 1986; Powers et al. 1986; González-Villaseñor and Powers 1990). Areas of intergradation were noted in northern New Jersey, on Long Island, in Chesapeake and Delaware Bays, and in the Potomac River (Able and Felley 1986).

Influences of temperature on embryonic development

Fish usually spawn at temperatures within a few degrees of the center of their embryonic zone of thermal tolerance. However, once spawned, the temperature change that the eggs can tolerate is roughly ±5.8°C for both temperate and tropical species (Herzig and Winkler 1986). While the thermal history of the embryo does not appear to alter the upper lethal temperature of the embryo, the thermal history of the parents apparently does (Hubbs and Bryan 1974). The upper lethal temperature is also influenced by other abiotic conditions of the environment including DO concentrations and salinity. The influence of environmental temperature on aerobic metabolism has been shown to be greater in embryonic and early larval stages than in later life (reviewed in Rombough 1997).

Females of *F. heteroclitus* contained mature eggs from the time water temperatures warmed to 11°C in the spring until the water temperature reached 18–19°C, as was pointed out above (Woods Hole, MA, Wallace and Selman 1981). Spawning of individuals of *F. heteroclitus* was found to begin when water temperatures reached 15°C (Patuxent River, MD, Morin and Hirshfield 1984). The development period of *F. heteroclitus* was found to be roughly two weeks regardless of latitude. Eggs deposited on a spring tide (beginning when the water reached a temperature of 15°C and ending at a later time determined by latitude), optimally developed and hatched on the next spring tide. That seemed to hold true over the entire range from Florida to Nova Scotia, though the reproductive season was shortest at the northern end of the range (DiMichele and Westerman 1997). They found that northern embryos (MA) had a faster temperature-specific rate of development than did southern embryos (FL), with Delaware embryos intermediate. Also, northern embryos were found to be more cold tolerant than southern embryos, which were more heat tolerant than the northern embryos. Field studies showed that embryos in their local environments developed at similar rates despite temperature differences among localities. This work and that of Conover (1990), Schultz et al. (1996), Yamahira and Conover (2002), and Conover et al. (2005) supported the concept of countergradient variation in developmental rates among *F. heteroclitus* populations along the Atlantic coast of North America. Higher growth rates were shown in newly-hatched individuals from northern populations held at elevated temperatures (21°C and 28°C) compared with those of southern populations, while growth rates were similar for the latitudinal groups at a lower temperature (17°C).

Among other cyprinodontoid species for which information on incubation temperatures was available, hatching of fertilized eggs of *J. floridae* took 10 days at 23°C (Baake, cited in Breder and Rosen 1966), and seven to eight days at ca. 27°C (Kaill 1967). Embryonic development rate of *J. floridae*, whose reproductive period extends from mid-April to mid-August (Foster 1967), evaluated over a restricted range of ambient temperature, was found to increase with increases in temperature in the range from 27°C to 35°C, but was unaffected by changes in salinity in the range from FW to 15. However, hatching success increased with salinity, but was unaffected by ambient temperature over the same ranges (St. Mary et al. 2004). Eggs of *C. rubrofluviatilis*, were found to show a tolerance of high incubation temperatures, 36.5°C, and adults of the species were found to have a wide thermal range for spawning, from 13°C to 34°C (Echelle et al. 1972b). Fertilized eggs of *Fundulus kansae* from southcentral OK, normally a summer spawning species, hatched at temperatures between 12.6°C and 35.8°C (Wilson and Hubbs 1972). Eggs of *C. macularius* showed a range of hatching time from 50 days at an environmental temperature of 14°C to four to five days at a temperature of 32°C (Kinne and Kinne 1962). Temperature range for successful hatching and development in eggs of *Fundulus parvipinnis*, a spring breeding species collected in southern California, was from 16.6°C to 28.5°C (Hubbs 1965). Hatching times varied from 45.5 days at a temperature of 17.2°C to 14.0 days at a temperature of 28.5°C. The response to changes in temperature was not linear over this range of ambient temperatures.

No evidence was found of temperature-dependent sex determination (TSD) in northern populations of *F. heteroclitus*, or of *C. variegatus*. Based on examples in other species of fishes with extended latitudinal distributions, and with annual life histories, it was expected that the most likely portion of the distribution of a species to show TSD would be at the extreme northern and southern limits of their distributions (Conover 1984; Conover and DeMondi 1991; Yamahira and Conover 2003).

DO requirements for development and hatching

A study comparing survival of embryonic and adult individuals of *F. heteroclitus* at low DO concentrations, showed stage 4 embryos having a 50% hatch rate at a DO concentration of

3.9 mg kg^{-1} (temperature, 20°C, salinity, 30–32). Development rates were retarded by DO concentrations $\leq$4.5 mg kg^{-1}. A 6-h median tolerance limit (TL_{50}) value of 0.80 mg kg^{-1}, with a range from 0.74–0.89 mg kg^{-1} (same temperature and salinity as of embryos), was found for adults. No mortality was noted at DO concentrations $\geq$2.2 mg kg^{-1}. It was concluded that successful embryonic development of this species required higher DO concentrations than those required by adult individuals (Voyer and Hennekey 1972), with values for adults somewhat higher in that study than those of Smith and Able (2003), discussed earlier.

Successful incubation of eggs of *F. heteroclitus* does not take place in salt marshes if siltation and regular episodes of very low DO concentrations prevail ($<$2.9 mg kg^{-1}) (Taylor and DiMichele 1983). Eggs were deposited in areas where they would be inundated only by waters of semi-monthly high tides. Spawning was found to occur on a variety of substrata among estuaries over the geographic range of the species, including on algal mats; on *Spartina alterniflora*; in empty shells of *Geukensia demissa*; in loose sand; and among plant roots, stems, and debris, depending to some extent on what substrata were available (Taylor 1986). The use of empty shells was found to be limited to the southern portion of the distribution of the species (Able and Castagna 1975; Kneib and Stiven 1978; Taylor et al. 1979; Able 1984; Taylor 1986), but not all individuals in that area spawned in shells; others spawned predominantly on *S. alterniflora* (Taylor et al. 1977). Hatching was found to occur only when the eggs that were laid at or near to spring high tide levels, were covered by water of the next spring high tide (DiMichele and Taylor 1980). Hatching in *F. heteroclitus* appeared to be triggered by lowered DO concentrations (mean effective concentration of 6.3 mg kg^{-1}) and hydration, and to be inhibited by DO concentrations >8.6 mg kg^{-1}. Levels of DO in high tide waters were usually found to range from 5.7 mg kg^{-1} to 8.6 mg kg^{-1}, stimulating hatching (DiMichele and Taylor 1980). They later suggested that very low DO concentrations simultaneously terminate diapause and initiate hatching in *F. heteroclitus* eggs (DiMichele and Taylor 1981). Other studies have been carried out involving individuals of *F. heteroclitus* in various life stages being subjected to hypoxic conditions. Embryos of *F. heteroclitus* developing in waters with low DO concentrations were found to hatch when their metabolic rates exceeded the rates at which oxygen was available to supply metabolic demands (DiMichele and Powers 1984). An experimental study of aerial incubation of eggs of *F. h. macrolepidotus* (artificial SW, sal., 10, 20°C) showed hatchlings from aerial incubation to average larger in size than those that were incubated with either shallow or deep submersion (Kidder et al. 2004).

The spawning period of *F. heteroclitus* was found to be significantly shorter at the northern end of its geographic range than at the southern end. Spawning was observed to take place from Feb. to Sept. at Sapelo Island, GA (Kneib 1984), Apr.-Sept., GA, (DiMichele and Westerman 1997); from early-May to late-Aug. (Brummett 1966) or March to Sept. (Kneib and Stiven 1978) near Beaufort, NC; from Apr. to Aug. in the Patuxent River, MD (Morin and Hirshfield 1984); May and June, MA (DiMichele and Westerman 1997); and from the end of May to mid-June in the Chezzetcook Inlet, Nova Scotia (Penczak 1985). That was consistent with evaluations of spawning periods of subtropical (FL and TX) populations of several other cyprinodontoid fishes which showed longer spawning periods than those of populations of the same species, or of other species, from higher latitudes (deVlaming, et al. 1978). Individuals of the Nova Scotia population of *F. heteroclitus* also differed from those of southern populations in life-history characteristics including early maturity, a short life span (high adult mortality in the second growing season), and a low fecundity (Penczak 1985).

Salinity effects on development

Salinity was found to have a significant impact on reproductive success in *F. heteroclitus*. Populations occupy waters that vary in concentrations from near FW to near SW, depending on the particular habitat in which individuals are located (Chidester 1916). There are also FW populations of the species (Denoncourt et al. 1978; Samaritan and Schmidt 1982). Individuals of *F. heteroclitus* maintained at a salinity of 30 were unable to produce fertilized eggs if placed into FW, while they showed ca. 80% success in 1/2 or full SW. Acclimating individuals to FW enhanced fertilization success in FW to 41%, 80% in 1/2 SW, but 0 in SW. Individuals from a FW population showed a fertilization success rate of 72% in FW, 80% in 1/2 SW, and 0 in SW (Palmer and Able 1987). Despite their euryhaline nature, developing individuals of *C. variegatus* were shown to have reduced rates of growth in waters with low concentrations of Ca^{+2}, K^{+}, Mg^{2+}, and Na^{+} (total concentrations of solutions producing a specific conductance of 431 ± 15 μS cm^{-1}). Reproductive success of adults was also severely reduced in the same range of dilution (Dunson et al. 1998).

Anthropogenic influences on reproductive patterns

Patterns of phenotypic variation among biochemical phenotypes of individuals of *F. heteroclitus* from nine localities along the north shore of Long Island, NY, and a tenth group from Mystic Isle, NJ, were compared (Mitton and Koehn 1975). One of the Long Island populations was from a cooling pond that received thermal waters from an electric-power generating plant where the water temperatures were 14–16°C higher than at the other eight Long Island stations; maximum water temperatures at the New Jersey station were 3–4°C higher than at the eight Long Island stations. Individuals from the cooling pond showed a high frequency of vertebral abnormalities, as well as morphological characteristics of individuals from populations at lower latitudes (Mitton and Koehn 1976). Vertebral abnormalities included such characteristics as numbers of vertebrae in the vertebral column, foreshortening, asymmetry, and fractured centra. Examples of other characteristics that differed between individuals from the anthropogenically warmed waters and from the ambient controls included: head length, snout length, inter-orbital width, and length of dorsal fin insertion. Individual fishes hatched at higher temperatures have been shown in laboratory experiments to be shorter and/or of lesser body masses than those hatched at lower temperatures (Blaxter 1992).

A field experiment evaluating timing of reproduction of individuals of *F. heteroclitus* was carried out in intake and discharge canals of the Chalk Point Steam Electric Station in the Patuxent River, MD (Morin and Hirshfield 1984). Those canals were in close proximity to one another, eliminating latitudinal differences in photoperiod. Water temperatures in the discharge canal averaged 4.1°C higher than in the inlet canal in 1981, and 3.3°C higher in 1982. Salinities were very similar between inlet and discharge canals, as were DO concentrations, which never dropped below 5.0 mg kg^{-1} in either year. Despite the proximity, there was said to be little if any interchange of individuals between the two canals as individuals of *F. heteroclitus* have limited home ranges. In both years the discharge population showed earlier reproductive activity than did the inlet population, ca. 10 days earlier in 1981 and ca. 20 days earlier in 1982. Spawning began when the water temperature rose above 15°C, and a semilunar reproductive cycle in synchrony with new and full moons became apparent by June.

Comparison of annual reproductive periods of two populations of *G. holbrooki*, both in ponds within 15 km of one another, near Aiken, SC on the Savannah River U.S. nuclear-production facility, showed significant differences in reproductive patterns. One of these ponds, Risher pond, an abandoned farm pond, showed ambient temperatures for the region, while the other, Pond C, received discharged cooling water from a nuclear reactor. When the reactor was operating, the temperature of discharged water was 40°C, above the lethal level for the fishes, which survived in refugia away from the area of discharge. While individuals from Risher pond showed reproductive activity from April to September, individuals from the Pond C population reproduced throughout the year (Meffe 1991).

The experiments discussed above illustrate the potential impacts that discharge of waters heated by various industrial processes, as well as changes in annual water-temperature patterns, might have on local fish populations. The majority of the cyprinodontoid fishes included in this discussion have reproductive periods that extend from spring to fall. However, reproductive periods among species, and among populations of a species, vary considerably with respect to earliest and latest dates of reproduction, especially over latitude for the widely distributed species. This is true of both the oviparous and live-bearing species. Some populations inhabiting warmer areas of the range of a species have been found to be reproductively mature in all seasons of the year, though their major reproductive periods are generally shorter, especially at more northern regions of their distributions. Examples of species populations that may show year-round reproduction in warmer areas include *A. xenica* (though generally February through August, Arndt 1971), *F. grandis* and *F. similis* (though generally spring through fall, Kilby 1955), *L. goodei* (Hellier 1967), and *L. parva* (Arndt 1971; Foster 1967). The only species among these cyprinodontoids found to spawn mainly in fall and winter was *F. pulvereus* (Simpson and Gunter 1956). Wilson and Hubbs (1972) expressed concern that thermal effluents, as from electrical power-generating plants, may have much greater effects on winter-spawning species, whose development would not normally encounter wide variations in ambient temperature, than on summer spawning species. That may not be of particular concern for the cyprinodontoid fishes considered here, as all have extended periods of reproduction, but with limited winter reproduction.

Despite all of the evidence for direct influences of abiotic environmental forces on hatching and development of cyprinodontoid species in salt marshes, especially of *F. heteroclitus*, it was suggested that adult reproductive activity, predation, and food limitation may be exerting more important influences on the abundances of resident species of salt-marsh fishes in a system where the most abundant fish species were *F. heteroclitus* and *F. luciae* (Kneib 1997).

Global-climate change: the potential to alter distribution patterns of indigenous species

Global-climate change is a phenomenon whose existence is attributed, at least in part, to human activities leading to increased concentrations in the atmosphere of CO_2 and other greenhouse gases. Sea-surface temperatures have shown two periods of warming over the past 100 years: first from 1920 to 1940, followed by periods of cooling; with a second period of warming beginning in the 1970s. The warming could be due to natural climatic variations, anthropogenic effects, or a combination of the two (Levitus et al. 2000). Ramifications of rapid increases in global air temperatures are widespread in the biosphere, encompassing changes in global climate patterns, rising sea levels, increasing water temperatures, and deviations from present patterns of precipitation, wind, and water circulation (Kennedy 1990). Efforts have been made to predict expected sequences of change in aquatic systems including in estuaries and near-shore marine habitats, in order to foresee potential alterations in ecosystem structure and function. These have been largely of two sorts: analyzing historical information relating air temperatures to water temperatures and evaluating changes in patterns of distribution of organisms (e.g., Dulcic and Grbec 2000); forecasting anticipated changes based on detailed computer models (e.g., Dulcic and Grbec 2000; Attrill and Power, 2002). The earth's climate has warmed by 0.6°C over the past century (Walther et al. 2002). The biological trends studied, despite confounding influences, match climatic-change predictions (Parmesan and Yohe 2003). However, there are significant difficulties in quantifying effects of changes in environmental quality on fish population dynamics (Rose 2000). Interpretations of evidence of impacts of global-climate changes on estuarine fishes and fisheries include many uncertainties about the future of affected species because of a lack of background information on various aspects of ecology and physiology of the involved fishes, especially from tropical areas (Roessig et al. 2004).

Four levels of effects on the biota have been suggested for evaluation (Hughes 2000): effects on physiology that could result directly or indirectly from changes in atmospheric CO_2 concentrations influencing temperature and precipitation patterns; effects on distribution patterns of organisms, noting that a 3°C change in mean annual temperature would produce a shift in the isotherm of ca. 300–400 km in latitude (temperate zone) or 500 m in elevation (species would be expected to move poleward in latitude or upward in elevation); effects on phenology that might alter timing of life cycle events, leading to decoupling of phenological relationships between species; and effects on adaptation. It would be expected that such changes, altering interactions among species, would ultimately result in stress on some species with the potential for extinctions, at least of regional populations. Higher water temperatures and increased freshwater delivery would be expected to alter estuarine stratification, residence time, and enhance eutrophication. Ocean warming would be expected to produce poleward shifts in distributions of marine organisms and alterations in habitat characteristics, potentially altering predator–prey and competitive relationships. Impacts of climate change may vary from system to system, with alterations in temperature being imposed on what may be systems already stressed by various types of pollution, habitat destruction, invasive species, harvest pressure, and extreme natural events, leading to unexpected results with respect to the resident organisms (Scavia et al. 2002).

One example of an alteration in species distribution initially thought to be at least partially a response to recent increases of sea level was the alterations in plant-species composition of salt marshes of eastern North America (Warren and Niering 1993). The common reed, *Phragmites australis*, which has been present in some salt marshes of the North American east coast for at least 3500 years (Orson et al. 1987), has in recent years become highly invasive. Its invasion has altered plant-species composition and physical characteristics of salt marshes along the Atlantic and Gulf coasts of North America (Fell et al. 1998; Weinstein and Balletto 1999; Windham and Lathrop 1999). That raised serious questions of utilization of such altered salt marsh areas by the native fauna, particularly fishes, both residents and seasonal visitors, and especially nursery species. For example, larval and juvenile abundances of *F. heteroclitus* were much reduced, or nursery functions altered, on *Phragmites*-dominated marsh surfaces compared to those of *Spartina* or *Typha* (Able and Hagan 2003; Able et al. 2003; Currin et al. 2003; Fell et al. 2003; Raichel et al. 2003). However, it was demonstrated that this was not a simple alteration in the distribution of an existing plant species, but rather that an invasive non-native strain of *P. australis* had displaced the native type in New England salt marshes. That form apparently has expanded its distribution southward, even into areas not previously known to have *Phragmites* (Saltonstall 2002). That clouded the issue of response to sea- level rises. Recent analyses have differed in interpretations as to why the non-native haplotype has become invasive in areas where the native haplotypes were not (e.g., Silliman and Bertness 2004; Vasquez et al. 2005). Issues related to global warming are unresolved with respect to this species.

Water temperature was suggested to be the most important environmental condition setting geographic limits of distribution of marine animals along the east coast of North America (Taylor et al. 1957). They suggested that temperature extremes were more important in this regard than mean temperatures. Possible influences of a warming temperature trend included: northward permanent extensions in distributions of populations of species that were formerly only seasonal migrants; changes in seasonal migration patterns, times of migration, and distributions of permanent residents; and geographical changes in abundances of permanent residents. Those responses might encompass altered timing of spawning and nursery migrations, changes in availability of food, or altered predator–prey relationships (Frank et al. 1990), and entire food chains might be affected by such temperature changes (Aebischer et al. 1990. The predicted changes in trophic relationships would result in increases in marine pelagic-species populations and decreases in benthic-fish populations (Frank et al. 1990). While examples of such changes have been observed in some Atlantic and North Sea species, the causal linkages have not always been clear (Holligan and Reiners 1992). In the present paper primary interest is in the potential impacts of persistent increases in water temperatures on estuarine and salt marsh systems of eastern North America with special reference to distributions and abundances of the cyprinodontoid fishes.

Will global warming alter geographical ranges of cyprinodontoid fishes?

Distributions of all resident fish species of estuaries/salt marshes potentially can be altered by changes in water temperatures, but not necessarily changes in water temperatures acting alone. Thus, it is difficult to predict whether any particular species of fish is likely to show changes in its geographic distribution following a general warming in the earth's climate, as distribution patterns may be determined by a number of interacting relationships, both biotic and abiotic, that have evolved through time. Also, the results of continued global warming may be manifested in a number of ways in addition to a rise in water temperatures. Most of the available information on influences of environmental conditions on individuals of the cyprinodontoid species discussed here relates to adult stages. Less information is available on hatching and development, which may be critical stages in altering distributions.

One study that does provide some insight into responses to climate changes in colonization/recolonization of inland waters is based on fossil records in the late Pleistocene to early Holocene, ca., 11,000 years B.P., in a site in ND (Newbrey and Ashworth 2004). The sequence of colonization of five species of fishes was explained on the basis of relative water-velocity tolerances and thermal tolerances of each species. The five species included individuals of *F. diaphanus*, two cyprinids, and a stickleback, along with a predator of the other four species, *Perca flavescens*. Individuals of *F. diaphanus* were late colonizers primarily because of their low water velocity tolerances, and secondarily because of their thermal requirements of higher temperatures, which included the range of temperatures necessary for spawning. No influence of the predator on prey species was found. Thus, alterations in certain environmental conditions, for example, temperature, may be used as predictors of changes in distribution patterns, even if alterations are not totally determined by such.

DO concentrations might interact with temperature in setting limits to population expansions toward higher latitudes, as oxygen-saturation levels decrease as the waters warm, though this might have greater impact on the distribution limits at lower latitudes. Virtually all, if not all of these cyprinodontoid species, have wide tolerance ranges with respect to salinity, at least as adults. All can inhabit waters of low ambient salinity, and most can survive in waters near to or beyond the salinity of SW. Thus, increasing environmental temperatures, and in some cases decreasing DO concentrations, would seem to be key abiotic features among these environmental conditions in determining such range alterations. The rates at which range expansions of various species of fishes, now limited at least in part by water temperatures, would show poleward extensions in distribution following continued increases in water temperatures might differ from one another among populations of a species as well as among species.

Among the present group of 28 cyprinodontoid species there were five southern species for which it appeared that ambient temperatures ranges/limits affected in some way their northern limits of distribution. No effort was made here to evaluate how the southern geographic-distribution limits of those species were established. Species identified were: *K. marmoratus*, *J. floridae*, *B. belizanus*, *G. rhizophorae*, and *P. latipinna*. All are known to be tolerant of wide ranges of ambient salinity, which would not seem to limit their distributions. Three of the species, *K. marmoratus*, *B. belizanus*, and *G. rhizophorae*, are primarily tropical, with individuals of *B. belizanus* having been introduced into Florida from Central America. The other two are apparently native to areas of south Florida as well as the Caribbean region. Two of those three, *K. marmoratus* and *G. rhizophorae*, are loosely associated with mangrove forests. Populations are also found in areas where mangrove is not present, and the presence of mangrove does not ensure the presence of individuals of one or the other of the species within geographical regions where they are found. Evidence that *K. marmoratus* may be limited, at least in part, by temperature in its geographic distribution, comes from observations made in Florida following an extremely cold period after which population sizes of the species appeared to have been greatly reduced near the northern boundary of its known distribution (Taylor 1993).

Individuals had previously been collected in Florida in the ambient temperature range as low as 5–7.7 (Taylor 1993) to 43°C (Harrington and Harrington 1961). However, it had been demonstrated in laboratory studies that individuals of *K. marmoratus* became moribund at an ambient temperature of 9°C (Taylor et al. 1992).

A lower lethal-temperature limit of 17°C was determined for individuals of *G. rhizophorae* in a laboratory study (Baumgarten cited in Getter 1982). It was affirmed that the distribution is not limited by ambient salinities, as individuals are capable of surviving in waters ranging from FW to hypersaline levels. Moreover, it was demonstrated (Getter 1982) that the northern limit of the Florida distribution of the species closely follows the winter low-temperature isotherm of 16.7°C for the area. It was also suggested that temperature limitation could operate through fertility, a function known to be temperature-sensitive in individuals of *G. rhizophorae* (Getter 1982).

The pike killifish, *B. belizanus*, a small, though voracious, poeciliid predator native to central America, was said to tolerate a wide range of ambient salinities and waters with low DO concentrations (Page and Burr 1991). Its distribution seems likely to be limited, at least in part, by low temperatures, as its LLT was found to be 9.7°C in a laboratory evaluation (FL, Shafland and Pestrak 1982). It is another likely candidate for a northward range extension accompanying a global warming trend.

A fourth species whose distribution might be extended northward is *J. floridae*, primarily a FW species but with populations in brackish waters, a species endemic to peninsular Florida (Page and Burr 1991; Gilbert and Williams 2002). Its distribution might be determined by its dietary requirements as the species is largely vegetarian (Foster 1967). However, populations are relatively easily maintained in laboratory situations (e.g., Foster et al. 1969; Smith 1973; Spehar 1976; Hedtke and Puglisi 1980; Hutchinson and Sprague 1987). Also, breeding populations have been established in other areas of the world, e.g., Borneo (Myers 1940), so they do not appear to be rigidly food-specific. Individuals of the species were reported as having been collected from nature in waters ranging in temperatures from 11 (Dickinson 1948) to 31.8°C (Brockmann 1974), and from 12.8°C to 37.0°C, at salinities from 0.3 to 17.7, and DO concentrations from 0.5 mg kg^{-1} to 12.1 mg kg^{-1} (Hale, unpubl., cited in St. Mary et al., 2004). While the known distribution suggests that individuals may encounter winter temperatures a bit lower than 11°C, it is likely that seasonal low temperatures influence the northern extent of their distribution.

A fifth species, *P. latipinna*, a livebearer, has a somewhat wider distribution than the previous four species mentioned, extending from Yucatan around the Gulf of Mexico to Key West, and along the Atlantic coast to North Carolina. Individuals have been taken at temperatures from 7.3°C (GA, Dahlberg 1972) to 39.2°C (FL, Carr and Giesel 1975), and tolerate a wide range of ambient salinities from FW to 70 in a FW population, and FW to 80 in a salt marsh population (FL, Nordlie et al. 1992). They survive at low DO concentrations without ASR and at lower concentrations with use of ASR (FL, Odum and Caldwell 1955; Timmerman and Chapman 2003). Populations have been established in many parts of the world (Herre 1929; Courtenay and Meffe 1989) suggesting that they are capable of thriving over a range of environmental conditions. Increased ambient temperatures might well allow for northward expansion of populations of this species.

Among the remaining 23 species, any or all might have their distributions altered by increased water temperatures in their environments. A few of these seem worthy of some speculation as to potential distributional alterations following continued global warming. A southern species, *F. grandis*, has a distribution that ends along the coast of northern Florida where it is replaced by *F. heteroclitus* (Duggins et al. 1989). The region of transition between these species is also the area of transition on the Atlantic coast between mangroves and salt marsh, ca. 27–29° N lat., north of which salt marsh becomes the dominant coastal ecosystem. The northern limit of mangrove forest development may be determined by frost stress (Kangas and Lugo 1990). That begs the question of whether the region of interchange between these fish species also involves such a temperature pattern and would move northward with warming of the coastal waters. It was noted in the section on temperature relations that the known LLT for adult *F. heteroclitus* (–1.5°C, Umminger 1971b) is lower than that of *F. grandis* (4°C, Umminger 1971a).

A northern species, *F. luciae*, was first recorded in Massachusetts waters in 1980 from the Palmer River (Hartel et al. 2002). Only in recent years has the extent of the present distribution of that species near the northern portion of its range been extensively studied (Hartel et al. 2002; Stallsmith 1999, 2004). Some earlier collections from New York and Connecticut have been reevaluated, finding specimens of the species that had been misidentified as of *F. heteroclitus* (Yozzo and Ottman 2003). Also, additional sampling has turned up specimens in estuaries in Connecticut where they seem especially associated with *P. australis* marshes (Osgood et al. 2003). Those findings raise the question as to whether the distribution of *F. luciae* has recently expanded in northern regions, possibly in association with *P. australis* marshes, rather than having been missed or misidentified. Both of these explanations seem plausible. Its known ambient temperature range extends from 4°C to 36°C for adults (VA, Byrne 1978), and from 15°C to 33°C for larval fish (NJ, Talbot and Able 1984). Individuals of the species can potentially occupy a wide range of salinity habitats (Griffith 1974; Kneib and Wagner 1994).

A regional approach to assessing possible range extensions of fish populations to higher latitudes accompanying global warming involves comparing distributions of key fish species across the Cape Cod zoogeographic boundary. An analysis of distributions of species across that boundary was made by Ayvazian et al. (1992), and provides a baseline for subsequent evaluations. Also, there are records extending back to 1886 of both air and near-surface water temperatures of the region (Woods Hole, MA, Nixon, et al. 2004). No significant trend in water temperatures was found at the site during the first 60 years of records, followed by a short period of warming, a period of cooling in the 1960s, followed by a significant trend in warming between the 1970s and 2002.

A total of 27 of the fish species that Ayvazian et al. (1992) reported from the Waquoit Harbor, MA estuary south of the Cape were not found in the Wells Harbor, ME estuary north of Cape Cod, a response thought to result from seasonal differences in water temperatures between the area south and north of the Cape. Five of the species included here, *F. diaphanus*, *F. heteroclitus*, *F. majalis*, *L. parva*, and *C. variegatus* were included in their group of species identified from Waquoit Harbor estuary, south of Cape Cod, but only one of which, *F. heteroclitus*, was included in the group found in Wells Harbor estuary, north of Cape Cod. Analyses of genetic patterns in individuals of *F. heteroclitus* from populations in the northern part of its range along the Atlantic coast have suggested that its range contracted and expanded in the north–south direction accompanying advances and retreats of glaciers during the Pleistocene (Ropson et al. 1990).

The known distribution of *F. diaphanus*, primarily a FW species, extends farther north beyond the Cape into the St. Lawrence River drainage (Page and Burr 1991), and the distribution of *F. majalis* also extends northward of Cape Cod (Relyea 1983; Duggins et al. 1989, 1995), but not as far north as Wells Harbor, ME (Ayvazian et al. 1992). The distribution of *F. majalis* was reported by several authors to have extended northward in recent times. Individuals appeared in Massachusetts Bay in the decade 1930–1940, though they may have gotten there by way of an enlarged Cape Cod Canal (Schroeder 1937). Individuals were first found in Great Bay, NH in 1950 (Taylor et al. 1957), and in increased numbers there in 1952 (Jackson 1953; Taylor et al. 1957). Individuals of *F. majalis* were reported from even farther north, in a salt pond near the mouth of the Kennebec River, ME in 1991, but not in succeeding years (1992, 1993, 1994) when collections were made in the same areas (Lazzari et al. 1999). Responses of individuals of *F. majalis* to low temperatures are known only from records of temperatures at which collections of the species were made, the lowest being 3.5°C (DE, Shuster 1959).

Since other features of coastal systems such as increased water levels would accompany global warming, this might well eliminate some potential physical barriers to occupying available habitats. Warming of coastal waters might also alter patterns of organic production along the coastline. Such changes may include an earlier beginning of the spring marine plankton bloom, and earlier spring increases in primary production in estuarine habitats. What this would do with respect to matching the timing of hatching and development of fish larvae (time, place, size, etc.) with the availability of necessary food resources, patterns of predation, and of competition, remains to be seen (McGurk 1984; Blaxter 1992).

Predictions were made of possible alterations of distribution of the anadromous species *Morone saxatilis* accompanying continued global warming, using results of two general atmospheric circulation models (GISS from NASA and GFCL from Princeton) (Coutant 1990). That species is distributed in the northern Gulf of Mexico and along the Atlantic coast from the St. Johns River, FL to the Gulf of St. Lawrence. Its Atlantic coastal distribution is quite similar to that of *F. heteroclitus*, and only slightly more extended to the north than that of *F. majalis*. Results of simulations using the two models differed somewhat in projections of expected air temperatures and precipitation patterns along the Atlantic coast from Florida to Nova Scotia. Simulations predicted that temperature increases would be greater in winter months (Dec., Jan., and Feb.) in the New Hampshire and Maine areas than at the latitudes of Georgia and Florida, where the greatest temperature changes would be in the warmer months (GA, June, July, and Sept.; FL, Mar., May, and June). Model predictions indicated that under some circumstances anticipated increases in air temperatures might not be manifested in increases in water temperatures in the area of the Gulf of St. Lawrence, depending on patterns and magnitudes of precipitation and runoff because they influence salinity and interactions of water-current patterns in that area. Such a situation might act as a barrier to further northward range extensions of species that now have populations with northern limits in that area, or those that expand northward to that region.

An example of how much is yet to be learned about how distributions and habitat utilization are shaped by environmental conditions for even a single species can be appreciated from an analysis of one of the best known of these cyprinodontoid species. Halpin (1997) found that utilization of specific habitats by individuals of *F. heteroclitus* varied seasonally in salt marshes of Narragansett Bay, RI. The areas in which they were found at any particular season represented only a small fraction of available habitats. It was known that individuals of the species were subjected to extensive changes in physical conditions of the salt marsh environment with every change in tide. How habitat occupation is actually determined at any particular time and in the various life stages is largely unknown (Halpin 1997).

Summary/Conclusions

Habitat occupation by populations of any species of estuarine fish is generally determined by a number of environmental conditions, their variations and interactions, with abiotic conditions including water temperature, DO concentrations, and salinity, (the three chosen for discussion in this paper) as well as pH, silt load, turbulence, substratum, and possibly others. These operate along with biotic influences of competition and predation in shaping patterns of distribution and abundance of various species. Cyprinodontoid fishes that have been found in estuaries/salt marshes of eastern North America were chosen for these evaluations because some of the species are often the most abundant and obvious residents in estuarine/salt marsh systems of North America. Many of these species show extensive latitudinal distributions as well as variations in characteristics of their estuarine habitats.

There are more eurythermal cyprinodontoids among these 28 species than stenothermal species. Seventeen of these have been taken from the field at, or shown in laboratory analyses, to tolerate temperature ranges from ≤10 to ≥30°C, with at least one more, *B. belizanus* likely also in this category. The only species among those being considered that has been shown to have a lower thermal limit above 15°C is *G. rhizophorae*. In most cases laboratory-determined, physiological-tolerance levels to elevated and reduced temperatures are higher and lower, respectively, than the temperature limits at which these fishes had been found in nature. Most of the exceptions involve lower thermal limits, where the tolerance limit and lowest temperature at which individuals of a species have been found in nature are roughly equivalent, frequently near the freezing point of waters that they generally inhabit. None of these 28 species appears to be exclusively limited to environments of consistently low temperatures. Cold fronts that rapid reduce water temperatures to near freezing levels have killed some of the most eurythermal of cyprinodontoid fishes, though reports of such events are few in number.

Variations in responses to environmental temperatures have been demonstrated between and among populations of a number of these species that have wide latitudinal ranges of distribution. Final thermal preferenda were found to be higher in populations of *F. diaphanus* from Pennsylvania than from Nova Scotia, and ULTs of *F. heteroclitus* showed lower highs in a Nova Scotia population compared to more southern populations. Southern populations of *G. affinis* showed lower values of UILTs and higher values of LILTs than northern populations. Conclusions in some studies of geographical variations in temperature responses were that variations were based on acclimations, while in others conclusions were that variations were genetically based.

Responses to low DO concentrations vary depending on temperature and salinity conditions, and especially on whether ASR is possible, supplementing DO uptake at reduced DO concentrations. The species found to be most tolerant of reduced DO concentrations were *F. heteroclitus* and *L. parva*. Other species that showed tolerance of low DO concentrations included *C. variegatus*, *G. holbrooki*, and *P. latipinna*. The only species among these 28 known to be especially sensitive to even modest hypoxia is *F. carpio*. Individuals of *K. marmoratus* show emersion when H_2S levels increase and/or DO concentrations reach critically low levels in the waters that they occupy. Only *F. grandis* of species discussed here has been shown to have anaerobic metabolism under hypoxic conditions. While hyperoxic conditions have been suggested to be detrimental to fishes in some situations, the only cyprinodontoid reported from waters showing hyperoxic levels, *F. diaphanus*, showed no evidence of gas-bubble trauma under the circumstances reported.

DO standards have been developed for estuarine habitats. These DO requirements are likely to be adequate for adult individuals of most of the cyprinodontoids considered here, with the notable exception of *F. carpio*. However, DO concentrations indicated as acceptable to adult fishes might be somewhat limiting to successful hatching and development of some of these species.

Sixteen of these cyprinodontoid species have been taken from the field at, or shown in laboratory analyses to tolerate, a range of ambient concentrations from FW or near FW, to salinities of ca. 70, or higher. Some of the other species have never been found at salinities higher than those of dilute brackish waters. Species with widest know tolerance limits include *C. variegatus* and a number of species of *Fundulus*. However, not all species of *Fundulus* have wide salinity tolerances. Generally, laboratory-determined salinity limits exceed the reported ranges of salinities at which individuals have been collected. However, individuals of *C. variegatus* apparently represent an extreme exception to this generalization. Evaluations of responses to various rates of change in salinities have not often been made in fishes, though they do appear to be important in determining survival of some species, even some highly euryhaline ones including *C. variegatus*. Individuals of several species of cyprinodontoids evaluated showed highest ULTs when maintained at an ambient salinity near to that of their normal blood osmotic concentration. However, individuals of *F. diaphanus* showed highest thermal preferences in its normal FW environment, while individuals of *F. heteroclitus*, showed highest thermal preferences when in its normal SW environment.

It seems obvious that temperature, DO concentrations, and salinities exert profound but varying influences on reproduction of these cyprinodontoid fishes. Significant differences have been demonstrated in reproductive patterns of *F. heteroclitus* among populations over its wide latitudinal range. Also, it has been shown that increases in water temperatures produced when estuarine/coastal waters are heated and discharged back into the estuarine system, can have a considerable impact on the reproductive patterns of local populations of a species.

The phenomenon of global warming raises questions of what its results might bring about with respect to alterations in distribution patterns of estuarine cyprinodontoid species, some with distributional ranges limited to warmer areas, and others with extensive latitudinal ranges of distribution. Predicted water-temperature changes accompanying global warming over the next 50–100 years may not threaten reproductive capabilities of populations of many fish species from the standpoint of lethal or sub-lethal effects, except for those at the limits of tolerable temperature ranges.

Suggestions were made as to some of these cyprinodontoid species that seem likely to show northward extensions in their distributions with continued global warming. Individuals of one of these species, *F. majalis*, have established more northerly populations in recent years, though that has not been attributed to climatic warming. A fundamental question that remains unanswered is will increases in water temperatures put cycles of organic production out of phase with reproductive cycles of fishes, cyprinodontoids as well as other species that reside in brackish or marine waters? There is still much to be learned before accurate predictions can be made as to influences of changes in global temperature patterns on habitat utilization and overall distributions of populations of any of these species. What the outcome will be for any of these 28 cyprinodontoid species remains to be seen.

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