



INVITED REVIEW

Patterns of Fish Reproduction at the Interface between Air and Water

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Synopsis Although fishes by nature are aquatic, many species reproduce in such a way that their embryos are exposed to air either occasionally or constantly during incubation. We examine the ecological context and review specific examples of reproduction by fishes at the air–water interface, including fishes that do and do not breathe air. Four modes of reproduction at the air–water interface are described across 18 teleost orders, from fresh water, estuaries, and sea water. Mode 1, the most common type of reproduction by fishes at the air–water interface, includes 21 families of mostly marine teleosts that spawn in water onto a substrate surface, on vegetation, or into hollow objects such as shells that will later be continuously or occasionally exposed to air. Although the eggs are emerged into air, many of these species do not emerge into air as adults, and only about half of them breathe air. Mode 2 involves six families of freshwater fishes setting up and guarding a nest and guarding on the water surface, either with bubbles or in vegetation. Most of these species breathe air. In Mode 3, annual killifishes in at least two families in seasonally dry habitats bury eggs in mud in temporary pools, then die before the next generation emerges. These species neither guard nests nor breathe air. Mudskippers (Gobiidae) breathe air and use Mode 4, excavating burrows in a soft substrate and then storing air in a subterranean chamber. In a variation of Mode 4, eggs are placed on bubbles within a nesting burrow by swamp eels (Synbranchidae). No fishes from basal taxa are known to place their embryos where they will be exposed to air, although most of these species breathe air as adults. The widespread but still rare, diverse forms of fish reproduction at the air–water interface across a broad taxonomic spectrum suggest repeated independent evolutionary events and strong selection pressure for adult fishes to protect their embryos from hypoxic waters, aquatic predators, pathogens, and UV radiation. Air-breathing by adult fishes appears to be de-coupled from air exposure of developing embryos or aerial emersion of adults during spawning.

Introduction

We traditionally describe fishes as aquatic vertebrates that complete the entire life cycle in water. This is true for 99% of fish species (over 35,000 species, Eschmeyer et al. 2018), roughly 50% of vertebrate species. Exceptionally, but quite importantly from the viewpoint of animal evolution and environmental adaptation, the remaining 1% of fish species, nearly 400, use air in various ways (Graham 1997, 2011). Some rely on air as a complementary oxygen source when water holds little oxygen, some others must breathe air even when water is rich in oxygen, and still some others, approximately 100 species, are amphibious and emerge from water to feed, escape

from predators, avoid poor water conditions, or reproduce (Sayer and Davenport 1991; Wright and Turko 2016). These fishes have attracted the interest of biologists for more than 100 years, resulting in a wealth of information on morphological, physiological, and behavioral adaptations to use the foreign but oxygen-rich medium for respiration, and to tap into environmental resources away from aquatic competitors (Graham 1997, 2011). Past studies have mainly dealt with adult fishes. Less attention has been paid to fishes emerged from water during early life.

In this review, we focus on fish reproduction at the interface between air and water. In shallow water or along shores of freshwater and seawater, egg-encased

embryos are exposed to air during their development, either occasionally or continuously. Eggs may be emerged whether or not the adults that produce them emerge into air themselves. Some of these fishes have the ability to breathe air, and use it to create an environment that ensures oxygen supply to embryos, such as bubble nests or air-filled chambers in subterranean burrows. Others lack air-breathing capacity and never emerge, or emerge very briefly for spawning. We seek to provide a framework for examining diverse modes of reproduction for numerous species of fishes that make use of the interface between air and water. Although some aspects of this approach may illuminate the evolutionary vertebrate transition from water to land (Graham 1997, 2011; Graham and Lee 2004; Schoch 2014), that is not the purpose of this paper. We consider how different fishes use beneficial aspects of both air and water to lay eggs and incubate embryos.

Ecological context

Aquatic hypoxia is present in many habitats where air-breathing fishes live. Many freshwater air-breathing fishes live in habitats where regional hypoxia may persist for a long time (Dehadrai and Tripathi 1976; Graham 1997). Stagnant tropical freshwater bodies are often hypoxic or even anoxic because of microbial action on the profuse aquatic vegetation continuously accumulating and decaying. Along marine coasts, intertidal pools may be well oxygenated during a flood tide by wave action, connection with the wider ocean, and daytime photosynthesis. However, at night pools may become hypoxic during ebb tides due to respiration by plants and animals in the absence of photosynthesis (Truchot and Duhamel-Jouve 1980). Air-breathing intertidal fishes emerge either actively or passively from normoxic or hypoxic water (Martin 2014). In tropical regions, water inundating mudflats, nearby creeks, and swamps can also be extremely hypoxic (Mazda et al. 1990; Okamura et al. 2010). Soft substrates in which highly amphibious mudskippers excavate burrows are often hypoxic or anoxic in the water and in burrows a few millimeters beneath the surface (Little 2000).

Hypoxic conditions do not support the high metabolism of developing embryos (Rombough 1988). One solution for embryos is to emerge eggs into air, where oxygen is abundant and diffuses more rapidly (Dejours 1981). Simultaneously, small anamniotic eggs must maintain hydration and avoid desiccation (Strathmann and Hess 1999). A similar need to balance oxygen availability and desiccation arises when a wet habitat dries up, either because of a receding

tide on the seashore or by evaporation of a freshwater pool during a dry season (Strathmann and Hess 1999; Martin et al. 2004).

Embryos are highly sensitive to hypoxia. Sublethal effects of hypoxia on fish embryos include delayed development, an increase in significant malformations, and a disturbed balance of sex hormones in the embryo (Shang and Wu 2004; Wu 2009). Eggs are essentially a passive entity, having no motility. Although fish embryos may be able to move perivitelline fluid by opercular movements (Wells et al. 2015), they are unable to initiate convective renewal of the external respiratory medium. In water, boundary layers must be thinned by placing eggs in a lotic environment, or by fanning, one of the most common parental behaviors in fishes.

Avoidance of hypoxia cannot be the only driving force for the evolution of spawning at the air–water interface, as fishes spawn at the air–water interface not only in oxygen-poor swamps and muddy shores, but also in oxygen-rich sandy and rocky coasts. In some cases, avoidance of aquatic predators or pathogens may be driving the evolution of terrestrial reproduction (Sayer and Davenport 1991; Wells 2007; Touchon and Worley 2015). Out of water, eggs are exposed to different predators, pathogens, UV radiation, and temperature extremes (Blaustein et al. 1997; Epel et al. 1999). These physical and biological challenges may explain why relatively few species of fishes take advantage of access to the steady reliability of oxygen at the air–water interface during early development. Even so, the variety of fish species that reproduce at the water’s edge truly is impressive.

The timing of return of water to terrestrial habitats may not be perfectly predictable. In such cases the incubating embryos may need to have flexibility to adjust development rates and hatching times (Bradford and Seymour 1985; Martin 1999; Moravek and Martin 2011), so that larvae can be safely returned to an aquatic habitat.

Teleost species with eggs that naturally incubate in air demonstrate that embryos develop faster and use less yolk reserves to produce larvae of the same size than embryos of the same species incubated in normoxic water (Tingaud-Sequeira et al. 2009; Wells et al. 2015). This suggests that terrestrial incubation of teleost eggs may have advantages beyond simple avoidance of hypoxia for the relatively long incubation of tidally synchronized embryos.

Phylogenetic context

All cartilaginous fishes have internal fertilization and most give birth to live young (Helfman et al. 2009).

None of these cartilaginous fishes is known to spawn at air–water interface or breathe air (Wourms and Demski 1993). Therefore, all fishes treated in this review are bony fishes. The adoption of air incubation appears in some teleost lineages as an isolated or independent event in one species, rather than a predictable sequence of gradual emergence higher and higher on shore (Martin and Swiderski 2001; Martin 2015). Because one may anticipate that the same ecological conditions that lead to the evolution of air-breathing in adult fishes may also select for reproduction at the air–water interface, Table 1 summarizes the known occurrences of air-breathing adults and embryos at the air–water interface for classes Sarcopterygii and Actinopterygii by order (phylogeny from Nelson et al. 2016). Air-breathing is known in at least 400 of about 35,000 species, or 1.1%. Spawning at the interface between air and water is seen in 104 species, or 0.3%. Only 0.3%, less than half of 1%, do both, indicating both that air-breathing is de-coupled from egg placement into air, and that air-breathing by adults is more widespread than egg emersion. At least 37 fish species that place eggs at the interface between air and water do not breathe air as adults (Table 5).

Reproductive modes in fishes

Reproductive mode for fishes is multifaceted, encompassing gender systems, spawning dynamics, modes of fertilization, mating systems, secondary sexual characteristics, and parental care (Wootton and Smith 2015). Balon (1975) developed classification schemes for guilds or modes of bony fish reproduction, separating three major types of reproduction into non-guarders, guarders, and bearers. He further subdivided each according to the spawning location, and called these 32 subdivisions guilds. Fish that spawn at the water–air interface are included in two guilds in both non-guarders and guarders. Later, Balon (1981) added another guild “terrestrial spawners” in the non-guarder type to incorporate spawning behaviors of *Fundulus*, *Menidia*, and *Galaxias*. However, neither Balon (1975, 1981, 1990) nor Wootton and Smith (2015) directly addressed the variety of methods that teleost fishes use to place eggs at the interface between air and water.

Both fishes and amphibians remain dependent on aquatic habitats as they typically hatch into aquatic larvae. A crucial difference is that amphibians usually become amphibious or terrestrial as adults, while the majority of fishes do not; only about 100 species of fish are known to exhibit variable degrees of amphibiousness (Graham 1997). Therefore initiating

life on land as terrestrial larvae, or bypassing the larval period (Crump 2015), have different consequences for amphibians than for fishes. To the best of our knowledge, all fishes breeding at the air–water interface have aquatic free-living, feeding larvae, and there is no known example of amphibious or terrestrial offspring among fishes.

Fish reproduction at the air–water interface: four modes

Our definition of reproductive modes for the fishes breeding at the air–water interface is simple, defined on the basis of the site of oviposition, and the way that eggs have access to air. We recognize four main types, most with subdivisions (Table 2).

In the first mode, beach-spawning fishes spawn in or out of water onto some substrate that will be continuously or occasionally exposed to air in the intertidal or supralittoral zone. This mode has many variations and is the most common type of reproduction by fishes at the air–water interface, found in marine, brackish, and freshwater habitats, in fishes that may or may not breathe air, with or without parental care. In the second mode, adult fishes guard eggs in a nest at the surface of fresh water. In the third mode, fishes bury resistant eggs in hypoxic mud, and in the fourth mode fishes excavate mud burrows, relying on parental care of the nest to help the embryos survive harsh conditions. Each of these will be discussed in detail below.

Air–water interface reproductive mode

1—Oviposition by fishes associated with a substrate, vegetation, or other objects that is intermittently or continuously out of water

Tidal emersion is the most commonly observed mode of spawning at the air–water interface. Fishes oviposit in water or air, on or in a substrate that will subsequently be intermittently or continuously out of water (Fig. 1A). Alternatively, some species broadcast eggs in water that will adhere to or settle onto a substrate and be exposed to air when tide recedes.

Spawning in these fishes may be aquatic, or the fish may emerge from water to spawn on a littoral substrate such as rocks or gravel, or onto vegetation or empty shells. By spawning high in the intertidal zone during a flood tide, the parents ensure that clutches will be emerged into air for hours or days as the tides subsequently ebb, but somewhat protected from desiccation and temperature extremes. This protects the embryos from temporary aquatic hypoxia that can occur during low tides. The return of tides is regular and predictable, and the timing of

Table 1 Phylogenetic context of air-breathing and reproduction at the air–water interface are shown for classes Sarcopterygii and Actinopterygii by order (phylogeny from Nelson et al. 2016)

Subclass	Superorder	Division	Order	Number of families	Total number of Species	Species with adults that breathe air	Species with embryos at air–water interface
Sarcopterygii			Coelacanthiformes	1	2	0	0
	Dipnoi	Dipnoi	Ceratodiformes	3	6	6	0
Actinopterygii			Polypteriformes	1	14	14	0
			Acipenseriformes	2	27	0	0
		Ginglymodi	Lepisosteiformes	1	7	7	0
		Halecomorphi	Amiiformes	1	1	1	0
		Teleostei	Elopiformes	1	2	2	0
			Albuliformes	1	12	16+	0
			Notacanthiformes	2	27	0	0
			Anguilliformes	19	938	0	0
			Hiodontiformes	1	2	0	0
			Osteoglossiformes	5	244	9+	0
	Clupeomorpha		Clupeiformes	5	405	0	1
	Alepocephali		Alepocephaliformes	3	137	0	0
	Ostariophysi		Gonorynchiformes	3	37	1	0
			Cypriniformes	13	4205	7	0
			Characiformes	24	2300	4	3
			Siluriformes	40	3730	9+	4
			Gymnotiformes	5	208	5	1
			Lepidogalaxiiformes	1	1	1	0
	Protacanthopterygii		Salmoniformes	1	223	0	0
			Esociformes	2	12	5	0
	Osmeromorpha		Argentiniformes	3	87	0	0
			Galaxiiformes	1	50	10	1
			Osmeriformes	5	47	0	4
			Stomiiformes	5	414	0	0
	Ateleopodomorpha		Ateleopodiformes	1	12	0	0
	Cyclosquamata		Aulopiformes	15	261	0	0
	Scopelomorpha		Myctophiformes	2	254	0	0
	Lamprimorpha		Lampriformes	6	22	0	0
	Paracanthopterygii		Polymixiiformes	1	10	0	0
			Percopsiformes	3	10	0	0
			Zeiformes	6	33	0	0
			Stylephoriformes	1	1	0	0
			Gadiformes	13	613	0	0
	Acanthopterygii		Holocentriformes	1	83	0	0
			Trachichthyiformes	5	68	0	0
			Beryciformes	8	104	0	0
			Ophidiiformes	5	531	0	0
			Batrachoidiformes	1	101	1	1
			Kurtiformes	2	349	0	0

(continued)

Table 1 Continued

Subclass	Superorder	Division	Order	Number of families	Total number of Species	Species with adults that breathe air	Species with embryos at air–water interface
			Gobiiformes	8	2167	41+	3
			Muguliformes	1	75	0	0
			Cichliformes	2	1764	0	0
			Blenniiformes	6	918	77+	5
			Gobisociformes	1	169	7	3
			Atheriniformes	8	351	0	4
			Beloniformes	6	283	0	0
			Cyprinodontiformes	10	1257	12	14
			Synbranchiformes	3	117	14	1
			Carangiformes	6	160	0	0
			Istiophoriformes	3	39	0	0
			Anabantiformes	4	207	83+	40
			Pleuronectiformes	14	772	0	1
			Syngnathiformes	8	338	0	0
			Icosteiformes	1	1	0	0
			Callionymiformes	2	202	0	0
			Scombrolabraciformes	1	1	0	0
			Scombriformes	9	192	0	0
			Trachiniformes	11	301	0	2
			Labriformes	3	630	0	0
			Perciformes	62	2248	1	0
			Scorpaeniformes	41	2092	10	15
			Moroniformes	3	22	0	0
			Acanthuriformes	18	168	0	0
			Spariformes	6	305	0	0
			Caproiformes	1	18	0	0
			Lophiiformes	18	358	0	0
			Tetraodontiformes	10	435	0	1
			Totals		31,178	343+	104

Notes: Total numbers of species are shown, followed by those that are known to breathe air as adults, and then number of species that spawn at the air–water interface. This list undoubtedly underestimates the number of species with these behaviors.

hatching or larval release may be related to the tides along with the timing of spawning (Taylor 1999; Martin et al. 2004), or wind waves (Frank and Leggett 1981), or local oxygen concentration (Taylor and DiMichele 1983).

As many as 21 families of teleosts are known to contain Mode 1 or beach-spawning species (Martin 2015). Most of these fishes are marine, but Rivulidae, Fundulidae, and Gobiidae are estuarine, Galaxiidae is diadromous, and Characidae is freshwater (Table 3).

We subdivide the 49 species into four groups based on the adult spawning behaviors.

Mode 1a includes 23 species in 9 families that show various levels of amphibious behavior (Martin 1993) and are either suspected or known to breathe air (Martin 2014). These fishes do not have specialized air-breathing organs, but use the skin, gills, and vascularized bucco-opercular mucosa for aerial gas exchange (Graham 1997). A variety of substrates are used to shield the embryos of Cottidae,

Table 2 Four reproductive modes and their subtypes at the interface between air and water, with example species

		Example species
Mode 1	Placement of eggs out of water for some or all of incubation	
	1a: Spawning aquatically in the marine intertidal zone at high tide	<i>Clinocottus acuticeps</i>
	1b: Emerging from water only to spawn	<i>Leuresthes tenuis</i>
	1c: Amphibious fish spawning out of water	<i>Andamia tetradactyla</i>
	1d: Freshwater fishes spawning out of water	<i>Copella arnoldi</i>
Mode 2	Placement of eggs at the water surface in a nest	
	2a: Nesting in or protected by floating vegetation	<i>Channa argus</i>
	2b: Bubble nesting	<i>Colisa lalia</i>
Mode 3	Burial of eggs in mud, embryos undergo diapause	<i>Austrolebias beloti</i>
Mode 4	Eggs are placed in a mud burrow	
	4a: Burrow contains an air space maintained by the parent(s)	<i>Periophthalmodon schlosseri</i>
	4b: Parent creates a bubble nest floating within the burrow	<i>Monopterus albus</i>

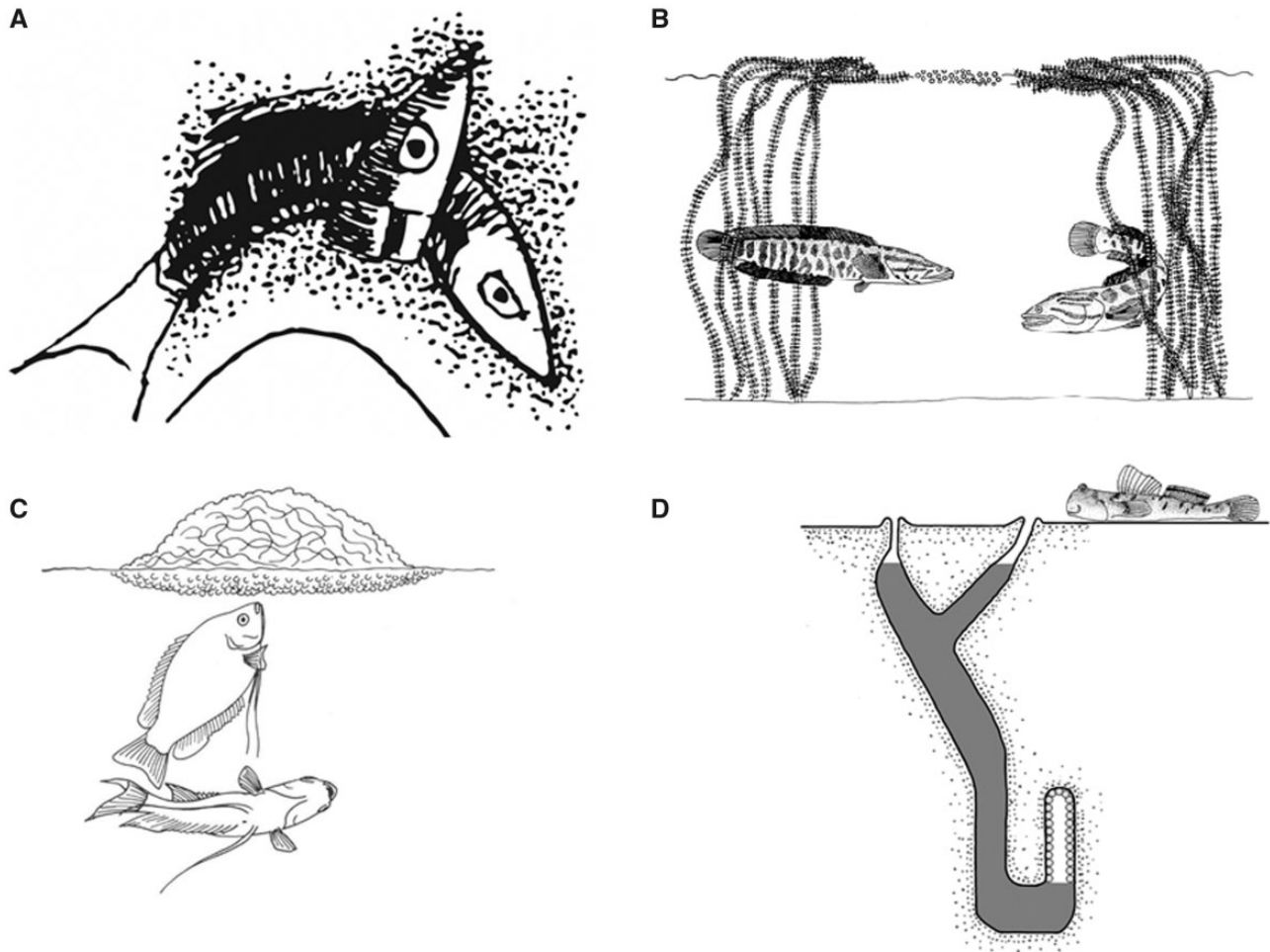


Fig. 1 Representative examples of reproductive modes. **A)** Mode 1b, California grunion *Leuresthes tenuis* spawn out of water, placing eggs high in the intertidal zone (from [Martin 1999](#)). **B)** Mode 2a spawning of snakehead *Channa argus* in a cleared area; eggs form a raft at the surface. Note the guarding adults nearby (modified from [Landis and Lapointe 2010](#)). **C)** Mode 2b spawning and egg guarding by the labyrinth fish *Colisa lalia* in a bubble nest (after [Miller and Jearld 1983](#)). **D)** Mode 4a, spawning in a burrow with an air chamber of the mudskipper *Periophthalmus modestus* (modified from [Matoba and Dotsu 1977](#)).

Table 3 At least 49 species are examples of Mode 1 fishes

Family	Species	Adult habitat	Mode	Eggs broadcast or placed	Spawning substrate	Egg type	Parental care	References
Ammodytidae	<i>Ammodytes hexapterus</i>	Subtidal	1a	B	Sand, Gravel	Adherent	No	Robards et al. (1999)
Atherinopsidae	<i>Colpichthys regis</i>	Subtidal	1a,b	P	Veg, Rubble	Non-adherent	No	Russell et al. (1987)
	<i>Leuresthes tenuis</i>	Subtidal	1b	P	Sand	Non-adherent	No	Griem and Martin (2000)
	<i>Leuresthes sardina</i>	Subtidal	1b	P	Sand	Non-adherent	No	Thomson and Muench (1976)
	<i>Menidia menidia</i>	Subtidal	1a	B	Vegetation	Adherent	No	Middaugh (1981)
Batrachoididae	<i>Porichthys notatus</i> ^a	Subtidal	1a	P	Rock	Adherent	Yes	Arora (1948)
Blenniidae	<i>Alticus kirkii</i> ^a	Intertidal	1a	P	Rock	Adherent	Yes (male)	Breder and Rosen (1966)
	<i>Alticus monochrus</i>	Intertidal	1a	P	Rock	Adherent	Yes	Bhikjee and Green (2002)
	<i>Andamia tetradactylus</i> ^a	Intertidal	1c	P	Rock	Adherent	Yes	Shimizu et al. (2006)
	<i>Coryphoblennius galerita</i>	Intertidal	1a	P	Rock	Adherent	Yes	Gonçalves and Almada (1998)
	<i>Lipophrys pholis</i> ^a	Intertidal	1a	P	Rock	Adherent	Yes	Almada et al. (1992)
	<i>Salarias pavo</i>	Intertidal	1a	P	Rock	Adherent	Yes	Almada et al. (1994)
Characidae	<i>Copella arnoldi</i>	Fresh water	1d	P	Vegetation	Adherent	Yes	Nelson and Krekorian (1976)
	<i>Brycon petrosus</i>	Fresh water	1d	?	Gravel	Adherent	No	Kramer (1978)
Clupeidae	<i>Clupea pallasii pallasii</i>	Subtidal	1a	B	Vegetation	Adherent	No	Jones (1972)
Cottidae	<i>Arteidius harringtoni</i>	Intertidal	1a	P	Rock	Adherent	Yes (male)	Ragland and Fischer (1987)
	<i>Arteidius lateralis</i>	Intertidal	1a	P	Rock	Adherent	No	Petersen et al. (2005)
	<i>Ascelichthys rhodorus</i> ^a	Intertidal	1a	P	Rock	Adherent	No	Petersen et al. (2004)
	<i>Clinocottus acuticeps</i>	Subtidal	1a	P	Vegetation	Adherent	No	Marliave (1981a)
	<i>Clinocottus analis</i> ^a	Intertidal	1a	P	Rock	Adherent	Yes	Wells (1986)
	<i>Enophrys bison</i>	Subtidal	1a	P	Rock	Adherent	No	DeMartini (1978)
	<i>Oligocottus maculosus</i> ^a	Intertidal	1a	P	Rock	Adherent	Yes (male)	Pfister (1996, 2007)
Fundulidae	<i>Trachidermus fasciatus</i>	Intertidal	1a	P	Shells	Adherent	No	Tsukahara (1952)
	<i>Fundulus heteroclitus</i> ^a	Subtidal	1a	P	Shells, vegetation	Non-adherent	No	Able and Castagna (1975)
	<i>Fundulus similis</i>	Intertidal	1a					Greeley et al. (1986)
	<i>Fundulus confluentus</i>	Estuarine	1a				No	Harrington (1959)
Galaxiidae	<i>Galaxias maculatus</i> ^a	Anadromous	1a	B	Vegetation	Non-adherent	No	McDowall (1968)
	<i>Galaxias brevipinnis</i>	Amphidromous	1a	B	Gravel	Adherent	No	O'Connor and Koehn (1998)
	<i>Galaxias fasciatus</i>	Amphidromous	1a	B	Gravel	Adherent	No	Mitchell and Penlington (1982)
	<i>Galaxias postvectis</i>	Amphidromous	1a	B	Gravel	Adherent	No	Charteris et al. (2003)
Gasterosteidae	<i>Gasterosteus aculeatus</i> ^b	Subtidal	1a	B	Rock	Non-adherent	No	MacDonald et al. (1995)

(continued)

Table 3 Continued

Family	Species	Adult habitat	Mode	Eggs broadcast or placed	Spawning substrate	Egg type	Parental care	References
Gobiesocidae	<i>Gobiesox maeandricus</i> ^a	Intertidal	1a	P	Rock	Adherent	Yes	Coleman (1999)
	<i>Gobiesox barbatulus</i>	Intertidal	1a	P	Rock	Adherent	Yes (male)	Pires and Gibran (2011)
Gobiidae	<i>Tridentiger barbatus</i>	Intertidal	1a	P	Shells	Non-adherent ^c	Yes (male)	Dótu (1957)
	<i>Tridentiger nudicervicus</i>	Intertidal	1a	P	Shells	Non-adherent ^c	No	Dótu (1958)
Osmeridae	<i>Mallotus villosus</i>	Subtidal	1b	B	Gravel, sand	Adherent	No	Frank and Leggett (1981)
	<i>Hypomesus japonicus</i>	Subtidal	1a	B	Gravel, sand	Adherent	No	Hirose and Kawaguchi (1998)
	<i>Hypomesus pretiosus</i>	Subtidal	1a	B	Gravel	Adherent	No	Penttila (2007)
	<i>Spirinchus starksi</i>	Subtidal	1a	B	Gravel	Adherent	No	Hart (1973)
Pholidae	<i>Pholis laeta</i> ^a	Intertidal, Subtidal	1a	P	Gravel	Adherent	No	Coleman (1999); Hughes (1985)
Pleuronectidae	<i>Lepidopsetta bilineata</i> ^c	Subtidal	1a	B	Gravel	Adherent	No	Penttila (1995)
Rivulidae	<i>Kryptolebias marmoratus</i> ^a	Estuarine	1c	P	Vegetation	Non-adherent	No	Abel et al. (1987)
Stichaeidae	<i>Anoplarchus purpureus</i> ^a	Intertidal	1a	P	Rock	Non-adherent	Yes (female)	Coleman (1999)
	<i>Xiphister atropurpureus</i> ^a	Intertidal	1a	P	Rock	Non-adherent	Yes (male)	Marliave and DeMartini (1977)
	<i>Xiphister mucosus</i> ^a	intertidal	1a	P	Rock	Non-adherent	Yes (male)	Marliave and DeMartini (1977)
Tetraodontidae	<i>Takifugu niphobes</i>	Subtidal	1a,b	B	Gravel	Non-adherent	No	Yamahira (1996)
Trichodontidae	<i>Trichodon trichodon</i>	Subtidal	1a	B	Sand	Adherent	?	Marliave (1981b)
Tripterygiidae	<i>Forsterygion nigripenne</i> ^a	Intertidal	1a	P	Rock	Adherent	Yes	Berger and Mayr (1992)
Zoaridae	<i>Austrolycus depressiceps</i>	Intertidal, Subtidal	1a	P	Rock	Adherent	Yes	Matalanas et al. (1990)

Notes: Adults typically live in the marine intertidal zone, but some are anadromous, subtidal, or freshwater. No species that broadcasts its gametes shows parental care in this group. There are likely to be many additional examples.

^aAir breathing has been confirmed by laboratory measurements.

^bWith filaments for attachment to a hard substrate.

^cKnown for only one population of the species.

Blenniidae, Gobeisocidae, Pholididae, Stichaeidae, and Tripterygiidae. Eggs of these fishes are all demersal, and may be adhesive to one another, or to the substrate, or neither. Some guard nests and others do not.

Some subtidal fishes also use Mode 1a, moving into the intertidal zone to spawn. They either do not emerge, or emerge briefly, and most of these apparently do not breathe air (Table 3). These include species that broadcast their eggs high in the intertidal zone, such as *Spirinchus starksi*, and *Hypomesus pretiosus* (Osmeridae) and the grass puffer *Takifugu niphobles* (Tetraodontidae). Other subtidal species attach eggs to the undersurface of intertidal boulders, or to vegetation by adhesion or filaments after release, such as Atlantic silversides (*Menidia menidia*) and Pacific herring, *Clupea pallasii pallasii* (Jones 1972). Some species hide their eggs under vegetation or other materials, such as *Fundulus heteroclitus* (Taylor 1999). The false grunion *Colpichthys regis* spawns as high on shore as possible at high tides beneath vegetation or rubble, where eggs are shaded during low tides (Russell et al. 1987).

A few species of fishes emerge from water during spawning for Mode 1b (Table 2). During highest spring tides, the California grunion *Leuresthes tenuis* (Atherinopsidae) and its congener, *L. sardina* the Gulf grunion, surf ashore, and as a wave recedes, females dig the tail into soft sand and oviposit about 10 cm below the surface while males contribute milt (Walker 1952). The adults emerge only briefly and are unable to breathe air (Martin et al. 2004). As the tides recede over the next few hours, the eggs remain buried on shore, damp but out of water for the duration of incubation. They rely on an environmental cue, the return of water during the following spring tides, to free the eggs and trigger hatching, releasing the larvae into the sea (Griem and Martin 2000). If tides are not high enough to cue hatching in the semilunar spring tides following the spawning run, the eggs can survive an additional 2 weeks of incubation and hatch with the next set of spring semilunar tides (Moravek and Martin 2011). The Osmerid *Mallotus villosus* spawns in shallow water or out of water during high wind wave events that are not synchronized by tides (Nakashima and Wheeler 2002).

In Mode 1c, the amphibious rockhopper blenny *Andamia tetradactylus* (Blenniidae) has terrestrial reproduction with paternal care. Spawning takes place out of water in a crevice between rocks located in the high intertidal zones (Shimizu et al. 2006). *Andamia tetradactylus* usually stay above water, attaching themselves to surfaces of rocks. A female spawns on the air-exposed wall or ceiling of a nest, followed by a

territorial male to fertilize, also in air. Males stay to guard eggs during both emersion and submersion of the nests. Eggs hatch 7–10 days later during a high tide.

The mangrove killifish *Kryptolebias marmoratus* (Rivulidae) has been found out of water in the wild and its eggs have been found emerged into air hidden under leaves or on the sides of crab burrows (Abel et al. 1987; Taylor 2012). This model organism is frequently bred in the laboratory, where it spawns on artificial substrates in water or in air (Wells et al. 2015), but its natural reproduction and oviposition have not been observed. As a self-fertilizing hermaphrodite, its reproductive activities may be cryptic, although males do occur (Turner et al. 2006). This species emerges into leaf litter and rotted logs and adults may remain out of water for weeks or months (Wright 2012). Thus natural reproduction may occur out of water in a manner consistent with mode 1a reproduction. The species apparently does not provide parental care to eggs, and eggs hatch in response to hypoxia (Wells et al. 2015).

An extreme example of spawning out of water is the freshwater splash tetra, *Copella arnoldi* (Characiformes), Mode 1d. The spawning pair leaps out of a stream to attach the eggs onto an overhanging leaf, then fertilize them. After this athletic encounter, the male stays in the water nearby and periodically agitates the surface of the stream to splash drops of water up onto the incubating eggs. When he is not splashing, the male moves slightly away from the nest, presumably to avoid the attention of predators attracted by the noisy activity. Spawning has been observed in aquaria with captive animals (Nelson and Krekorian 1976), where eggs adhere to glass aquarium walls above the water line. Eggs of another Characiform, *Brycon petrosus*, have been found under vegetation or in mud out of water near its home streams although terrestrial spawning has not been observed (Kramer 1978).

Most fishes spawn aquatically, including amphibious intertidal fishes. Among the fishes that emerge from water to spawn, only *A. tetradactylus* and *K. marmoratus* breathe air (Table 3).

Parental care is variously present, although less likely in non-air-breathing species. Parental care of the eggs is present for many intertidal species of Blenniidae, Cottidae, Gobiidae, and Stichaeidae, and a few species of Gobiisocidae and Pholidae (Coleman 1999; DeMartini 1999), even when eggs are out of water. At least two subtidal Cottids spawn intertidally. *Clinocottus acuticeps* (Marliave 1981a) and *Enophrys bison*, with males that guard the nest when it is submerged but leave the area during low tide (DeMartini 1978). Male mating success may improve

if he guards multiple clutches simultaneously (Hastings and Petersen 2010). No fish that broadcast eggs in Mode 1 shows parental care (Table 3).

Only a few subtidal species show care for eggs spawned in the intertidal zone (Martin 2015). The plainfin midshipman, *Porichthys notatus*, normally subtidal, sets up a nest territory under an intertidal rock or boulder. The male remains with the eggs, often with more than one clutch at different stages of development (Arora 1948), guarding them throughout embryonic development into the larval phase. Male midshipmen have the ability to breathe air (Martin 1993) and a high tolerance for aquatic hypoxia during the breeding season (Craig et al. 2014).

Air–water interface reproductive mode

2—Oviposition to a nest at the water surface

This mode has two distinct forms, either a nest of bubbles, or a nest surrounded by vegetation. Both forms are seen in fresh water species that breathe air (with rare exceptions), and both involve parental care throughout incubation (Table 4).

Mode 2a, many species of snakehead fishes (Anabantiformes, Channidae) move vegetation to create an open circular area for spawning buoyant eggs at the water surface. Eggs float inside the matrix of plant debris in the center of the nest, without any accumulation of bubbles (Fig. 1B). Snakeheads consist of two genera, *Channa* native to Asia and *Parachanna* from Africa (Courtenay and Williams 2004). Almost all *Channa* species that build a nest for spawning show biparental guarding of the nest and hatchlings. Both *Channa* and *Parachanna* parents fiercely attack any animals (including humans) approaching the nest. Reproductive ecology is relatively well known for *Channa* species, mainly because several are important food fish and the target of aquaculture in Asian countries, while very little is known for *Parachanna* (Kpogue et al. 2013).

Spawning into a bubble nest, Mode 2b, is best represented by labyrinth fishes in Anabantidae (5 species) and Osphronemidae (26 species), but not known in Helostomatidae of the same suborder (Anabantoidei, Rüber et al. 2006). It is also known in three species of Siluriformes in Callichthyidae, one species of Cypriniformes in Hepsetidae (Merron et al. 1990), and one species of Gymnotiformes in Gymnotidae. These are all freshwater fishes from tropical latitudes. We did not differentiate foam nests and bubble nests because the difference is subtle, relying on the consistency of the nests, and the number and the size of the bubbles.

Male labyrinth fish gulp air and blow bubbles to create a mucus-covered bubble nest at the water's

surface or in a few species underside of a submerged overhanging object (Fig. 1C). Eggs are attached to the fine bubbles in the nests by the male or both parents, so that embryos develop in conditions higher in oxygen than the surrounding hypoxic water (Miller and Jearld 1983; Linke 1991). Labyrinth fish eggs are either demersal, meaning they would sink on their own (*Betta splendens*, *Pseudosphromenus cupanus*, and *Trichopsis pumila*), or buoyant (some species of *Microctenopoma* and *Colisa lalia*, Linke 1991).

In Callichthyidae, bubble-nest spawning is best described for *Hoplosternum littorale*, *H. thoracatum*, and *Callichthys callichthys* (Mol 1993). In nests of *H. littorale*, the eggs are sandwiched between the bubbles floating in the water surface and overlying plant materials, such that the eggs are not in contact with hypoxic water of the habitat (Carter and Beadle 1931). Bubble nests of *H. thoracatum* and *C. callichthys* are guarded by the male and are much simpler, but essentially play the same role of insulating the eggs from oxygen-poor habitat water.

Hepsetus odoe is the only species of Hepsetidae known to build bubble nests (Merron et al. 1990). The bubble nest of *H. odoe* is a dome-shaped aggregation of tightly packed bubbles, with eggs embedded in the lower zone but above the water surface (Merron et al. 1990), guarded by both parents.

Limited information on the breeding of *Electrophorus electricus* (Assunção and Schwassmann 1995) suggests a male fish builds a bubble nest in residual backwater cohabited by the bubble-nesting *H. thoracatum* (see above), and guards his nest and hatched larvae.

Generating a bubble nest requires the ability to gulp air, and most listed species are air-breathers, via different methods. The air-breathing organ of labyrinth fishes consists of the lobular protrusion of variable complexities from the epibranchial of the first gill arch (labyrinth) encased in the suprabranchial chamber (Graham 1997; Tate et al. 2017). Adults of all three Callichthyidae species breathe air through a highly vascular section of the intestine (Graham 1997). *Electrophorus electricus* uses richly vascularized epithelium inside the mouth for air breathing (Johansen et al. 1968). In contrast, *H. odoe* probably does not breathe air (Merron et al. 1990).

Air–water interface reproductive mode 3—Burial of eggs in mud with eggs entering diapause to survive

Muddy substrates are fine, closely packed sediments that obstruct movement of water or oxygen. Fishes

Table 4 Mode 2 fishes that place eggs in a nest at the water surface are all freshwater species and all guard the nests

Family	Species	Substrate	Egg type	References
Anabantidae	<i>Microctenopoma fasciolatus</i> ^a	Bubble	Buoyant	Linke (1991)
Osphronemidae	<i>Betta splendens</i> ^a	Bubble	Demersal	Linke (1991)
	<i>Colisa lalia</i> ^a	Bubble	Buoyant	Linke (1991)
	<i>Pseudosphromenus cupanus</i> ^a	Bubble	Demersal	Linke (1991)
	<i>Trichopsis pumila</i> ^a	Bubble	Demersal	Linke (1991)
Channidae	<i>Channa argus</i> ^a	Surface vegetation	Buoyant	Courtenay and Williams (2004)
	<i>Parachanna obscura</i> ^a	Surface vegetation	Buoyant	Kpogue et al. (2013)
Callichthyidae	<i>Hoplosternum littorale</i> ^a	Bubble and vegetation	Adherent	Mol (1993)
	<i>Hoplosternum thoracatum</i> ^a	Bubble	Adherent	Mol (1993)
	<i>Callichthys callichthys</i> ^a	Bubble	Adherent	Mol (1993)
Hepsetidae	<i>Hepsetus odoe</i>	Bubble	Adherent	Merron et al. (1990)
Gymnotidae	<i>Electrophorus electricus</i> ^a	Bubble	Adherent	Assunção and Schwassmann (1995)

^aAbility to breathe air.

that reproduce in mud require unique strategies for embryo survival.

A well-studied example of burial of eggs in a mud substrate is seen in annual fishes (Cyprinodontiformes: Nothobranchiidae and Aplocheilidae, Berois et al. 2016a). Annual fishes inhabit seasonal, ephemeral fresh water pools in Africa and Central and South America, and live only 9 months from hatching to death. These fishes bury eggs in a substrate (*Austrolebias*) or oviposit on a substrate that is immediately covered by more settling substrate (*Nothobranchius*, Passos et al. 2016). As the pools dry up, adults die, but embryos in the mud survive extremely hypoxic subsurface conditions (Wourms 1972; Podrabsky et al. 2016). Adults are not amphibious and do not breathe air. Technically these embryos are not emerged into air but they are out of water, in a hypoxic terrestrial environment (Podrabsky et al. 2016). The embryos become metabolically depressed, requiring so little oxygen to survive that they do not move, grow, or even metabolize oxygen for months at a time (Podrabsky et al. 2007, 2010).

When the rains return, new stages of development are initiated. These reproductive modes include embryonic diapause, best studied for *Austrolebias bellottii*, *A. nigripinnis*, and *A. viarius* in the South America and for *Nothobranchius furzeri* in Africa (Berois et al. 2016b; Cellerino et al. 2016; Martin and Podrabsky 2017). Loureiro and de Sá (2016) listed 31 genera in the suborder Aplocheiloidei, including 3 genera in Nothobranchiidae, and 28 in Rivulidae, as “annual,” suggesting that there may be more species than those listed with the capacity for embryonic diapause to survive seasonal drought.

Air–water interface reproductive mode 4—Reproduction within a burrow excavated in soft substrate

Mode 4a is seen among highly amphibious mudskippers of the family Gobiidae (Jaafar and Murdy 2017). Mudskippers spawn in burrows excavated in hypoxic intertidal mudflats. This requires a sophisticated array of adaptations for successful incubation (Ishimatsu and Graham 2011; Martin and Ishimatsu 2017). Mudskipper burrows are excavated on the mudflat below the highest spring tide, so that the burrow opening is inundated by seawater during high tide, but open to air during low tide. During the reproductive season, the water-filled burrow may extend into a J-shape or U-shape, providing space for an egg chamber (Fig. 1D). This chamber then is filled with air by the male or the parents, one mouthful at a time during a low tide (Ishimatsu et al. 1998). The air stored under the surface is monitored by the male guarding the burrow. He replaces the air as needed so that oxygen levels are maintained high enough to meet the metabolic demand of the embryos (Etou et al. 2007), even during high tide when the burrow entrance is underwater (Lee et al. 2005). The male continues his parental care by perceiving when the embryos are ready to hatch, then removing the air to immerse the eggs in water, triggering them to emerge and swim free of the burrow as larvae (Ishimatsu et al. 2007). Apart from the air inside the chamber, the water-filled burrow is severely hypoxic (Ishimatsu et al. 1998, 2007).

Direct evidence for this type of burrow spawning is known for three species of mudskippers

(*Boleophthalmus pectinirostris*, *Periophthalmodon schlosseri*, and *Periophthalmus modestus*; Hong et al. 2007; Toba and Ishimatsu 2014; Ishimatsu et al. 2009). Air deposition in an egg chamber was stated for four other mudskippers (*Periophthalmus magnuspinnatus*, Baeck et al. 2008; *Periophthalmus minutus*, Takeda et al. 2011; *Scartelaos gigas*, Kim et al. 2011; and *S. histophorus*, Okinawa Prefecture 2000), but direct evidence is lacking. The extremely hypoxic conditions in the burrows of all mudskippers so far studied indicate air deposition during breeding is ubiquitous (Martin and Ishimatsu 2017). Burrow nesting under fully aquatic conditions is probably the ancestral condition for this group, as seen in fully aquatic gobies (Cole 2010). It is not clear at this time whether the actual spawning event occurs out of water, or whether air is added to the chamber after the eggs have been deposited. It is somewhat difficult to imagine a large mudskipper such as *P. schlosseri* defying gravity, clinging to the ceiling of an air-filled chamber without the support of seawater (Ishimatsu and Gonzales 2011), but the truth is we do not know how the act of spawning occurs in the burrow.

Mudskippers are highly amphibious and some breathe air more efficiently than they breathe water, but none of them has specialized air-breathing organs. They use the skin, gills, and vascularized buccopericardial mucosa for aerial gas exchange (Ishimatsu 2012, 2017), as in some of the mode 1a fishes.

Mode 4b reproduction is rare, known for only one species of Synbranchidae. Combining aspects of both burrow and bubble nesting, a male *Monopterus albus* (as *M. javanensis*) deposits bubbles in his U-shaped burrow to which fertilized eggs were attached (Wu and Liu 1942). These authors stated that the eggs are probably laid in the immediate vicinity of the breeding burrow and the male fish subsequently carries them in his mouth to the bubbles in the interior of the burrow. Matsumoto and Iwata (1997) observed egg incubation of *M. albus* in an aquarium, and confirmed that a male repeatedly added bubbles into an artificial plastic nest through his mouth, and the demersal eggs were then embedded in the bubbles of the nest. After hatching, the male starts mouth brooding the larvae. There may be other fishes that use this method, but bubbles were not observed in reproductive burrows of congener *M. cuchia* (Banerji et al. 1981) or related species *Synbranchus lamprea* (Favorito et al. 2005). Aerial respiration occurs through the richly vascularized inner mucosae of the buccopharyngeal cavity and the anterior esophagus in *M. albus* (Iversen et al. 2013) and *S. marmoratus* (Eduardo et al. 1979).

Basal bony fishes

As we have seen, air-breathing fishes do not necessarily incubate eggs in air. Most of the so-called primitive or basal groups of fishes are air-breathing, living in hypoxic waters and remaining aquatic during active life. Our extensive literature survey indicates that none of these fishes spawn at air–water interface, although little is known and some descriptions are unclear.

Among the three genera of lungfishes, *Protopterus* and *Lepidosiren* (Lepidosireniformes) spawn in severely hypoxic, heavily vegetated waters of the tropics, whereas the spawning waters of *Neoceratodus* (Ceratodontiformes) are better oxygenated.

Neoceratodus forsteri does not build a nest, but lays eggs attaching to submerged macrophytes or underwater roots of water hyacinth or terrestrial trees in shallow water of rivers and lakes (Kemp 1984, 1986). No parental care of the eggs has been reported.

In contrast, *Protopterus* builds a breeding nest in stagnant swamps. The nest of *P. aethiopicus* was formed within the densely matted roots of the papyrus or in soil sediment, and the opening may be exposed to air (Greenwood 1958). The eggs rest on the bottom of the chamber (Johnels and Svensson 1954). In the single burrow of *P. aethiopicus* that was analyzed, burrow water was severely hypoxic (Greenwood 1958).

Lepidosiren paradoxa also builds a breeding nest. Carter and Beadle (1930) described eggs contained in a mass of weed and plant debris at the end of a horizontal burrow located in mud at the bottom of the swamp. Dissolved oxygen level of the nest water was not determined, but the water at the bottom of the swamp was reported to be anoxic (Carter and Beadle 1930). None of these early papers examined how the eggs of *Protopterus* and *Lepidosiren* could develop in such extremely low oxygen conditions.

To the best of the authors' knowledge, no definite observations have been published for oviposition or fertilization of any species of Polypteriformes in the wild. Budgett (1901) stated that the eggs were deposited in the shallow lagoons along the main river in the rainy season and that the eggs adhere to submerged twigs or water plants. The male guards the nest and may thrash his tail to agitate the water, presumably aerating the eggs. Nothing is known about reproductive behavior of *Erpetoichthys calabaricus* in the wild, but Britz and Bartsch (1998) reported that in captivity the eggs of the fish were released onto the aquatic vegetation with no exposure to air.

Species of Amiiformes (*Amia calva*) or Lepidosteiformes (*Lepisosteus* and *Atractosteus* spp.) do not build a breeding nest but spawn demersal, adhesive eggs onto benthic stones, woody debris, and other objects lying on the bottom, or onto aquatic vegetation (Dean 1896, 1899; Frenette and Snow 2016).

Among Osteoglossiformes, breeding behavior for the four families, Osteoglossidae, Notopteridae, Mormyridae, and Gymnarchidae, has been studied. Both *Arapaima gigas* and *Heterotis niloticus* (Osteoglossidae) form nests in shallow, plant-rich areas (Budgett 1901; Castello 2008), but neither of them appears to use air to supply oxygen to the embryos. *Chitala chitala* (Notopteridae) in the wild lay demersal eggs that will not be exposed to air (Singh et al. 1980). The eggs of *Hyperopisus bebe* (Mormyridae) are laid in the shallow depression of the swamp bottom, and attached to the rootlets of the grasses accumulated by the parent (Budgett 1901). Finally, Budgett (1901) described a nest of *Gymnarchus niloticus* (Gymnarchidae) in the swamp, without details on the position of the eggs, although Odo et al. (2013) stated that *G. niloticus* deposited eggs on submerged grasses in their experimental ponds.

Reproduction at the air–water interface, air-breathing capacity, and parental care

Table 5 shows reproductive mode at the air–water interface by family, along with parental behavior. Air-breathing is significantly but weakly correlated with Mode 1 reproduction (Spearman's Rank correlation coefficient $r=0.56$, $P=0.001$, $N=49$ species). Mode 2 reproduction is strongly correlated with air-breathing ($r=0.99$, $P<0.0001$, $N=38$ species). In Mode 3, no adults breathe air, and in mode 4, all are known to breathe air. Parental care at the air–water interface is strongly correlated with air-breathing ($r=0.93$, $P<0.0001$, $N=102$ species). Among species that guard nests at the air–water interface, 63 of 66 species breathe air.

Discussion

The use of air by fishes has long attracted biologists, but the focus has usually been on adults. This is not surprising because the variety of morphological, physiological, and biochemical adaptations to air in adults of these fishes is amazingly elaborate, as if we are seeing experimental exploitation of air. The use of air by fishes also has important implications for survival of embryos. What impresses us is the rich

repertoire of the behaviors that parents exhibit to ensure embryonic survival. Behavior is more labile than morphology or physiology; animals can change their reproductive behavior as long as the egg-encased embryos can tolerate the new conditions.

Oviposition, the choice of a specific habitat or substrate for embryos, is a form of parental care (Coleman 1999). No fish species that broadcasts its eggs is known to have parental care, so egg hiding or spawning on a specific substrate may be all the care that ovipositioning parents provide. Egg-encased embryos are more resilient than aquatic larvae (Frank and Leggett 1981; Bradford and Seymour 1985). Gametes can be broadcast in water but often are spawned close together on land (Strathmann 1990), perhaps to minimize desiccation risk. Unlike larger amphibian eggs, fish eggs generally are not embedded in a protective gel matrix, and this may further constrain fishes from placing their eggs in air–water interface because of the desiccation risk. In the marine intertidal zone, fishes may place their eggs beneath boulders or beach sand, in mussel shells, or under construction rubble. Intertidally, hiding eggs under vegetation or well-drained substrates may provide cooling shade and protect against UV damage or over-heating (Blaustein et al. 1997; Rice 2006) as well as slowing evaporation.

Reproductive mode 1, spawning at the water's edge, may have evolved both as an adaptation to avoid aquatic predation and increase access to oxygen for the eggs. About half of these species breathe air, and placing eggs at the air–water interface in Mode 1 is significantly but weakly correlated with air-breathing. Nest guarding by parents is variable in Mode 1, present in fewer than half of these species (Table 5). Only two species that do not breathe air guard nests at the air–water interface.

Mode 2, placing eggs on the water's surface in vegetation or bubble nests, avoids hypoxia, and parental guarding reduces predation risk. All Mode 2 species show nest guarding by parents and almost all breathe air (Table 4).

Reproductive mode of annual fishes (Mode 3) requires eggs resistant to harsh environmental conditions such as desiccation and hypoxia, allowing species to survive when all other life stages perish. Adults do not survive to guard nests, and do not breathe air (Table 4).

Reproductive Mode 4, using burrows with an air phase or bubbles to hide clutches, combines protection from both hypoxia and predators. All Mode 4 species breathe air and guard the nests (Table 5).

Table 5 Reproductive Mode at the air–water interface by family for 18 orders and 32 families in class Osteichthyes, subclass Actinopterygii, infraclass Neopterygii (classification by Nelson et al. 2016)

Order	Family	A-b adult	A-b no. spp.	AWI mode	AWI no. species	Guard yes	Guard no
Clupeiformes	Clupeidae	No	0	1a	1		1
Characiformes	Characidae	No	0	1d	2	1	1
	Hepsetidae	No	0	2a	1	1	
Siluriformes	Callichthyidae	Yes	30	2b	4	4	
Gymnotiformes	Electrophoridae	Yes	1	2b	1	1	
Galaxiiformes	Galaxiidae	Yes	10	1a	2		2
Osmeriformes	Osmeridae	No	0	1a	4		4
Batrachoidiformes	Batrachoididae	Yes	1	1a	1	1	
Gobiiformes	Gobiidae	Yes	28+	4a	3	3	
Blenniiformes	Blenniidae	Yes	74+	1a	5	5	
	Labrisomidae	Yes	2	1c	1	1	
	Tripterygiidae	Yes	1	1a	1		1
Gobiesociformes	Gobiesocidae	Yes	7	1a	4	4	
Atheriniformes	Atherinopsidae	No	0	1a	2		2
	Atherinopsidae	No	0	1b	2		2
Cyprinodontiformes	Aplocheilidae	No	0	3	3		3
	Fundulidae	Yes	4	1a	8		8
	Nothobranchiidae	No	0	3	2		2
	Rivulidae	Yes	5	1c	1		1
Synbranchiformes	Synbranchidae	Yes	14	4b	1	1	
Anabantiformes	Anabantidae	Yes	24	2b	5	5	
	Osphronemidae	Yes	44	2b	26	26	
	Channidae	Yes	14+	2a	2	2	
Pleuronectiformes	Pleuronectidae	No	0	1a	1		1
Trachiniformes	Trichodontidae	No	0	1a	1		1
	Ammodytidae	No	0	1a	1		1
Scorpaeniformes	Cottidae	Yes	5	1a	8	4	4
	Pholididae	Yes	5	1a	2	2	
	Stichaeidae	Yes	5	1a	4	4	
	Zoarcidae	No	0	1a	1	1	
	Gasterosteidae	No	0	1a	1		1
Tetraodontiformes	Tetraodontidae	No	0	1a	1		1
			274+		102	66	36

Notes: Mode 1 is the most diverse both phylogenetically and behaviorally. In Mode 2, most species breathe air and all guard nests. In Mode 3, no species breathes air nor do they guard nests. In Mode 4, all known species breathe air and all guard nests. Species in 18 of 32 families breathe air. A-b indicates some species have air-breathing adults. AWI indicates reproduction at the air–water interface.

Factors driving reproduction at air–water interface

Oxygen

Aquatic hypoxia characterizes spawning sites of many fishes that reproduce at the air–water interface, just as in habitats of air-breathing fishes (Taylor and DiMichele 1983; Dehadrai and Tripathi 1976; Cochran and Burnett 1996; Martin and Ishimatsu 2017).

Taylor and DiMichele (1983) demonstrated that Mode 1a eggs of *F. heteroclitus* failed to develop in subtidal and mid-intertidal levels of a salt marsh. Experimentally excluding siltation from the cause of embryonic death, they concluded that severe hypoxia at low tide was responsible for the observed mortality. Embryos placed at the usual, higher tide levels showed 100% hatching. The subterranean environment for embryos of annual fishes (Mode 3) is

severely hypoxic or anoxic during both the rainy and dry seasons due to physicochemical characteristics of the soils (Podrabsky et al. 2016). Fishes using Mode 3 have several periods of embryonic diapause with metabolic and developmental arrest. For Mode 4a, Etou et al. (2007) found 100% mortality in embryos of the mudskipper *P. modestus* within 1 h in water at 10% oxygen saturation, although the level of dissolved oxygen was even lower in burrow water in their natural habitats (Ishimatsu et al. 2007).

Salinity

Fish reproduction at the air–water interface occurs in fresh water, estuaries, and seawater. The fishes with reproductive Mode 1, the most diverse category with respect to the number of families and species, are mostly marine, with roughly 30% of them migrating into brackish or even freshwater (Table 2). It is somewhat difficult to conceive why salinity might provoke a shift in reproduction from water to an air–water interface.

Predation

Tidal fluctuation may provide a refuge for embryos in the upper intertidal zone, which aquatic predators cannot reach, although such placement exposes adults and embryos to terrestrial predation (Middaugh 1981; Martin and Raim 2014). Very few studies have examined impact of aquatic or terrestrial predation on the survival of terrestrial fish eggs or spawning adults (Martin 2015). Tewksbury and Conover (1987) found that embryonic survival of *M. menidia* was higher when placed in the high intertidal zone, the natural spawning height, than in the subtidal zones in field experiments. Further, the observed difference in embryonic survival was negated by caging embryos, leading to the conclusion that the main cause of embryonic mortality was predation. On the other hand, survival of terrestrial eggs of *Galaxias maculatus* was not different after 28 days between exclusions and non-exclusions in the natural spawning water's edge, although mice and slugs were confirmed to feed on eggs (Hickford et al. 2010).



Cannibalism of eggs may occur after spawning. The California grunion *L. tenuis* buries its eggs in sand on shore, but if some eggs wash out in waves, conspecific adults consume them (Cavanagh et al. 2014). The eggs of *T. niphobles*, the grass puffer, are toxic to all predators except conspecifics. Males feed on eggs they encounter during spawning event (Uno 1955). This species spawns high in the intertidal zone, even though embryonic survival improves lower in the intertidal

zone (Yamahira 1996), suggesting that potential loss from cannibalism may be greater than the actual loss due to desiccation or physical stress.

Early development in fishes at the air–water interface

Egg type and size

Fishes that select a particular location or habitat type for the clutch generally produce demersal eggs that sink, in contrast to fishes that spawn in the water column and release floating pelagic eggs (Pauly and Pullin 1988; Shine 1989; Martin 2015). Demersal eggs may be larger because of greater yolk provisioning, and clutches may hold fewer eggs than pelagic spawners. Species with demersal eggs are found in all four modes at the air–water interface. If eggs are adherent, attachment to aquatic vegetation or other substrates may prevent burial and exploit local water currents during periods of submergence. In air, egg size can be larger because diffusion of oxygen is more rapid, and boundary layers around embryos are thinner (Strathmann and Hess 1999).

Buoyant eggs are seen in Mode 2l  eggs floating in vegetation and in some bubble nests (Mode 2a  but not the Mode 4b nests with bubbles in burrows. Rather than floating free in the water, these eggs are carefully captured and placed in a matrix of bubbles either on the water surface or in a burrow, then guarded by parents.

Some of the largest anamniotic eggs are laid by the amphibians with terrestrial foam nests (Shine 1989). The eggs of amphibians laid in air tend to be larger than those deposited in water (Wells 2007). The larger amphibian eggs also may develop longer than aquatic eggs before hatching, to a more advanced state or even to tiny froglets, avoiding the aquatic larval stage altogether (Crump 2015).

The largest teleost eggs known are incubated in the rocky intertidal zone by the zoarcid *Austrocyclus depressiceps* (Mode 1a, Matallanas et al. 1990). Of course some sharks and rays produce even larger eggs that are fully aquatic. Egg pouches for elasmobranchs tend to hold only one or two eggs, maximizing the surface area available to the developing embryo for oxygen, but with a far lower reproductive output than teleosts. Larger terrestrial anamniotic eggs may allow plasticity in hatching time and incubation duration when the return of aquatic conditions is unpredictable (Moravek and Martin 2011).

There is no evidence for internal fertilization, ovoviviparity, or viviparity among those fishes, although these are seen in other species of fishes and some

terrestrially breeding amphibians (Haddad and Prado 2005). *Artedius* species with reproduction Mode 1 copulate, but actual fertilization of the eggs occurs after oviposition (Petersen et al. 2005).

Larval type

No fish that spawn at the air–water interface are known to have larvae that rely on maternal provisioning and do not feed, direct developing juveniles, or terrestrial larvae (although eggs of *M. villosus* sometimes hatch terrestrially, Frank and Leggett 1981). Even the larvae of the most terrestrial fishes, the mudskipper *P. modestus*, show no morphological or behavioral modification from other aquatic goby larvae and live as plankton for 40–45 days before starting to invade land (Kobayashi et al. 1972). Larvae of the highly amphibious blennies *Alticus monochrus* and *A. tetradactylus* have not been described, but larvae of all blennid species studied to date are planktonic (Watson 2009).

Variation and plasticity of the reproductive mode

The reproductive behaviors we have categorized into these modes are by no means fixed for each corresponding fish group but may vary between species of a given taxon and populations within a species. For example, Rüber et al. (2006) provided information on the spawning behavior of 57 species of labyrinth fishes. Bubble-nest building, Mode 2b, occurs in 31 species, of which 28 show male parental care, one shows biparental care, and the remaining two have not been studied for parental care (Table 5). Other reproductive modes seen in labyrinth fishes include mouth-brooding in 12 species, of which 10 show male parental care. Aquatic substrate nesting and attachment of clutches to plants on a substrate are known in one species each, with male parental care of the eggs. Another nine species spawn free buoyant eggs and show no parental care, and the reproductive habit is unknown for the remaining four species. Free spawning and the release of buoyant eggs are thought to be the plesiomorphic anabantid reproductive style (Cambrey 1997).

Assuming that bubble-nest building is an adaptation for reproduction in hypoxic waters, one might expect that those species with reproductive Mode 2b have higher dependency on air breathing (and better developed labyrinth organs) than in other labyrinth fishes. Comparative morphometric data of the accessory respiratory organs are scarce for anabantid species. Unfortunately, the relative importance of aerial and aquatic oxygen uptake has been examined for

only limited number of anabantid fishes (Graham 1997), with no obvious trend between the proportion of oxygen uptake from air and reproductive behaviors. However, this may be deceiving because oxygen uptake from air varies with both biotic and abiotic factors, and above all it has been almost always determined using adults. It is probably more important to examine the relationship between the micro-environment of embryos (particularly dissolved oxygen concentration) during development, and reproductive modes that parent fish employ. Many anabantid fishes have spawning peaks at the start or during the rainy season (Munro 1990) when plenty of water fills rivers, ponds, and swamps, which should increase the availability of oxygen in water. There are, however, anabantid species that are reported to breed in the hot dry season, such as *B. splendens*, *Trichopsis schalleri*, and *T. vittata*. Reproductive seasonality may have strong influence on the evolution of particular reproductive modes because of oxygen availability at the time of spawning.

Although less diverse, snakeheads show two types of spawning behaviors similar to labyrinth fishes: mouth brooding in *Channa gachua* and *C. orientalis*, and Mode 2a for the rest of the genus (Courtenay and Williams 2004). These species prefer clear pools, shallow streams (*C. gachua*), or clean freshwater pools (*C. orientalis*), presumably less hypoxic than the stagnant water habitats of other snakeheads though they may also occur in swamps and other more hypoxic water (Courtenay and Williams 2004). *Channa gachua* is a facultative air-breather, able to extract sufficient amounts of oxygen from well-aerated water, in contrast to most other *Channa* species that are obligate air-breathers (Ishimatsu and Itazawa 1983; Olson et al. 1994).

Intraspecific variation in spawning behavior has been documented for several fishes spawning at the air–water interface. Capelin, *M. villosus*, spawn not only intertidally but also subtidally to the depth of 280 m. These populations spawning in each habitat seem not to be genetically differentiated, but environmental conditions, particularly temperature and substrate size, presumably have strongly influence on the choice of spawning site by this fish (Nakashima and Wheeler 2002; Davoren 2013).

In other examples, threespine stickleback *Gasterosteus aculeatus* typically spawn subtidally in an elaborately built nest and show paternal care, but a subgroup within a population of white threespine stickleback in Nova Scotia lay eggs intertidally and show no parental care (MacDonald et al. 1995; McKinnon and Rundle 2002). A population of rock sole *Lepidopsetta bilineata* in Puget Sound,

Washington, spawns eggs intertidally that are exposed to air during low tide, whereas other members of the same species breed subtidally (Penttila 1995). *Enophrys bison* was reported to spawn intertidally in Puget Sound by DeMartini (1978), but subtidally in the Vancouver region, approximately 150 km north (Kent et al. 2011). These differences suggest spawning behavior is plastic and may change readily within populations without concomitant genetic divergence.

Gene expression differs in eggs when they are out of water rather than submerged (Tingaud-Sequeira et al. 2009). Eggs of many of these species may adjust to their current habitat with changes in transcripts during emersion and submergence (Thompson et al. 2017). Research in this fertile area has just begun; future studies are likely to find multiple adaptations for terrestrial incubation the embryos and egg envelopes.

Basal bony fishes

It is noteworthy that none of the basal bony fishes reproduce terrestrially, despite that most of them have the capacity of breathing air and that these non-teleosts have much longer history of evolution than teleosts. These fishes live in very hypoxic environments of tropical freshwater bodies. Early investigators revealed nearly anoxic conditions in the nests of African lungfishes, but they reported that the eggs were laid on the bottom of the nests. Effectiveness of nest water splashing by the African lungfish (Budgett 1901) or of the vascular filaments on the pelvic fin in South American lungfish (Urist 1973) have been suggested for augmenting oxygen supply to developing embryos, but Lima et al. (2017) refuted the claim for *L. paradoxa*. Many of these investigations were conducted decades ago or earlier, and even though they are surprisingly detailed, it is probably necessary to re-investigate reproductive ecology of the primitive fishes using modern techniques. Reproductive seasonality may be important for these species.

Summary

Over 100 species of Actinopterygian fishes in 32 families and 18 orders have evolved diverse methods for placing developing eggs at the interface between air and water. Oviposition may require the preparation of a nest site or burrow, or may exploit natural substrates such as rocks or shells or sand. Embryos at the air–water interface do not necessarily breathe air as adults, while conversely many fishes known to breathe air as adults are fully aquatic in their early lives. Parental care for species that spawn at the air–water interface is highly correlated with air-breathing

adult fishes. The physiology, ecology, and behavior described in these four reproductive modes differ and undoubtedly are present in additional species in alternative forms, providing many rich opportunities for future studies.

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