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## FRESHWATER TO SEAWATER TRANSITIONS IN MIGRATORY FISHES

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The transition from freshwater to seawater is integral to the life history of many fishes. Diverse migratory fishes express anadromous, catadromous, and amphidromous life histories, while others make incomplete transits between freshwater and seawater. The physiological mechanisms of osmoregulation are widely conserved among phylogenetically diverse species. Diadromous fishes moving between freshwater and seawater develop osmoregulatory mechanisms for different environmental salinities. Freshwater to seawater transition involves hormonally mediated changes in gill ionocytes and the transport proteins associated with hypoosmoregulation, increased seawater ingestion and water absorption in the intestine,

and reduced urinary water losses. Fishes attain salinity tolerance through early development, gradual acclimation, or environmentally or developmentally cued adaptations. This chapter describes adaptations in diverse taxa and the effects of salinity on growth. Identifying common strategies in diadromous fishes moving between freshwater and seawater will reveal the ecological and physiological basis for maintaining homeostasis in different salinities, and inform efforts to conserve and manage migratory euryhaline fishes.

## 1. INTRODUCTION

The understanding of euryhalinity in migratory fishes has been investigated over the past century in numerous studies, but the focus has mainly been on salmonid fishes (see [McCormick, 2013](#), Chapter 5, this volume). In recent decades, however, more research has centered on other families including the lampreys, sturgeons, anguillid eels, herrings, and tilapias. Functional approaches to defining life history patterns (e.g. [Elliott and Dewailly, 1995](#); [Elliott et al., 2007](#); [Franco et al., 2008](#)) have effectively defined estuarine guilds based on use patterns to inform estuarine ecology. Estuaries provide critical habitat for many migratory species ([McLusky and Elliott, 2004](#); [Rountree and Able, 2007](#)) and are relied upon for rearing, feeding, spawning, or simply serving as a corridor of migration ([Elliott and Hemingway, 2002](#)). This chapter will focus on the transition from freshwater (FW) to seawater (SW), which is an integral part of the life history of many migratory fishes. For most migratory fishes, such a transition generally punctuates longer residence times at more stable salinities.

Migrants between FW and SW are collectively termed “diadromous” and geographic patterns of diadromy have been well described ([McDowall, 1987](#)). General trends in occurrence are linked to productivity differences between FW and SW habitats ([Gross, 1987](#); see also [Shrimpton, 2013](#), Chapter 7, this volume). The success or failure of these migrants is largely dependent upon the timing of migration in the context of biotic and abiotic environments ([McCormick et al., 1998](#); [Limburg, 2001](#)), size at migration ([Saloniemi et al., 2004](#)), and physiological preparation for changing environment (e.g. [Zydlewski et al., 2003](#)). While the estuary serves as a migratory corridor between the ocean and inland waters ([Lobry et al., 2003](#)), it can also serve as an important staging area for physiological acclimation (e.g. [McCormick and Saunders, 1987](#)), growth opportunity, and predator avoidance ([Klemetsen et al., 2003](#); [Lepage et al., 2005](#)).

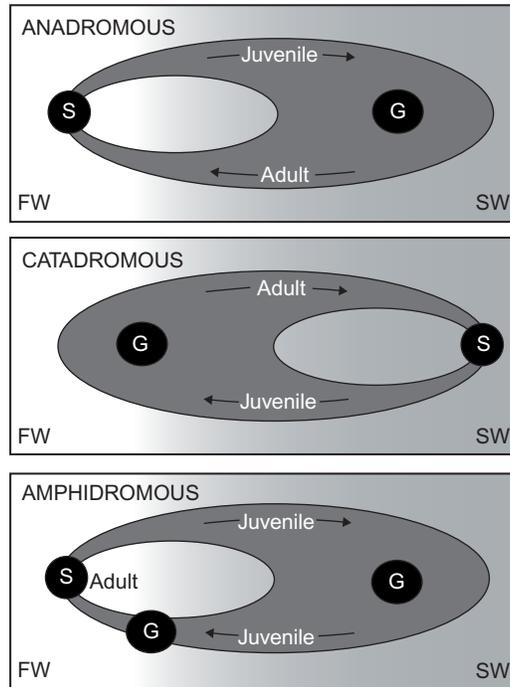
The idealized descriptions of anadromy, catadromy, and amphidromy remain useful and defining archetypes for most euryhaline migrations. These terms have considerable history (Myers, 1949; McDowall, 1987, 1988, 2007) and are widely applied (although the use of the term “amphidromy” continues to evolve). While they are useful heuristic constructs, there is a growing appreciation for the complexity of life histories. Many species exhibit divergent behaviors within a population – or an individual. These divergent movements can be, and have been argued to be, trophic movements rather than “true migrations” (Myers, 1949; Dingle, 1996) but some of the distinctions are difficult to determine empirically. The overview that follows is not intended to be exhaustive, or to define terms (as such contributions have been prominently noted). Rather, what follows is a sampling of the diversity of migratory patterns, with some consideration of those patterns that do not fit neatly into the three general patterns of diadromy. The physiological mechanistic and behavioral patterns that allow these fish to exploit the estuarine environment as part of their life history as they move from FW to SW are also discussed.

## 2. LIFE HISTORY PATTERNS

### 2.1. Anadromy

Anadromous fishes spawn in FW and the young (usually) remain in this dilute environment for some period before making a directed seaward migration. As adults, these fish return to FW to reproduce (Fig. 6.1). The period in SW is generally associated with accelerated growth opportunities and, as a result, greater fecundity. This group is exemplified by salmonines (McDowall, 1988; McCormick, 1994) but it is a conspicuous strategy across many species. Although phylogenetically distant, sea lampreys (*Petromyzon marinus*) have a distinct FW phase (ammocoete) that typically lasts for 3–7 years followed by a parasitic phase at sea, which is characterized by rapid growth as they ingest large quantities of blood from (mainly) fish (Hardisty and Potter, 1971; Beamish and Potter, 1975). Juvenile downstream migration is linked to a metamorphosis as the eyeless, suspension feeding, sediment-dwelling ammocoete transforms into a silvered, metamorph with distinct eyes and an adult-like oral disc (Youson and Potter, 1979). Seaward migration is bimodal, occurring in spring and fall (autumn), associated with flow events (Beamish and Potter, 1975; McCormick et al., 1997).

Some sturgeon species have well-defined anadromous migrations, while others make multiple movements into the estuary habitat through their life



**Fig. 6.1.** Idealized patterns of diadromous migration. Life histories proceed in a clockwise fashion. Width of dark gray band represents variation in the salinity to which a given life stage may be exposed. Shading on right side of panels indicates increased salinity. G: periods of growth; S: spawning.

history (Doroshov, 1985). Atlantic sturgeons (*Acipenser oxyrinchus*) migrate from the ocean into riverine habitat to spawn, and juvenile anadromous sturgeons gradually enter SW within several years (Rochard et al., 2001; Wilson and McKinley, 2004). Green sturgeons (*Acipenser medirostris*) enter SW earlier than other sturgeon species, within 1–3 years (Allen and Cech, 2007). Their eggs are relatively large and juveniles grow rapidly (Deng et al., 2002); these may be adaptations for early entry into the estuary.

Anadromous clupeids such as the American shad (*Alosa sapidissima*) undergo migrations from coastal rivers of North America (Leggett and Carscadden, 1978). Adults enter FW when river temperatures are between 14 and 20°C (Leggett and Whitney, 1972). Spawning occurs in open water beyond tidal influence, and the young generally remain in FW until autumn.

The downstream migration of juvenile American shad is linked to declining river temperatures (O'Leary and Kynard, 1986). The use of otolith microchemistry has greatly informed the complexity of life history diversity within this and other alosine species to demonstrate varied use of the estuary by juveniles (Limburg, 1998).

Moronids demonstrate great flexibility in their anadromous life history. For striped bass (*Morone saxatilis*), there are fully FW populations at the northern and southern extents of their range (Rulifson and Dadswell, 1995; Haeseker et al., 1996; Carmichael et al., 1998), although anadromous spawning migrations that ensure early development occurs in low salinities are the norm (Gemperline et al., 2002; Wingate and Secor, 2008). Similarly, white perch (*Morone americana*) have considerable diversity in migratory patterns linked to the estuary (Hanks and Secor, 2011). These fish spawn in FW before returning to the estuary where they reside through the winter (Setzler-Hamilton, 1991; Kerr and Secor, 2009). Larvae are associated with the low-salinity zone of the estuarine turbidity maximum and young-of-the-year juveniles are subsequently found rearing in both FW and SW (North and Houde, 2001). Members of the same population can be either resident or migratory (Kerr et al., 2009), diverging in behavior only after transitioning into the juvenile stage (Kraus and Secor, 2004).

## 2.2. Catadromy

Catadromous fishes spawn in SW and move into FW for a period of growth (Fig. 6.1). While catadromy is more commonly associated with tropical latitudes, American (*Anguilla rostrata*), European (*A. anguilla*), and Japanese eels (*A. japonica*) exemplify the temperate pattern of catadromy (Lecomte-Finiger, 1983; Sorensen, 1984). These fish are spawned in tropical ocean waters and leptocephalus larvae are carried passively towards coastal areas (Beumer and Harrington, 1980; Tsukamoto et al., 2003) before invading the estuary as “glass eels”. These juveniles acquire pigmentation and migrate upstream to varying extents as “yellow eels”. This growth phase can be as long as 20 years before seaward migration as an adult “silver eel” (Hourdry, 1995).

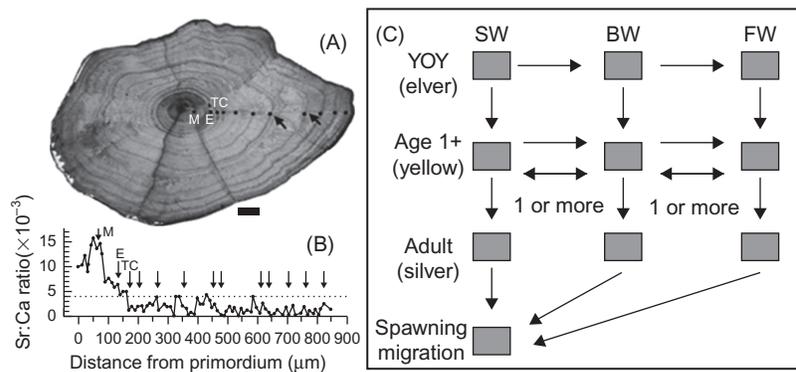
Although conventional wisdom has assumed that the majority of eel juveniles pass through the estuary (Tesch, 1977; Feunteun et al., 2003; Fontaine et al., 1995), recent work demonstrates that many eels rear in elevated salinities (Morrison and Secour, 2003; Arai et al., 2006; Thibault et al., 2007; Jessop et al., 2008), making them facultative in their catadromy. Facultative FW entry is related to energy status (Edeline, 2007; Bureau du

Columbier et al., 2011), where slower growing eels migrate farther upstream into FW, perhaps to avoid competition with conspecifics. These FW migrants may comprise a large proportion of migrating adults (12–25%) (Jessop et al., 2004; Morrison and Secour, 2003). Juveniles that rear in the estuary for an extended period before recruiting into FW may also move back and forth from FW to the estuary as subadults (Jessop et al., 2002, 2006, 2008). Recent work using telemetry and Sr:Ca ratios (Daverat et al., 2006; Thibeault et al., 2007; Arai et al., 2009; Shrimpton, 2013, Chapter 7, this volume) has provided convincing evidence for this variation (Fig. 6.2).

Although less well characterized, non-anguillid fishes also express catadromous life histories. Mulletts (Mugilidae) (Anderson, 1957; Nordlie, 2000; Cardona, 2006) and a few species of the Galaxiidae (Pollard, 1971) are considered catadromous. Some species of tropical and subtropical gobies and some sculpins may also be considered catadromous (McDowall, 2007), although they have also been classified as amphidromous.

### 2.3. Amphidromy

The use and application of “amphidromy” has been less precise than either “anadromy” or “catadromy”. For anadromous and catadromous migrations, patterns are tightly linked with reproduction (Klemetsen et al.,



**Fig. 6.2.** Facultative catadromy in American eel. Using electron microprobe analysis of otoliths (A) Sr:Ca ratios along transects can be measured (B) to retrospectively infer movements between freshwater (FW) (low ratio) and seawater (SW) (high ratio). Arrows indicate onset of metamorphosis (M), elver phase (E), and habitat transition (TC). Based on such inferred histories (C) facultatively catadromous eels may employ a variety of contingent behaviors which exploit FW and estuarine habitats to different extents. BW: brackish water. Reproduced with permission from Jessop et al. (2008).

2003; Quinn and Myers, 2004). In contrast, amphidromy has been characterized by trophic movements between FW and SW such that there is a growth phase in each biome. “Freshwater” and “seawater” amphidromous patterns have been described (Myers, 1949; McDowall, 1987, 1988, 1992) and attributed to species such as shortnose sturgeon (*Acipenser brevirostrum*) (Bain, 1997; Bemis and Kynard, 1997) and tarpon (*Megalops* sp.) (Myers, 1949) based on early use of the term. As terminology has been sharpened, however, these species fit the definition more poorly. Here, the more precise definition of McDowall (2007) with specific criteria is employed. Amphidromous fishes migrate seaward as larvae, experience a brief growth phase in SW (or brackish water, BW), and return to FW as small juveniles (usually less than 50 mm). This definition restricts the term to what has previously been defined as “FW amphidromy” (the use of “FW” and “SW” amphidromy, as in McDowall, 1988, 1992, has been dropped). There is a clear distinction between amphidromy and other diadromous fishes. In general anadromous and catadromous fishes reduce or cease feeding altogether upon entry of the habitat in which they will spawn (McDowall, 2004), whereas amphidromous species have an extended secondary growth phase in FW which is followed by spawning (Keith, 2003) (Fig. 6.1).

The majority of amphidromous fishes are found in the southern hemisphere in the intertropical area. Particularly in island habitats, amphidromy can be the dominant life history form (McDowall, 1999), as exemplified by galaxiids (e.g. genus *Galaxias*). Spawning of amphidromous galaxiids takes place in FW, followed by the larval growth phase in SW (Waters et al., 2001) and then the return to rivers for the extended growth period (McDowall, 1990). Although this is the general pattern, larvae may be retained in the BW of the estuary before returning into FW river systems (David et al., 2004). Similarly, the red-tailed goby (indigenous to islands of the Indian Ocean and Pacific Ocean) spawns in FW followed by a short pelagic growth period in the ocean (Keith and Marquet, 2002; Keith, 2003). Amphidromous Sicydiine gobies enter into SW environment hours after hatching, whereupon they enter a growth phase lasting 3–6 months (Keith et al., 2008; Lord et al., 2010).

Migration back to FW habitats is generally associated with a striking metamorphosis (Nishimoto, 1996; Nishimoto and Kuamo’o, 1997; Balon, 1990; Schoenfuss et al., 1997) that includes changes in skull morphology including a shift from a subterminal to terminal mouth. Many gobies develop fused pelvic fins during the period of FW entry, allowing them to hang onto rocks and invade upstream habitat above waterfalls (Fitzsimons et al., 2002; Taillebois et al., 2011). *Lentipes concolor*, found in the Hawaiian Islands, is known to make impressive inland movements up waterfalls

greater than 600 m in height (Nishimoto and Fitzsimons, 1986; Englund and Filbert, 1997).

In bullies (*Gobiomorphus* spp.) and galaxiids, the completion of an amphidromous life history can be facultative (Hicks et al., 2010). Larvae may successfully develop in FW lakes even where ocean access is possible (Closs et al., 2003; David et al., 2004; Hicks, 2012). The degree to which this indicates plasticity within an individual rather than variability within a population is unclear. Amphidromous species seem to be marked by lower maternal investment than resident relatives. These fish have smaller eggs and a less developed state at hatching, presumably adaptations for passive downstream drift. Congeneric species that are completely fluvial in their life histories hatch as larger, precocious young that can hold position in stream flows. Such differences are observed among gobies of the genus *Rhinogobius* and Japanese FW sculpin of the genus *Cottus* (Goto, 1990; Goto and Andoh, 1990; Iguchi and Mizuno, 1999).

#### 2.4. Freshwater-Linked and Seawater-Linked Estuarine Movements

Rather than being linked to a distinct growth or reproductive phase, FW-linked estuarine migrants are generally opportunistic in their use of the estuary. These fish generally experience salinity transitions that are transient and usually low in salinity. Such patterns are best described as trophic movements rather than migrations between environments. There is great variation in osmotic tolerance among FW species. Ictalurid catfish and yellow perch (*Perca flavescens*) have extremely low tolerances to salinities above 1 ppt (Lutz, 1972; Furspan et al., 1984), yet other “stenohaline” FW species are commonly observed in estuaries (Lowe et al., 2009). Juvenile centrarchids are commonly found in the upper parts of estuaries (Hackney and de la Cruz, 1981; Rozas and Hackney, 1983; Rogers et al., 1984) and it is likely that the salinity gradient defines the extent of downstream abundance. Limits to survival in BW may be restricted by limited osmoregulatory capacity (Peterson, 1988; Meador and Kelso, 1990), by reduced growth (Meador and Kelso, 1990; Peterson, 1991), or by preventing successful spawning (Tebo and McCoy, 1964).

Local populations of FW-linked fishes may be adapted to tolerate increased or fluctuating salinity. Some largemouth bass (*Micropterus salmoides*) have developed greater tolerance to ion perturbation, rather than increasing osmoregulatory capacity in elevated salinities (Meador and Kelso, 1990; Lowe et al., 2009). Other centrarchids may likewise tolerate modest salinities typical of an upper estuary. Peterson (1988) demonstrated that red-ear sunfish (*Lepomis microlophus*) osmoregulated effectively up to

8 ppt. Local adaptation to salinity exposure has also been observed in western mosquitofish (*Gambusia affinis*) (Purcell et al., 2008).

While FW-linked movements are generally opportunistic, many SW species are dependent upon the estuary for the early part of their life history (Boesch and Turner, 1984; Kneib, 1997; Beck et al., 2001; Able, 2005). Because of the clear link of movement into the estuary to these fishes' life histories, such movements can be considered migrations. The importance of the estuary is often demonstrated by the strong link between estuarine conditions and SW recruitment (Elliott et al., 1990; Thiel and Potter, 2001). In general, these fish experience stable SW salinity for most of their life cycle, and exploit the near-shore or estuary habitat at the larval and juvenile stages. The facultative use of lower salinities confounds the use of diadromous definitions. These SW fish lay pelagic eggs, often near the coast or in the lower estuary, and parental investment is defined by selection of spawning site (Wootton, 1999; Elliott and Hemingway, 2002; DeMartini and Sikkel, 2006; Elliott et al., 2007).

Many benthic-oriented SW fishes have distinct settling patterns [e.g. seaboard goby (*Gobiosoma ginsburgi*) (Duval and Able, 1998) and window-pane flounder (*Scophthalmus aquosus*) (Neuman and Able, 2002)], such that larvae develop and take up residence in estuaries or coastal habitats (Able et al., 2006). SW-linked halibut (*Paralichthys californicus*), summer flounder (*P. dentatus*), and turbot (*Pleuronichthys guttulatus* and *P. ritteri*) spawn near the coast and larvae metamorphose and settle as juveniles near or in the estuary and remain there through the early part of their life history (Moser, 1996; Gibson, 1997; Love, 1996; Sackett et al., 2007, 2008; Herzka et al., 2009). Juvenile flatfish (e.g. *Solea solea* and *Solea senegalensis*) select areas based largely on abiotic conditions such as structure, temperature, and salinity (Vinagre et al., 2007, 2009). Although variable, many juvenile flatfish are likely to experience only narrow salinity fluctuations at or near full-strength SW (Herzka et al., 2009; Fairchild et al., 2008).

Other SW-linked fishes have pelagic larvae (e.g. gilthead sea bream, *Sparus aurata*) which hatch in the ocean and are recruited into coastal waters. Juveniles migrate further into estuaries, where they experience a wide range of salinities, up to 60 ppt (Ben-Tuvia, 1979; Tandler et al., 1995). Distribution of these fish is strongly influenced by prey availability (Timmons, 1995) and recruited young of the year experience rapid growth (Rountree and Able, 1992; Szedlmayer et al., 1992). Pinfish (*Lagodon rhomboides*) (Sparadae) spawn in the ocean (Muncy, 1984) and larvae are recruited into the estuary (Warlen and Burke, 1990). Juveniles subsequently exploit benthic habitats for several months (King and Sheridan, 2008).

European anchovy (*Engraulis encrasicolus*) is a conspicuous example of a SW-linked species that facultatively exploits estuarine habitat (Suzuki et al.,

2008; Hibino et al., 2006). Some fish complete their life history in a saline environment, while others use low-salinity reaches of the estuary as a rearing habitat (Morais et al., 2010). For these fish, spawning occurs in the lower estuary and larvae develop and move into the upper reaches of the estuary before migrating downstream after this period of growth (Chicharo et al., 2001). Similarly, sea bass (*Lateolabrax japonicas*) spawn offshore and the young migrate inshore populating both estuaries and surf zones as juveniles (Fuji et al., 2010). Conspecifics can therefore have very different osmotic experiences.

Many SW-linked fishes can dominate the upper reaches of the estuary where salinity approaches FW, necessitating tolerance to low salinities in these fish (Weisberg et al., 1996; Whitfield, 1998; Maes et al., 2005; Hoeksema and Potter, 2006). Juveniles remain in estuarine environments over wide temporal and spatial periods. Winter flounder (*Pseudopleuronectes americanus*) remain in the estuary for 2 years before moving into the ocean (Pereira et al., 1999). Ladyfish (*Elops saurus*) are found over a wide range of salinities, although rarely in FW (McBride et al., 2001). Spotted grunter (*Pomadasys commersonnii*) spawn in the ocean and developing juveniles recruit into estuaries, where they remain for a period of 1–3 years (Wallace and Van der Elst, 1975; Heemstra and Heemstra, 2004) and display strong site fidelity (Childs et al., 2008).

## 2.5. Estuarine Fishes

Estuarine fishes reside in the zone of fluctuating salinity through all periods of their life history, but individuals within a given cohort may experience substantial variability in salinity. These fish often gravitate to BW for spawning and are considered in detail in Marshall (2013, Chapter 8, this volume). Estuarine species are exemplified by black sea bream (*Acanthopagrus butcheri*), which can be found in salinities from 0 to 60 ppt (Hoeksema et al., 2006; Hindell et al., 2008; Sakkabe and Lyle, 2010) and generally complete their life cycle within the upper and middle part of an estuary (Butcher and Ling, 1958; Hindell, 2007; Hindell et al., 2008). For this species, moderate salinities are required as poor recruitment is correlated with high FW delivery into the estuary (Sakabe, 2009). The mummichog (*Fundulus heteroclitus*) may best exemplify estuarine species. This fish completes its life history within salt marshes (Taylor et al., 1979) and undergoes limited movements (Lotrich, 1975; Teo and Able, 2003). These remarkable fish may undergo daily fluctuations in salinity, from near FW to full-strength SW as the tide ebbs (Griffith, 1974). Estuarine fishes are not considered further in this chapter but are discussed by Marshall (2013, Chapter 8, this volume).

### 3. MOVEMENT PATTERNS

#### 3.1. Control of Migration

The choice of “when and where” to spawn can have profound effects on the life history strategy assumed by the progeny. White perch spawn over a protracted period (North and Houde, 2001) and a greater proportion of resident (versus anadromous) fish occur in faster growing late-spawned cohorts (Kerr and Secor, 2010). Amphidromous ayu (*Plecoglossus altivelis*; Osmeriformes) move downstream in anticipation of spawning (Tsukamoto et al., 1987; Iguchi et al., 1998), which may be advantageous for young in that it reduces their seaward migratory distance. Similarly, *Galaxias maculatus* adults move downstream to spawn at the head of tide (McDowall, 2008). For amphidromous fishes, this does not appear to be a widespread pattern. Others, such as the Amur goby (*Rhinogobius brunneus*), show no indication of such prespawn movement patterns.

The internal condition of the organism influences its behavior during migration. Sea lamprey metamorphosis and subsequent survival during the prefeeding (parasitic phase), downstream migration is dependent upon the availability of sufficient lipid energy stores during these non-trophic periods (Lowe et al., 1973; Beamish et al., 1979; Youson, 1997). Similarly, the propensity for anguillid glass eels to migrate is dependent upon energy stores (Bureau du Colombier et al., 2007, 2009; Bolliet and Labonne, 2008). It has been hypothesized that the facultative diadromy observed in anguillids is linked to an individual’s response to its own metabolic status (Edeline, 2007). While downstream migration of juvenile American shad may be more concerted in the fall (O’Leary and Kynard, 1986; Zydlewski and McCormick, 1997a,b), retrospective otolith analysis reveals a more protracted migration that is influenced by size (Limburg and Ross, 1995; O’Donnell and Letcher, 2008). Similar variability and correlation with size have been reported for other clupeid species, e.g. allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*), in terms of both the timing of migration and extent of residence in the estuary (Taverny, 1991; Lochet et al., 2008).

Endogenous rhythms are ubiquitous and are the underpinning of activity patterns and migrations in all animal clades (Dingle, 1996, 2006). For salmonines, timing of the development of SW tolerance is species specific and cued by photoperiod and modified by other environmental factors (Boeuf, 1993; Hoar, 1988; McCormick, 1994). Diurnal cycles are linked to redistributions of fish within estuaries (Rountree and Able, 1993; Gray et al., 1998; Miller and Skilleter, 2006; Hagan and Able, 2008). Larval and juvenile green sturgeon exhibit a diel pattern of migration that peaks at night

(Kynard et al., 2005) and photoperiod has been suggested as the major driver of preparatory adaptation in this fish (Allen et al., 2011).

Many estuarine fishes exhibit a demonstrable pattern of activity linked to tidal stage, e.g. toadfish (*Halobatrachus didactylus*) (Campos et al., 2008), and with demonstrated circatidal rhythms such as those seen with juvenile plaice (*Pleuronectes platessa*) (Burrows, 2001) and the juvenile intertidal blenny (*Zoarces viviparus*) (Cummings and Morgan, 2001). Vertical migration of glass eels in response to tidal currents remains one of the most conspicuous examples of circatidal patterns (McCleave and Wippelhauser, 1987; Wippelhauser and McCleave, 1988). In the absence of a tidal *zeitgeber*, the pattern dampens (Bardonnet et al., 2003), even with photoperiod information (Dou and Tsukamoto, 2003).

Behavioral patterns established by endogenous rhythms are sculpted by other cues for migration. Eel movements occur preferentially under low-light or high-turbidity conditions, e.g. European eel (Bardonnet et al., 2005). Migration into the estuary is linked to spring tides and therefore moon phase (Jellyman, 1979; McKinnon and Gooley, 1998; Tsukamoto et al., 2003). Patterns of upper estuary use by flatfish juveniles (e.g. *Plecoglossus altivelis* and *Lateolabrax japonicus*) may be facultative and linked to the diurnal flood tides (Ohmi, 2002). Olfactory cues such as those resulting from decaying organic material (e.g. decomposition of plants/animals) may serve to attract coastal juvenile anguillids (Sorensen, 1986; Sola, 1995), indirectly indicating lower salinity (Sola and Tongiorgi, 1996).

Temperature is considered a driving factor in the timing of spawning and migrations (Livingston, 1976; Marshall and Elliott, 1998; Witting et al., 1999). The relative roles of other factors (e.g. salinity, dissolved oxygen, FW input) can be masked through covariance (Morin et al., 1992; Potter et al., 1986; Valiela, 1995; Fraser, 1997). Temperature, however, may limit the use of FW habitat and estuaries for many fishes (Attrill and Power, 2002, 2004). White perch and striped bass spawning is cued by the initial rise in temperature during spring (Rutherford and Houde, 1995; Secor and Houde, 1995). Temperature is thought to provide a threshold for the initiation of upstream migration in anguillid eels, e.g. shortfinned eel (*A. australis*) (Kearney et al., 2009) and European eel (Creutzberg, 1961; Tesch, 2003).

For American shad juveniles, temperature in FW may serve as a migratory cue through its influence on hyperosmoregulatory ability. Anadromous American shad are fully competent to enter into SW at larval juvenile transition, months before autumnal migration. As temperatures decline, these fish cease feeding and downstream migration is hastened (Backman and Ross, 1990; Zydlewski and McCormick, 1997b). Below 10°C shad juveniles rapidly decline in osmoregulatory ability (Chittenden, 1972; Zydlewski and McCormick, 1997b). Late SW entry at low temperatures also

comes with a physiological cost because it may impact survival (Zydlewski et al., 2003).

Downstream movements of young amphidromous fishes (e.g. gobiids and eleotrids) appear to be cued by seasonal and short-term changes in stream flow (Fitzsimons et al., 2002). Similarly, migration back into FW is also associated with rain events (Delacroix and Champeau, 1992). Flow may also clear the stream mouth, thus facilitating passage (Fitzsimons and Ogorman, 1996). Postlarvae congregate near the shore and initiate diurnal migrations, indicating a visual component of upstream searching (Miller, 1984; Fievet et al., 1999; Lim et al., 2002). Actively migrating amphidromous gobies select FW rather than SW and preferentially select stream-origin water over well water (Fitzsimons et al., 2002).

### 3.2. Passive and Active Movement in the Estuary

Migratory fishes can use estuary habitats for protracted periods, ranging from weeks to years (Able et al., 2005). For structure-oriented species such site fidelity can be strong (Able et al., 1995; Tupper and Boutilier, 1995), as seen in juvenile winter flounder (*Pseudopleuronectes americanus*) in which movements were limited to a 100 m zone for up to 3 weeks (Saucerman and Deegan, 1991). Similar observations were made in juvenile plaice (*Pleuronectes platessa*) over several weeks (Burrows et al., 2004). These fish also exhibited strong homing if displaced up to 3.5 km offshore (Riley, 1973). Resource ranging (Dingle, 1996) and site fidelity were observed in young of the year summer flounder (*Paralichthys dentatus*). These fish exhibited site fidelity, but made daily movements of up to 1 km (Szedlmayer and Able, 1993). Flounder move onto the mudflats with high tide to feed and return to deeper water at low tide (Wirjoatmodjo and Pitcher, 1984; Raffaelli et al., 1990).

The importance of shallow littoral zones for small fish is well established in estuarine ecology (Boesch and Turner, 1984; Loneragan et al., 1986; Manderson et al., 2004) because it affords some protection from predators (Paterson and Whitfield, 2000; Ruiz et al., 1993) and provides abundant feeding opportunities (Orth et al., 1984; Rozas and Odum, 1988). Movements synchronous with twilight periods into estuarine intertidal mudflats (Vinagre et al., 2007) may also reduce risk of predation (Cowley and Whitfield, 2001; Steinmetz et al., 2003; Zydulis and Kontautas, 2008).

Passive forces can be largely attributed to the volitional retention within or movement through the estuary by migrating fishes. Larval fish have limited mobility due to both size and morphology. Initial movements are therefore influenced by the selection of spawning sites (Boehlert and Mundy, 1988). Tidal currents can transport and retain inorganic material (Postma,

1961) and passively drifting organisms alike (de Wolf, 1973; Jager and Mulder, 1999). Such advective tidal transport occurs as larval fish sink during low-current velocities and are lifted in the water column by turbulence on an incoming tide. Thus, tidal currents are responsible for egg and early larval movement inshore (Power, 1984; Able and Fahay, 1998; Werner et al., 1999).

Rapid seaward migration may be critical for the larvae of some amphidromous species so that SW entry is synchronous with the transition from endogenous to exogenous feeding. Iguchi and Mizuno (1999) estimated that more than half of the Japanese goby (*Rhinogobius brunneus*) may starve during downstream migration in long river systems owing to a lack of appropriately sized prey in streams (Tsukamoto, 1991). Goby larvae passively drift downstream during the night (Iguchi and Mizuno, 1990, 1991; Moriyama et al., 1998) and actively remain in the water column by alternating movement towards the surface and sinking during rest periods (Kinzie, 1993; Balon and Bruton, 1994; Keith et al., 1999). These larvae accomplish this migration at the diminutive size of 1–4 mm in length (Han et al., 1998; Keith et al., 1999). For amphidromous fishes that re-enter FW at a small size, inshore and estuarine movements can also be dependent upon tidal currents, e.g. *Awaous guamensis* (Keith et al., 2000) and *L. concolor* (Nishimoto and Kuamo'o, 1997). Larvae are transported mostly by currents, as has been frequently observed for other fish (Borkin, 1991; Hare and Cowen, 1996), but larvae may also actively swim (Balon and Bruton, 1994; Cowen et al., 1993; Leis and Carson-Ewart, 1997; Stobutzki and Bellwood, 1997; Fisher et al., 2000).

Many SW-linked fishes move into temperate estuaries during the postflexion larval stage (Miskiewicz, 1986; Strydom et al., 2003) or during the juvenile stage (Wasserman and Strydom, 2011). This period is marked by physiological, behavioral, and morphological shifts that can occur synchronously with transition to nursery habitat (Balon, 1984; Kaufman et al., 1992; Able et al., 2006). Migration to these “critical zones” in the estuary favors successful recruitment (Dovel, 1971). Some pelagic juvenile species such as menhaden (*Brevoortia tyrannus*) rely on the strength of a tide to enter the estuary (Joyeaux, 1999). Passive forces may be sufficient to explain the invasion of the estuary by pufferfish (*Takifugu rubripes* and *T. xanthopterus*). These fish are moved inshore to the upper estuary by residual currents in the lower vertical stratum of the estuary (Yamaguchi and Kume, 2008).

Some larval fish exploit currents in order to move inland (Jenkins and Black, 1994; Jenkins et al., 1999). Oliveira et al. (2006) demonstrated through hydraulic modeling that passive individual recruitment to the estuary is dependent on FW flow. Vertical movements, however, can

effectively move and retain organisms even under high flow conditions. Such a mechanism of selective tidal transport exploits the vertical velocity profile that approaches zero at the bottom during a period of opposing flow. Thus, a fish can control directional movement in areas of reversing flows while minimizing the energetic cost of swimming (Fortier and Leggett, 1983; Miller, 1988). The ability to maintain position in the estuary by selectively populating vertical habitat is a commonality in larval fish retained in the estuary (Creutzberg, 1961; Hobbs et al., 2006), developing as both behavioral and sensory abilities increase (Forward et al., 1999; Tolimieri et al., 2000). The degree to which these fish have active control of position is logically correlated with an increase in swimming ability (Clark et al., 2005; Leis et al., 2006). Many fish exhibit a clear pattern to estuarine entry linked to size and development. Bay anchovy (*Anchoa mitchilli*) in the Chesapeake Bay are spawned in the lower estuary (Zastrow et al., 1991; Rilling and Houde, 1999; Schultz et al., 2003) and the juveniles are recruited into low-salinity waters at the head of tide as they grow (Dovel, 1971; Kimura et al., 2000). The prevalence of vertical patterns is also correlated with tidal magnitude (Graham and Sampson, 1982).

Tidal transport is not limited to larval fish, and this mechanism of movement into and through the estuary is shared by many catadromous anguillid species (Jellyman, 1979; Sheldon and McCleave, 1985; Sugeha et al., 2001; Dou and Tsukamoto, 2003; Tesch, 2003). Selective vertical movement of glass eels drives upstream progress (McCleave and Kleckner, 1982), resulting in an accumulation of these juveniles at the head of tide (Gascuel, 1986; McCleave and Wipplehauser, 1987; De Casamajor et al., 1999). At this point, upstream progress necessitates the initiation of active swimming (Creutzberg, 1961).

#### 4. OSMOREGULATORY COMPETENCE

As euryhaline fishes move between SW and FW, an obvious requirement is the maintenance of plasma osmotic concentration (Blaber, 1974; Mehl, 1974; Martin, 1990). Steady-state plasma ions are generally higher in SW-acclimated fish than in FW (Holmes and Donaldson, 1969; Allen and Cech, 2007; He et al., 2009) but regulated within a relatively narrow range (McDonald and Milligan, 1992; Evans et al., 2005). Even larval fishes tightly regulate internal osmolality with respect to external salinities (280–360 mOsm; Varsamos et al., 2005). In FW, fish use hyperosmoregulatory strategies to offset the osmotic influx of water and to counter passive ion losses. On the other hand, hypoosmoregulatory strategies are used to

offset ion influx and dehydration in more saline waters (Evans, 1999; Varsamos et al., 2005). Fishes in SW must also offset the uptake of divalents such as  $Mg^{2+}$ ,  $SO_4^{2-}$ , and  $Ca^{2+}$ , which can occur passively across the gills, or through the ingestion of food and water.

The gills, digestive tract, and kidneys play important roles in osmoregulation in both saline and FW environments. Gill ionocytes (also known as mitochondrion-rich cells and chloride cells), first noted by Keys and Wilmer (1932) in American eel, play a critical role in ion excretion, as definitively demonstrated by Foskett and Scheffey (1982). The excretion of  $Na^+$  and  $Cl^-$  excretion by these SW ionocytes relies upon ouabain-sensitive, basolateral  $Na^+/K^+$ -ATPase (NKA) pumps, which maintain the low intracellular  $Na^+$  concentrations required to promote the excretion of  $Cl^-$  and  $Na^+$  across the gills (Karnaky et al., 1976, 1977; Silva et al., 1977). Ion extrusion also involves the transport of  $Cl^-$  and  $Na^+$  into the ionocyte via a basolateral  $Na^+, K^+, 2Cl^-$  cotransporter (NKCC), resulting in sufficiently high intracellular  $Cl^-$  concentrations to generate the electrochemical gradient needed to promote  $Cl^-$  excretion via an apical cystic fibrosis transmembrane conductance regulator (CFTR) channel normally found within the small apical pit of SW ionocytes (reviewed by Marshall, 2002; Evans et al., 2005; Marshall and Grosell, 2006; Edwards and Marshall, 2013, Chapter 1, this volume). The resulting local accumulation of negative charge then promotes paracellular  $Na^+$  excretion between adjacent ionocytes and accessory cells or other ionocytes linked with relatively shallow tight junctions (Sardet et al., 1979). FW fishes actively take up  $Na^+$  and  $Cl^-$  via FW ionocytes on the gill filament and lamellar epithelium (reviewed by Perry, 1997; Wilson and Laurent, 2002; Marshall, 2002; Evans et al., 2005; Edwards and Marshall, 2013, Chapter 1, this volume). The large bulbous, apical surface of the FW ionocyte is studded with numerous microvilli, increasing the surface area for ion uptake. Like the SW ionocytes, the basolateral surface of FW ionocytes is enriched with NKA transporters, but it is apical  $H^+$ -ATPase pumps and the basolateral NKA that establish the inward electrochemical gradient that promotes  $Na^+$  influx via apical  $Na^+$  channels. Chloride is taken up via apical  $Cl^-/HCO_3^-$  exchange and a presumed basolateral  $Cl^-$  channel (Perry, 1997; Marshall, 2002; Evans et al., 2005 for reviews).

To counteract osmotic water losses across the gills, SW-acclimated fish drink SW, relying on gill-mediated ion excretion to counter the resulting salt load (Smith, 1932; Keys, 1933). In general,  $Na^+$  and  $Cl^-$  are actively taken up in the esophagus, which lowers the osmolality of the ingested SW prior to its reaching the intestine (Hirano and Mayer-Gostan, 1976), where the majority of water uptake takes place (Grosell, 2011). The excess  $Na^+$  and  $Cl^-$  is then removed from the blood via the gill SW ionocytes. Water uptake is further driven by the alkalization of the gut contents in the posterior

intestine, resulting in the generation of  $\text{CO}_3^{2-}$  and the formation of  $\text{CaCO}_3$  precipitates in the gut lumen, which further lowers the osmolality of the intestinal fluids, promoting water uptake (Grosell, 2006, 2011; Wilson et al., 2009). The gut also plays an important role, along with the kidneys, in the excretion of divalents such as  $\text{SO}_4^{2-}$ ,  $\text{Mg}^{2+}$ , and  $\text{Ca}^{2+}$ . Glomerular filtration rate (GFR) and urinary flow rate (UFR) are much lower in SW fishes. In FW fishes, on the other hand, the kidneys reabsorb  $\text{Na}^+$  and  $\text{Cl}^-$  and act as a “bilge-pump” that excretes copious amounts of dilute urine (Beyenbach, 2004; Marshall and Grosell, 2006; Evans et al., 2005; Edwards and Marshall, 2013, Chapter 1, this volume). Although it had been widely accepted that fish do not drink in FW, it now appears that there is some water ingestion, but at rates far below those observed in SW fishes (Marshall and Grosell, 2006).

#### 4.1. Patterns of Osmoregulatory Competence

The fundamental mechanisms of transitioning from FW to SW are similar across all groups of euryhaline fishes. In general, there is a replacement of FW ionocytes with SW ionocytes, usually accompanied by an increase in gill NKA activity, increased drinking, and decreased urine output (Folmar and Dickhoff, 1980; Hoar, 1976, 1988; McCormick, 2001; Evans et al., 2005). While increasing NKA is generally observed during SW acclimation, an increase in this NKA activity can also be observed in fish transferred from SW to FW (Bystriansky and Schulte, 2011), underscoring the shared reliance of osmoregulatory mechanisms on this transporter in either environment. In addition to these homeostatic adjustments, factors such as life stage, behavior, and body size are key factors affecting survival following FW to SW transfer (Hoar, 1988; Folmar and Dickhoff, 1980). While there appears to be great commonality in the mechanisms of osmoregulation across clades of migratory fishes (Hoar, 1988; Evans, 1993; Marshall and Grosell, 2006), there is great variation in the developmental patterns of osmoregulatory competence for life in SW.

In assessing patterns of salinity tolerance, McCormick (1994) described three general pathways by which SW tolerance might be developed: (1) development at an early age; (2) gradual acclimation associated with increasing size; and (3) environmentally cued development as a juvenile “preparatory adaptation”. Such processes are well characterized for salmonines, which represent only one group of migratory fishes. Development is a major driver for salmon that enter SW soon after hatching [e.g. fall Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), and pink salmon (*O. gorbuscha*)], but the underlying mechanisms are not yet clearly worked out. On the other hand, the role of the preparatory adaptation of smolting is very

well characterized and extensively described for Atlantic salmon (*Salmo salar*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*). This preparatory adaptation minimizes osmotic perturbations as these fish transit the estuary (McCormick and Saunders, 1987; Hoar, 1988; McCormick, 2013, Chapter 5, this volume). In brook trout (*Salvelinus fontinalis*) there are no apparent physiological changes and survival in SW depends upon gradual acclimation and body size (McCormick and Naiman, 1984). While these patterns are not mutually exclusive, this construct presents testable hypotheses that can be systematically applied to explain the patterns observed in other clades (as in Allen et al., 2011; see below).

#### 4.1.1. DEVELOPMENT AT AN EARLY AGE

Osmoregulation begins with embryonic development (Alderdice, 1988), but the focus of this section will be on the mechanisms seen posthatch. Prior to the development of the gills, larval fishes have to counter diffusional ion losses that mainly take place across the body surface using ionocytes located in the integument (Tytler and Bell, 1989; Tytler et al., 1993; Rombough, 2007). The ionoregulatory capacity appears to be somewhat lower in these early life stages compared to later in development, as internal osmolality can vary widely in larval fishes, from 250 to 540 mOsm (Varsamos et al., 2005). SW-linked larval fishes may survive in BW, and be tolerant to very dilute salinities (Yin and Blaxter, 1987). Even as yolk-sac larvae, Atlantic herring (*Clupea harengus*) maintain low blood osmolality with respect to a saline environment (Holliday and Blaxter, 1960), as does the lump sucker (*Cyclopterus lumpus*) (Kjörsvik et al., 1984). Plaice (*Pleuronectes platessa*) yolk-sac larvae display an impressive pattern of regulation from low salinities to full-strength SW with minimal perturbation (Holliday, 1965; Holliday and Jones, 1967).

There are many other examples of early ontogenic changes in capacity for salinity (see excellent review by Varsamos et al., 2005). In many SW-linked fishes there is an ontogenic shift in the capacity to osmoregulate in the early postembryonic stages, e.g. in European sea bass (*Morone labrax*) and starry flounder (*Platichthys stellatus*) (Hickman, 1959). The amphidromous goby (*Chaenogobius urotaenia*) has the ability to enter higher salinity immediately posthatch, but performs poorly in FW. Larvae moved into 50% SW survived for more than 30 days, while those in FW lived less than a week (Katsura and Hamada, 1986). A similar trend was observed in the goby (*Awaous guamensis*) when larvae were held in either 34 ppt SW or FW (Ego, 1956).

Striped mullet (*Mugil cephalus*) display osmotic perturbations during FW and SW exposure as young larvae, but osmoregulatory ability increases quickly through development (Nordlie et al., 1982). For these fish, early development of hypoosmoregulatory capacity may reflect an adaptive

“spread the risk” strategy. Remaining in the estuary during early development may be just as likely an outcome as being recruited into full salinity and these fish are prepared for either. Indeed, these fish are capable of survival in full-strength SW very early in development, when they are still quite small (just over 40 mm) (Nordlie et al., 1982). In many cases, osmoregulatory competence in early life stages involves developmentally dependent restructuring and/or modifications to osmoregulatory organs including the gill, gastrointestinal tract, and kidneys (Varsamos et al., 2005; Rombough, 2007). For instance, in gilthead sea bream (*Sparus aurata*) osmoregulatory capacity is increased during development as ionocytes shift from the integument to the gills (Bodinier et al., 2010).

#### 4.1.2. ACCLIMATION AND SIZE

Many teleosts can be gradually acclimated to increased salinity and either correct or establish new steady-state internal ion concentrations (Holmes and Donaldson, 1969; Jacob and Taylor, 1983; Evans, 1984). The ability to acclimate gradually to increasing ion concentrations, or in response to abrupt transfer to SW, can be profoundly influenced by size. For example, in tilapia (*Oreochromis aureus* and *O. niloticus*) the ontogeny of salinity tolerance is positively correlated with body size although there is no apparent developmental stage associated with this increase (Watanabe et al., 1985). Similarly, increased salinity tolerance has been linked to size in gilthead sea bream (*S. aurata*) (Bodinier et al., 2010) and European sea bass (Varsamos et al., 2001). Such patterns have been postulated to reflect the relatively reduced shift in diffusional surface with respect to increased volume achieved during growth, thereby reducing the burden of osmoregulation in larger fish (Allen et al., 2009).

With the notable exception of green sturgeon (Allen et al., 2009, 2011), the pattern of late SW entry of most sturgeon juveniles is consistent with the hypothesis that these fish do not have a discrete preparatory adaptation for SW entry, but slowly acquire the ability through an increase in size. The general behavioral paradigm has been that juvenile sturgeon migrate seaward over a period of years (Vladykov and Greeley, 1963), remaining in the estuary, and perhaps exploiting the lower metabolic costs associated with a lesser osmotic differential. Size-mediated increase in osmoregulatory ability has been documented in several sturgeon species, e.g. Gulf sturgeon (*A. oxyrinchus*) (Altinok et al., 1998), white sturgeon (*A. transmontanus*) (Amiri et al., 2009; McEnroe and Cech, 1985) and shortnose sturgeon (Ziegeweid et al., 2008). The behavior of Atlantic sturgeon indicates an avoidance of high-salinity environments at small sizes (Brundage and Meadows, 1982; Dovel and Berggren, 1983; Bain, 1997). There is also some evidence of staging in the

estuary by European sturgeon (*A. sturio*) juveniles. This may indicate a period of acclimation prior to SW entry (Rochard et al., 2001).

Fish may actively occupy regions of moderate salinity in order to acclimate. Contact with increased salinities can elicit greater salinity tolerance in several sturgeon species, e.g. Gulf sturgeon (Altinok et al., 1998), white sturgeon (McEnroe and Cech, 1985), and Adriatic sturgeon (McKenzie et al., 2001). Anguillid glass eels may stratify in SW low in the estuary, perhaps to gradually make the transition into FW. Further up in the estuary these fish are more evenly distributed through the water column in FW (Adam et al., 2008). Similarly, the return to FW in amphidromous gobies may be linked to body size, based on the consistent sizes of species upon return (Keith et al., 2002). These fish may persist in the estuary for several weeks (Font and Tate, 1994), although it is unclear whether this is linked to the ability to osmoregulate or whether it reflects a size-dependent metamorphosis, or both.

#### 4.1.3. DEVELOPMENTAL STAGE

Direct SW transfer is often used to characterize the ontogeny of salinity tolerance (Varsamos et al., 2001; Watanabe et al., 1985; Zydlewski and McCormick, 1997a; Allen et al., 2009, 2011). In many species SW tolerance is, after all, correlated with migration and seasonal movements (Varsamos et al., 2005). For some species, this connection is relatively clear. The parr–smolt transformation in salmonines is a synchronized shift in behavior, morphology, and physiology linked to seaward migration resulting in a rapid transition through the estuary (Schreck et al., 2006; McCormick, 2013, Chapter 5, this volume) that limits vulnerability to predators (Kennedy et al., 2007). Yet in other species, the ontogeny of salinity tolerance and of preparatory adaptation is the backdrop for a wide array of life history contingencies. For instance, in anguillids, glass eel metamorphosis and acclimation to FW are associated with irreversible changes to the gut structure (Ciccotti et al., 1993; Rodriguez et al., 2005). Body size and life stage are important determinants of osmoregulatory competency in saltwater. As illustrated below, however, in most cases these variables are part of a suite of processes associated with other preparatory adaptations that determine osmotic scope through a species's life history.

## 5. PREPARATORY ADAPTATION AND MECHANISTIC TRENDS

### 5.1. Anadromous Fishes

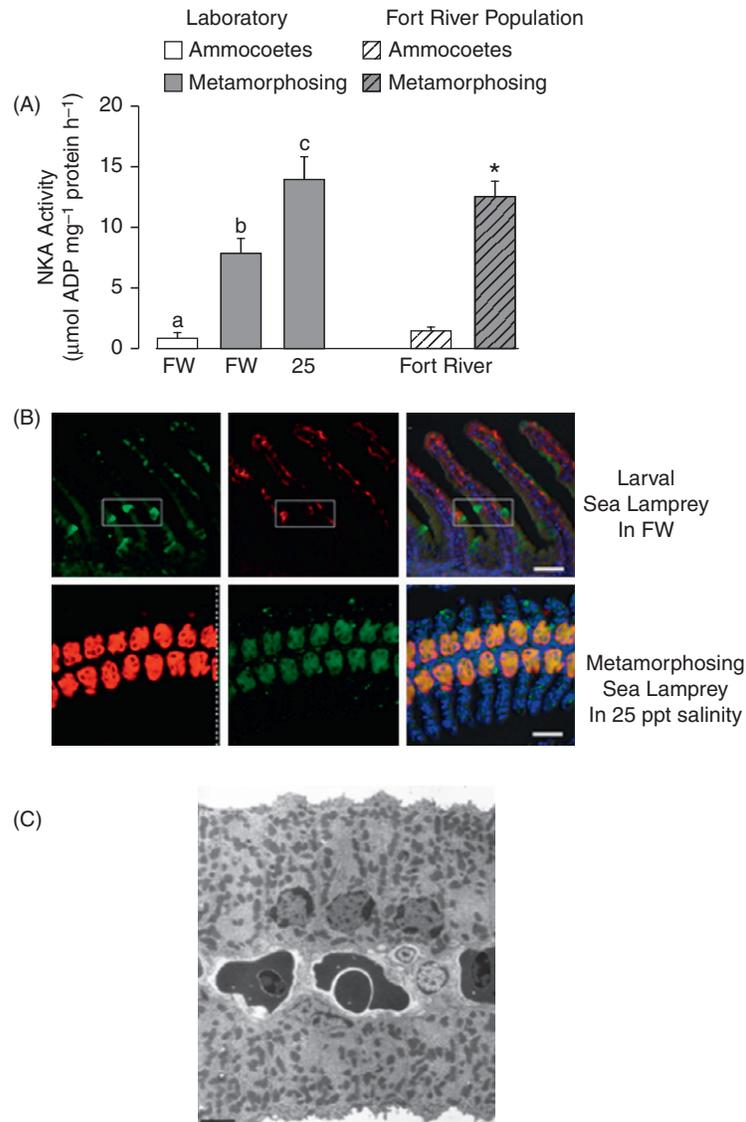
#### 5.1.1. LAMPREY

All of the anadromous lampreys have an SW parasitic phase, in which they attach themselves to potential prey/hosts, which include not only

large-bodied teleost fishes (Farmer, 1980; Renaud et al., 2009) but also elasmobranchs (Jensen and Schwartz, 1994; Wilkie et al., 2004; Gallant et al., 2006) and even cetaceans (Nichols and Tschertter, 2011). Before this parasitic phase, anadromous lampreys spend the first several years of their lives burrowed in the substrate of FW streams as functionally blind suspension feeding larvae, known as ammocoetes (Youson, 1980; Rovainen, 1996). Upon metamorphosis these relatively sedentary ammocoetes undergo marked structural and physiological changes that include a reorganization of the feeding apparatus in which the oral hood of the ammocoete is replaced by an oral disc and rasping tongue that is used to penetrate the hide and/or tear pieces of flesh from their hosts/prey in the parasitic stage (Youson, 1980, 2003; Renaud et al., 2009). The gills also switch from a unidirectional flow through gill to a tidally ventilated gill in which water is actively pumped in and out of gill pouches in order to continuously use the mouth for attachment to its parasitic host (Rovainen, 1996; Wilson and Laurent, 2002). Metamorphosis is a size-dependent process, reflecting the large stores of lipid needed to sustain the animal during this non-trophic life phase (Lowe et al., 1973; O'Boyle and Beamish, 1977; Holmes et al., 1994; Youson, 1997).

Development of SW tolerance is tightly linked to metamorphosis (Beamish, 1980a,b; Morris, 1980; Richards and Beamish, 1981) and upregulation of osmoregulatory capacity (Reis-Santos et al., 2008). The ammocoetes are exclusively FW, and incapable of surviving in even dilute SW for more than a few days (10–15 ppt; Beamish et al., 1978; Reis-Santos et al., 2008). As in other fishes, the lamprey gill epithelium is comprised of pavement cells and lower numbers of mucus cells (Bartels and Potter, 2004; Evans et al., 2005). Differences in ionocyte structure differentiate lamprey gills from those of other fishes. The ammocoete gill has two types of ionocytes: ammocoete ionocytes (referred to as ammocoete MR cells in Bartels and Potter, 2004) and a population of intercalated ionocytes (Bartels and Potter, 2004), which are solitary and found between adjacent pavement cells in this life stage (Reis-Santos et al., 2008). The ammocoete ionocyte is distinct from the typical teleost ionocyte and the intercalated ionocyte in that it lacks an extensive tubular network, and has only minimal apical exposure and microvilli.

During metamorphosis, the ammocoete ionocytes lying between lamellae of the gills are replaced by SW ionocytes (Peek and Youson, 1979), which are subsequently lost during the upstream spawning migration (Bartels and Potter, 2004). The intercalated ionocytes are retained (or reappear) only in FW, implying a role in ion uptake. The emergence of SW ionocytes at metamorphosis is accompanied by increased activity and abundance of gill NKA (Reis-Santos et al., 2008) (Fig. 6.3A). Like teleost SW ionocytes, lamprey SW ionocytes have an extensive tubular network, but they lack the



**Fig. 6.3.** Preparative physiological adaptation and seawater (SW) ionocytes in anadromous sea lampreys. (A) In both laboratory-held and river-captured sea lampreys, metamorphosis was accompanied by a marked increase in  $\text{Na}^+/\text{K}^+$ -ATPase (NKA) activity in freshwater (FW), and further increases occurred in 25 ppt SW (25). (B) NKA protein (red) and  $\text{H}^+$ -ATPase protein (green) were immunolocalized in ammocoete ionocytes on the lamellae in FW (upper panel), but immunofluorescence was restricted to ionocytes in the interlamellar spaces in SW-acclimated (metamorphosing) animals (lower panel). Differential interference contrast images of merged

apical crypt that is characteristic of analogous teleost SW ionocytes (Bartels et al., 1998). Characteristic features of the SW ionocyte are their plate-like appearance and propensity to be distributed in rows at the base of the filament (Fig. 6.3B,C). These SW ionocytes extend into the interlamellar region, probably with leaky paracellular junctions between adjacent cells (Bartels and Potter, 2004). These changes in gill ultrastructure are remarkably reminiscent of those that characterize smoltification in euryhaline salmonid fishes, which also normally includes an upregulation of NKA capacity and reliance on SW ionocytes (see McCormick, 2001; Evans et al., 2005 for excellent reviews). Like smolting salmonids, postmetamorphic lampreys take on a silvery sheen owing to the deposition of guanine in the epithelium (Youson, 1980). Despite the subtle but significant differences in gill ultrastructure, the mechanism of  $\text{Na}^+$  and  $\text{Cl}^-$  extrusion in lamprey also appears similar to that of SW teleosts. Evidence for the NKCC is limited in lampreys, but using the T4 antibody to this protein (which cannot distinguish between NKCC1 and NKCC2) this cotransporter has been identified in sea lamprey ionocytes (S. Edwards, S. Blair and M. P. Wilkie, unpublished observations). While a CFTR-like protein has not yet been described in lampreys, its presence also seems likely.

Like other SW fishes, lampreys drink while in SW (Pickering and Morris, 1970; Rankin et al., 2001), with water absorption probably taking place across the anterior intestine down osmotic gradients generated by  $\text{Na}^+$  and  $\text{Cl}^-$  uptake by enterocytes (Pickering and Morris, 1973). The divalent ions ( $\text{Mg}^{2+}$  and  $\text{SO}_4^{2-}$ ) are not taken up by the intestine (Pickering and Morris, 1973) and are instead excreted in the very low amounts of urine and via defecation (Pickering and Morris, 1973; Rankin et al., 2001).

The role of lamprey kidneys in SW has been described in upstream migrant river lamprey (*Lampetra fluviatilis*) reacclimated to 50% SW. Pickering and Morris (1973) noted that kidney UFRs were extremely low after exposure to these hyperosmotic conditions. Further studies by Logan et al. (1980) demonstrated that it was mainly marked reductions in GFR (through a reduction in the number of renal corpuscles) that resulted in the 90% reduction in UFR observed. As in many SW teleosts, lamprey urine is either hypoosmotic or isosmotic to SW, and mainly concentrated with  $\text{Mg}^{2+}$  and  $\text{SO}_4^{2-}$ , and  $\text{Cl}^-$  (Logan et al., 1980).

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images of NKA,  $\text{H}^+$ -ATPase protein, and DAPI (nuclear marker) to illustrate colocalization of the two transport proteins. (C) Electron micrograph illustrating that the SW ionocytes of lamprey (pouched lamprey, *Geotria australis* shown) are arranged in columns or rows, containing extensive tubular invaginations, but unlike teleost ionocytes, lack an apical crypt. Scale bar: 3  $\mu\text{m}$ . Data and images in panel A and B from Reis-Santos et al. (2008); electron micrograph in panel C adapted from Bartels and Potter (2004) with permission.

The contribution to lamprey ion and osmoregulation made by the ingestion of isosmotic fluids from their teleost hosts has yet to be investigated. Such physiological parasitism could explain why NKA activities tend to decrease with age and with body size in SW-acclimated sea lamprey (Beamish, 1980b). Fossil evidence suggests an SW origin for lampreys (Shu et al., 1999; Gess et al., 2006), implying that ancestral lampreys were likely to be anadromous (Gill et al., 2003). However, the conspicuous presence of the FW population of *P. marinus* in the Laurentian Great Lakes indicates that anadromy may be facultative in this species, or that rapid adaptation is possible (Lawrie, 1970; Eshenroder, 2009). Whether or not the several other FW populations of parasitic lampreys, including members of the *Ichthyomyzon*, *Entosphenus*, and *Lampetra* genera (Potter and Gill, 2003), have retained some of the features associated with anadromy remains an open but intriguing question. Comparative work considering endocrine control of ionocyte structure and function in relation to SW tolerance in postmetamorphic juveniles may inform the evolutionary radiation of lamprey species.

Little is known about the hormonal factors involved in the preparative changes involved in the FW to SW transition in lampreys, but metamorphosis is well described and depends upon gradual increases in the thyroid hormones thyroxine ( $T_4$ ) and triiodothyronine ( $T_3$ ) in the larval phase. These increases are followed by a precipitous drop in both hormones that is thought to trigger metamorphosis (Youson, 1994, 2003; Youson and Manzon, 2012). It is notable that these “low” levels are near the peak concentrations known to initiate metamorphosis in amphibians (Youson, 2003), and could therefore be at physiologically relevant levels that are sufficient to play a role in the development of SW tolerance. In fact, thyroid hormones play an important role in preparatory adaptation of salmonines to SW by initiating the upregulation of corticosteroid receptors, which is critical for ensuring that the cortisol-induced upregulation of SW ionocytes takes place in these fishes (Evans et al., 2005). The recent finding that 11-deoxycortisol is the functional mineralocorticoid in lampreys (Close et al., 2010) could represent a turning point in our understanding of preparatory adaptation in these basal vertebrates. Indeed, 11-deoxycortisol administration to lampreys results in a marked increase in gill NKA activity, a prerequisite for downstream migration and SW acclimation (Close et al., 2010).

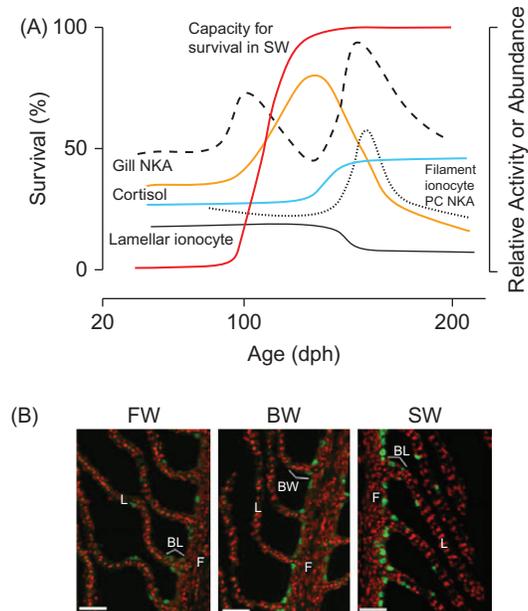
#### 5.1.2. STURGEON

Salinity tolerance is related to ontogeny in the anadromous sturgeons, with body size being directly proportional to the ability of the fish to hypoosmoregulate in SW environments (Altinok, 1998; Allen and Cech,

2007; Allen et al., 2009, 2011). Amiri et al. (2009) noted that larger juvenile white sturgeon experienced lower mortality and a lower onset of osmotic disturbances when transferred to SW. Similar findings were reported by Altinok et al. (1998) for Gulf sturgeon (*A. oxyrinchus*) using fish of identical age (13 month posthatch) but grouped by size (110–170, 230–270, and 460–700 g). Smaller fish suffered greater osmotic stress (increases in plasma osmolality,  $\text{Na}^+$ , and  $\text{K}^+$ ) and mortality following direct transfer from FW to SW (25 ppt). Following 96 h exposure to SW, however, plasma ions returned towards FW values in the larger fish, but  $\text{Na}^+$  remained elevated in the smaller fish. Many sturgeon species require prior exposure to BW to make the transition from FW to SW (McKenzie et al., 1999). White and green sturgeons readily tolerate acute transfer from BW to the full-strength SW, but are less tolerant of acute transfer to FW (Potts and Rudy, 1972). Blood ion concentrations and patterns of  $\text{Na}^+$  uptake are similar to those of teleosts. Transfer to SW also leads to decreased water permeability, with reduced urinary flow being mainly for the elimination of divalents such as  $\text{Mg}^{2+}$  and  $\text{SO}_4^{2-}$  (Potts and Rudy, 1972).

Size alone is not sufficient to explain patterns of osmotic competence in green sturgeon. There is a clear link between an ability to control plasma osmolality and age. Allen and Cech (2007) acclimated three different life stages of green sturgeon (100, 170, and 533 days posthatch age) to FW (<3 ppt), BW (10 ppt), and SW (33 ppt). There was significant mortality (23%), lower growth, and osmotic perturbations in the youngest group, but older fish experienced no change to osmolality or  $\text{Na}^+$  concentration, and only minor changes in plasma  $\text{Cl}^-$ . Thus, the green sturgeon has the ability to completely acclimate to SW after 1.5 years, and life-stage dependent preparatory adaptation for SW residence is probably essential. Indeed, there was no relationship between body mass and plasma osmolality when green sturgeons were acclimated to SW over 7 weeks (Allen et al., 2009). Green sturgeon survived short-term transfer to SW after a gradual acclimation in BW at 4.5 months, but by 7 months they were capable of withstanding direct transfer with no mortality, and minimal osmotic perturbations (Fig. 6.4A) (Allen et al., 2011).

The development of increased osmoregulatory ability coincides with a peak in cortisol that was followed by peaks in thyroid hormones and the upregulation of gill and pyloric ceca NKA activity and abundance (Fig. 6.4A) (Allen et al., 2009). Cortisol, with growth hormone (GH), drives the proliferation of gill SW ionocytes in euryhaline teleosts. Thyroid hormone is thought to have permissive effects that include the upregulation of corticosteroid receptors in the gill (Takei and McCormick, 2013, Chapter 3, this volume). These changes occur at the time when decreased swimming performance and other behavioral shifts associated with downstream



**Fig. 6.4.** Preparatory adaptation in the anadromous green sturgeon. Seawater (SW) tolerance in green sturgeon is linked to ontogeny (A), with full SW tolerance developing in less than 5 months (red line). Tolerance is linked to a steady increases in plasma cortisol (orange line), and increased gill (dashed line) and pyloric ceca (dotted line)  $\text{Na}^+/\text{K}^+$ -ATPase (NKA) activity. Marked decreases in ionocyte abundance on the lamellae (black) are coincident with increases in filamentary ionocyte abundance (blue). dph: days posthatch. (B) Gill ionocytes rich in NKA (green) on the lamellae (L) are more numerous in freshwater (FW) than brackish water (BW) and SW. The intensity of the immunostaining on the filament located ionocytes (F), particularly at the lamellar base (BL), was also greater in SW. Scale bar: 10  $\mu\text{m}$ . Drawing based on Allen et al. (2011); micrographs were obtained, with permission, from Allen et al. (2009); micrographs obtained with permission from Allen et al. (2009).

migration occur (Kynard et al., 2005). This is the first evidence of a preparatory developmental stage in sturgeon and may reflect a preparatory adaptation of this species to enter SW at a relatively young age (Brown, 2007). Such preparatory adaptation may be triggered by external factors such as photoperiod (Allen et al., 2011), but whether this or other factors are involved requires further investigation. It remains to be determined whether similar preparatory strategies for SW acclimation are used by other migratory sturgeon, but this certainly represents an exciting and important direction of future study.

There has been very limited work on the underlying molecular mechanisms of ionocyte function in the sturgeon, but the general structure

and function of sturgeon ionocytes are similar to those of teleosts. As in teleosts, sturgeon switch from an FW ionocyte to an SW ionocyte as they transition from FW to SW (Fig. 6.4B) (Altinok et al., 1998; McKenzie et al., 1999; Martinez-Alvarez, 2005; Allen et al., 2009, 2011; Sardella and Kültz, 2009; Zhao et al., 2010). The most detailed microscopic examination, using transmission electron microscopy, suggests that the SW ionocyte of at least one species, the Adriatic sturgeon (*A. naccarii*), has an apical crypt (Martinez-Alvarez et al., 2005), implying the presence of an apical  $\text{Cl}^-$  channel. An accompanying NKCC has been localized to the ionocyte in green sturgeon, which is upregulated during SW acclimation (Sardella and Kültz, 2009). Similarly, immunohistochemical localization indicates that the basolateral membrane of SW ionocytes is enriched with NKA (McKenzie et al., 1999; Allen et al., 2009; Sardella and Kültz, 2009; Zhao et al., 2010). Sardella and Kültz (2009) also noted a downregulation of the V-type  $\text{H}^+$ -ATPase with SW acclimation in green sturgeon, consistent with a decreased role for  $\text{H}^+$ -ATPase coupling to drive  $\text{Na}^+$  uptake in saltwater environments.

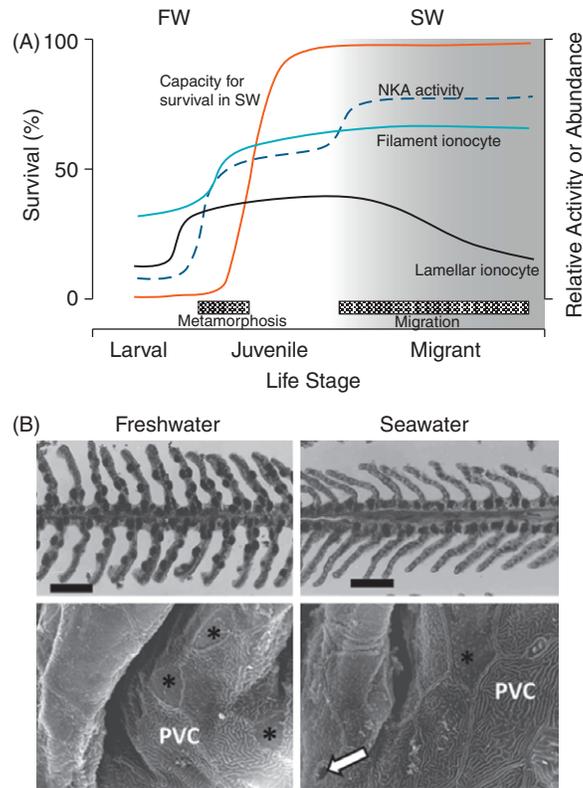
There is some direct evidence that sturgeon drink during SW acclimation, as demonstrated by exposing FW-acclimated Siberian sturgeon (*A. baeri*) to elevated salinity (Taylor and Grosell, 2006). In the green sturgeon, the concentrations of  $\text{Na}^+$  and  $\text{Cl}^-$  are markedly lower in the stomach compared to ambient SW, suggesting that the water is desalinated in the esophagus en route to the stomach (Allen et al., 2009). The ion concentrations decline further in the anterior–mid intestine, and in the rectum, which probably generates more favorable lumen–blood osmotic gradients in this region (Allen et al., 2009). As in SW teleosts there is circumstantial evidence for high rates of luminal  $\text{Cl}^-/\text{HCO}_3^-$  exchange in the intestine, based on lower  $\text{Cl}^-$  concentrations, more alkaline pH, and the presence of solid mucus tubes associated with precipitates comprised mainly of  $\text{Ca}^{2+}$ ,  $\text{CO}_3^{2-}$ , and  $\text{HCO}_3^-$  (Allen et al., 2009). Thus, like its teleostean counterparts, it appears that the sturgeon maximizes water uptake through a combination of ion uptake in the esophagus and intestine, and  $\text{Cl}^-/\text{HCO}_3^-$ -mediated base extrusion in the intestine to cause precipitation of solutes such as  $\text{Ca}^{2+}$  in the form of  $\text{CaCO}_3$  (Grosell, 2011). Although increased NKA, NKCC, and aquaporin in the gut are likely to be involved, this has yet to be examined in sturgeons.

### 5.1.3. ALOSINE FISHES

Several anadromous clupeid species spawned in FW develop SW tolerance at the larval juvenile transition, e.g. allis shad (Leguen et al., 2007; Bardonnet and Jatteau, 2008) and American shad (Zydlewski and McCormick, 1997a). Development of larval American shad can occur at

salinities greater than isosmotic (Limburg and Ross, 1995) but development of the gills at the larval–juvenile transition is necessary for survival in full SW (Zydlewski and McCormick, 1997a). This ontogeny is likely to afford some success of eggs and larvae displaced to the estuary before migration occurs. In temperate rivers, migration can be protracted into the fall; thus a wide window of SW entry is allowed. Size does affect migration. Larger juveniles are recruited into migration earlier in the season (Limburg, 1996; O'Donnell and Letcher, 2008) but there appears to be no increase in SW tolerance at the time of migration (Zydlewski and McCormick, 1997a,b). In allis shad, however, additional development of SW tolerance has been linked to size of the juvenile (Leguen et al., 2007), which corresponds with the timing of SW entry (Lochet et al., 2009).

In spite of being competent to enter SW early in development, migratory juvenile American shad in FW have markedly higher gill NKA activities than their non-migrant counterparts (Zydlewski and McCormick, 1997b). Remarkably, this increase in NKA is linked to marked reductions in hyperosmoregulatory ability in FW, as indicated by declines in plasma  $\text{Cl}^-$ . When held under FW conditions in the laboratory past the period of migration, dramatic 70% reductions in plasma  $\text{Cl}^-$  and increased mortality occur. This decline is delayed, but not prevented, in juvenile shad held constant at 24°C (Zydlewski and McCormick, 2001). Thus, declining hyperosmoregulating capacity probably represents a developmental shift, a “preparatory adaptation”, associated with the FW to SW migratory period, although its adaptive significance is perplexing. As this reduction in ability to osmoregulate in FW is hastened by declining temperature, this development probably defines a window for successful ocean migration in temperate American shad populations (Zydlewski et al., 2003) (Fig. 6.5). The increased gill NKA in migrant American shad in FW is likely to be related to upregulation of ion uptake mechanisms. Increased NKA corresponds to a significant increase in ionocyte abundance in the gills, particularly on the lamellae (Zydlewski and McCormick, 2001; Zydlewski et al., 2003) (Fig. 6.5). In FW, these cells have a large surface and appear similar in morphology to FW ionocytes implicated in ion uptake in teleosts. As ionocytes on the lamellae proliferate, they begin to cover an increasing proportion of the respiratory surface (Zydlewski and McCormick, 2001). The proliferation and enlargement of ionocytes during seaward migration may present a considerable energetic challenge to late migrant shad or may directly interfere with respiration and other gill functions. In both American shad and alewife (*A. pseudoharengus*), acclimation to SW is associated with a marked increase in gill NKA activity, loss of ionocytes on the gill lamellae, and increased size of filamental ionocytes (Fig. 6.5) (Zydlewski et al., 2001; Christensen et al., 2012). Detailed immunohistochemical examination of the alewife gill has demonstrated that



**Fig. 6.5.** Preparatory adaptation in American shad. (A) Seawater (SW) tolerance develops at the larval–juvenile transition in American shad, accompanied by parallel increases in gill  $\text{Na}^+/\text{K}^+$ -ATPase (NKA) and filamental and lamellar ionocytes as the gills are formed. FW=freshwater. (B) As shown by light (scale bar: 10  $\mu\text{m}$ ) and scanning electron microscopy, freshwater ionocytes are numerous on both the gill lamellae and filament with large apical surfaces (as indicated by \*). During SW acclimation, total ionocyte numbers decrease and cells are restricted to the filament. Apical crypts characteristic of SW ionocytes are formed (arrow). Data modified from Zydlewski and McCormick (2001) and Zydlewski et al. (2003). Light micrographs reproduced with permission from Zydlewski and McCormick (2001).

the FW and SW ionocytes are indistinct from those of other teleosts (Christensen et al., 2012). SW ionocytes have basolaterally located NKA and NKCC1, and an apical CFTR channel embedded in the apical crypt of the cells. The CFTR appears to be colocalized with the  $\text{Na}^+/\text{H}^+$  exchange protein 3 (NHE3), which is likely to be important for acid–base regulation in SW (Evans et al., 2005). SW ionocytes are arranged in diads or triads, which probably facilitates paracellular  $\text{Na}^+$  extrusion through the formation of leaky

tight junctions (Christensen et al., 2012; Edwards and Marshall, 2013, Chapter 1, this volume).

The FW to SW transition in alewife leads to increased gill NKA activity and abundance on the basolateral membrane. NKCC abundance also increases (Christensen et al., 2012). Based on similar increases in gill NKA activity and changes in SW ionocyte distribution following SW acclimation (Zydlewski and McCormick, 1997a, 2001), the fundamental mechanisms can be presumed to be the same in American shad.

The decline in osmoregulatory competence seen in American shad with prolonged residence in FW suggests that it is an obligate anadromous species (Zydlewski et al., 2001). However, alewives appear to be facultative in the expression of anadromy, as demonstrated by their ability to regulate internal  $\text{Na}^+$  (Stanley and Colby, 1961) and  $\text{Cl}^-$  (Christensen et al., 2012) during prolonged or even permanent residence in FW (Scott and Crossman, 1973). American shad residence in FW is apparently curtailed by the temporal loss of hyperosmoregulatory ability in FW (Zydlewski and McCormick, 1997b, 2001; Zydlewski et al., 2003) and these fish are rarely successful if landlocked (von Geldern, 1965; Lambert et al., 1980). Like American shad, similar reductions in ionoregulatory competence have also been reported in alewives exposed to cold temperatures following prolonged periods in FW, which may have contributed to the sudden die-offs of alewives that frequently occurred in the Great Lakes during the 1960s and 1970s (Stanley and Colby, 1971). There is a population of landlocked American shad in California (von Geldern, 1965; Lambert et al., 1980), not to mention several landlocked populations of shad, including the allis shad (*A. alosa*) and twaite shad (*A. fallax*), in Europe (Bianco, 2002; Bagliniere et al., 2003; Jolly et al., 2012). Direct comparisons between the anadromous and landlocked Alosines could help to tease out the relative importance of physiological preparation in these fishes.

#### 5.1.4. TEMPERATE BASSES

The approximately 50 species of temperate basses inhabit FW, estuaries, and marine environments. Some, including the striped bass (*Morone saxatilis*) and white perch (*Morone americana*), are anadromous, spawning in FW and typically migrating towards the sea as juveniles (Scott and Scott, 1988). However, schools of juveniles often remain in estuaries, with occasional forays into FW that may last for several months or longer (Scott and Scott, 1988). The period of preparatory adaptation for SW appears to be minimal in the striped bass following hatching. While tolerance to increased salinity is limited during the yolk-sac and larval stages, juvenile striped bass are able to tolerate up to 10–15 ppt salinity only a few months after hatching (Tagatz, 1961; Otwell and Merriner, 1975; Kane

et al., 1990; Grizzle and Mauldin, 1994; Winger and Lasier, 1994; Secor et al., 2000; Cook et al., 2010). Survival at higher salinities is positively correlated with warmer water temperatures in juvenile white perch and striped bass, perhaps due to limitations in ATP supply at lower temperatures. Reduced power for NKA pumps may therefore reduce gill-mediated  $\text{Na}^+$  and  $\text{Cl}^-$  extrusion (Hurst and Conover, 2002; Hanks and Secor, 2011). This may explain why these fishes tend to overwinter in lower salinity regions of the estuary, when the metabolic demands of osmoregulation would be less than at higher salinities (Hurst and Conover, 2002). Indeed, marked reductions in energy stores have been reported in young-of-the-year white perch following acclimation to 16 ppt salinity compared to more dilute waters (Hanks and Secor, 2011).

Studies on striped bass, the most studied of the temperate basses, indicate that transfer from FW to SW is associated with transient increases in plasma  $\text{Na}^+$  and osmolality that generally recover to pretransfer levels within 24 h (Madsen et al., 1994; Tipsmark et al., 2004). In both SW and FW, NKA and CFTR appears to be localized to large cells, which are presumably ionocytes, found at the base of the lamellae and in the interlamellar spaces (Madsen et al., 2007). Ionocytes appear early in the ontogeny of the striped bass, when they are mainly restricted to the gill filaments in larvae, followed by a shift to the lamellae in the juvenile stages (43 days posthatch) (Hirai et al., 2002). As suggested earlier, such findings imply that there may be two populations of ionocytes, a filamental population involved in osmoregulation at higher salinities and an FW population needed for hypoosmoregulation in more dilute waters. King and Hossler (1991) proposed that the rapid acclimation of FW-acclimated striped bass to SW was related to the restructuring of the ionocytes characterized by extensions of the apical membranes of ionocytes, which were associated with increased  $\text{Cl}^-$  efflux. These ionocytes were replaced within 7 days by cells displaying the distinct apical crypts characteristic of SW ionocytes, but ionocytes similar to those seen in FW were still retained. These early findings therefore suggest that the striped bass retains some of the physiological machinery required for osmoregulation in both SW and FW.

Unlike many other anadromous migrating fishes, SW acclimation is associated with only minor changes in gill ionocyte number or distribution (King and Hossler, 1991; Madsen et al., 1994), although the surface area of individual cells increases slightly (Madsen et al., 1994, 2007). Neither NKA activity nor protein abundance ( $\alpha 1$  subunit) changes greatly following FW to SW (Madsen et al., 1994, 2007; Tipsmark et al., 2004) or SW to FW transfer (Tipsmark et al., 2004). Nor does CFTR messenger RNA (mRNA) expression or protein abundance appreciably change in response to greater salinity (Madsen et al., 2007). On the other hand, NKCC mRNA expression and protein abundance markedly increase following FW to SW transfer,

consistent with a switch from ion uptake in FW to ion extrusion in SW (Tipsmark et al., 2004).

Like the estuarine killifish (*Fundulus heteroclitus*) (see Marshall, 2013, Chapter 8, this volume), the striped bass appears to be in a “state of readiness” to control osmotic balance in the event of sudden changes in salinity (Madsen et al., 2007). Madsen et al. (2007) have speculated that the striped bass uses an “ionocyte shift-reuse” strategy in which the CFTR is translocated to the basolateral membrane from its typical apical location, while the NKCC1 is internalized (or removed) from the basolateral membrane. Such reorganization would rapidly convert the ionocyte from a salt-secreting to salt-absorbing cell, in which  $\text{Cl}^-$  uptake would presumably take place via apical  $\text{Cl}^-/\text{HCO}_3^-$  exchange followed by basolateral uptake via the CFTR, and  $\text{Na}^+$  uptake would take place via epithelial  $\text{Na}^+$  channels coupled to  $\text{H}^+$ -ATPase-mediated proton extrusion. However,  $\text{H}^+$ -ATPase activity is quite low in striped bass compared to other FW fishes such as the brown trout (*Salmo trutta*), suggesting that higher basal rates of NKA activity or abundance may be needed to help generate the low intracellular  $\text{Na}^+$  concentrations needed to generate favorable inwardly directed  $\text{Na}^+$  electrochemical gradients in FW (Tipsmark et al., 2004). Indeed, there may also be a functional switch in NKA indicated by differential mRNA expression of the NKA  $\alpha 1$  subunit, shifting from the “FW”  $\alpha 1a$  to the “SW”  $\alpha 1b$  isoform, as described in rainbow trout (Richards et al., 2002). While intriguing, evidence for the ionocyte shift-reuse model is lacking. Approaches using *in vitro*, immunohistochemical, and immunoblotting approaches may be productive ways to elucidate intracellular signaling pathways that control ion uptake and extrusion in the gills of striped bass transitioning between FW and SW. However, it would also be advisable to combine such approaches with direct measurements of unidirectional movements of  $\text{Na}^+$  and  $\text{Cl}^-$  across the gills to better relate the changes in ion uptake and diffusive loss to events occurring at the cellular, subcellular, and molecular level of the gills.

While physiological adjustments to changes in salinity are rapid, endocrine regulation is likely to play an important but slightly different role in mediating the FW to SW acclimation in the striped bass. Consistent with its role in SW acclimation in other species (Marshall, 2002), cortisol increases following FW to SW transfer in striped bass (Madsen et al., 1994). However, the importance of cortisol remains unresolved (Tipsmark et al., 2007). Exogenous cortisol administration has no effect on the expression of gill NKA or CFTR mRNA levels *in vivo*, and actually suppressed CFTR expression in isolated gill tissue *in vitro* (Madsen et al., 2007). Kiilerich et al. (2011) recently demonstrated that cortisol and 11-deoxycorticosterone activated the mitogen-activated protein (MAP) kinase signaling cascade in

striped bass. Thus, even subtle, transient increases in hormone levels could activate or inactivate CFTR, NKCC1, and NKA (or other critical proteins) via phosphorylation pathways. As in other fishes, ionocytes are not regulated by corticosteroids alone. In combination with cortisol, epidermal growth factor (EGF) may play a key role in striped bass osmoregulation by regulating CFTR function via the MAP kinase pathway (Madsen et al., 2007). However, the role of cortisol plus EGF in the acquisition of SW tolerance remains unresolved as experiments with isolated gill cells have demonstrated a downregulation of CFTR abundance, rather than the expected increase following FW to SW transfer (Madsen et al., 2007). Insulin-like growth factor-1 (IGF-I) may also be critical because IGF-I receptor mRNA expression is upregulated in ionocytes following FW to SW transfer (Tipsmark et al., 2007). Increased plasma IGF-I has been shown to play an important role in smoltification in salmonines (Sakamoto et al., 1995). However, exogenously administered IGF-I impairs the hypoosmoregulatory ability of striped bass, suggesting that its fundamental actions differ from those reported in salmonines (Tipsmark et al., 2007). It is more likely that IGF-I is involved in FW acclimation as it promotes prolactin release in striped bass pituitaries (Fruchtman et al., 2000). Work on the molecular signaling pathways controlling osmoregulation in striped bass, as well as other species including estuarine killifish (Marshall, 2013), is still in its early stages, but should fill in many gaps in our understanding of the processes controlling salt excretion by marine fishes.

Based on the rapid corrections to osmotic balance in striped bass with SW acclimation, changes in gut ion and water transport capacity are likely to occur in parallel to those taking place in the gill. Madsen et al. (1994) reported that the water transport capacity of the mid-intestine doubled with a 35% increase in intestinal NKA activity following FW to SW transfer (Madsen et al., 1994). Increased drinking rate occurs in 1-month-old striped bass following transfer from FW to BW (5 ppt) (Grizzle and Cummins, 1999). Like the gills, the intestine and the kidneys are probably also in a state of “readiness” to allow striped bass to rapidly adjust to changes in external salinity. However, most of the work thus far has focused on physiological adjustments occurring in the gills. Given the importance of the gut and kidneys in SW osmoregulation, studies focusing upon the temporal plasticity of these organ systems in response to changes in salinity are clearly warranted.

## 5.2. Catadromous Fishes

### 5.2.1. ANGUILLIDS

As described earlier, newly hatched eel larvae (leptocephali) are transported on ocean currents from ocean spawning grounds to intertidal

areas where they transform into glass eels. These juveniles accumulate at the head of tide before initiating active swimming upstream. This delay in migration may be associated with morphological and physiological preparation for the riverine environment as they transition to pigmented “yellow eels” (Jellyman, 1977; McCleave and Wippelhauser, 1987; Pease et al., 2003). There is, however, no obvious shift in osmoregulatory capacity at this stage. Glass eels make the transition from SW to FW without notable changes in water content (Wilson et al., 2007) or plasma osmolality (Seo et al., 2009). Glass eels captured in the lower tidal area are already competent to osmoregulate in FW (Wilson et al., 2004).

Recent findings using telemetry and Sr:Ca ratios in otoliths suggest that northern temperate eels are facultatively catadromous (Tsukamoto et al., 2001; Daverat et al., 2006; Thibeault et al., 2007; Arai et al., 2009), with some animals persisting in the estuary and making sorties into FW (Fig. 6.2) (Jessop et al., 2008; see also Shrimpton, 2013, Chapter 7, this volume). Yellow eels must therefore be robust to the changes in salinity that occur through the tidal cycle and the gills play a critical role. Gill ionocytes are distributed on both the lamellar and filamental epithelium of the yellow eel (Thomson and Sargent, 1977; Sasai et al., 1998). In Japanese eel, two types of ionocytes, acidophilic type A and weakly acidophilic type B ionocytes, are present (Shirai and Utida, 1970). The type B ionocytes (referred to as CCs by the authors) were differentiated from type A based on their smaller size, smaller mitochondria with less distinct cristae, and a less elaborate tubular network (Shirai and Utida, 1970; Utida et al., 1971). More recent work revealed that these basolateral invaginations are rich in NKA (Marshall, 2002; Evans et al., 2005).

Abrupt transfer of yellow eels from FW to SW is accompanied by an initial increase in ionocyte abundance and size (Keys and Wilmer, 1932; Olivereau, 1970; Utida et al., 1971; Thomson and Sargent, 1977), and parallel increases in gill NKA activity (Kamiya and Utida, 1968; Utida et al., 1971; Thomson and Sargent, 1977; Rankin, 2009) and abundance (Cutler et al., 1995a,b). In Japanese eel it is the type A ionocytes that increase in number and size, followed by the gradual elimination of the type B ionocytes after 2 weeks in SW (Shirai and Utida, 1970).

While such plasticity is of inherent value when fish are faced the uncertain salinity of the estuary, an increase in active  $\text{Na}^+$  and  $\text{Cl}^-$  extrusion capacity in full-strength SW probably results in greater energetic costs. However, otolith Sr:Ca ratio data also indicate that growth is much less in FW-dwelling yellow eels and those spending prolonged periods in BW or SW (Jessop et al., 2008; Cairns et al., 2009; Lamson et al., 2009). Therefore it remains unclear what the relationship is between energy expenditure and osmoregulatory capacity in the yellow eel. It would be informative to determine the energetic costs that transient excursions into SW from FW or

BW have on yellow eels, compared to silver eels that are undergoing physiological preparation for their seaward migration.

The transition from the yellow to silver stage (“silvering”) in anguillid eels is perhaps the most obvious change associated with the initiation of seaward migration and reproductive maturation (e.g. [Utida et al., 1967](#); [Thomson and Sargent, 1977](#); [Fontaine et al., 1995](#); [Lignot et al., 2002](#); [Tesch, 2003](#); [Acou et al., 2005](#); [Kalujnaia et al., 2007](#); [van Ginneken et al., 2007b](#)). Silvering also marks a period of physiological preparedness for the eel’s extended, terminal stay in SW (see [Tesch, 2003](#); [Rankin, 2009](#) for recent reviews). However, there appears to be no difference in the SW tolerance of yellow and silver eels ([Rankin, 2009](#)).

Gill ionocyte abundance changes little during silvering ([Thomson and Sargent, 1977](#); [Sasai et al., 1998](#)): ionocytes on the lamellae of the gill are lost, while ionocyte size and number on the gill filament increase ([Fontaine et al., 1995](#); [Sasai et al., 1998](#)). These shifts result in modest increases in NKA activity in FW, which further increases after exposure to SW ([Thomson and Sargent, 1977](#); [Sasai et al., 1998](#); [Rankin, 2009](#)).

As in the clupeids (see above), the loss of lamellar ionocytes implicates these cells in ion uptake, while the filamental ionocytes are probably for salt extrusion ([Sasai et al., 1998](#); [Sakamoto et al., 2001](#)). Detailed ultrastructure analysis also noted a more extensive tubular network and greater numbers of mitochondria in filamental ionocytes ([Doyle and Epstein, 1972](#); [Fontaine et al., 1995](#)). Accessory cells were also observed in close association with the ionocytes in both yellow and silver eels, which would be consistent with a greater capacity to excrete  $\text{Na}^+$  and  $\text{Cl}^-$  in SW ([Fontaine et al., 1995](#)).

“Silvering” may be associated with reduced FW osmoregulatory capacity, as evidenced by the loss of lamellar ionocytes; the silver eel may in fact be at a point of no return. The decrease in branchial aquaporin 3 (AQP3) mRNA ([Cutler and Cramb, 2002a](#); [Tse et al., 2006](#)) and protein ([Lignot et al., 2002](#)) reported in SW-acclimated eels could also compromise FW osmoregulatory capacity by impairing cell volume control and other physiological processes in ionocytes ([Cutler et al., 2007](#)). Indeed, disturbances to ion homeostasis (demineralization) may be an important trigger of FW to SW migration in silver eels ([Dutil et al., 1987](#); [Durif et al., 2009](#)), but this hypothesis requires further investigation.

There is ample evidence that FW to SW transfer by eels is accompanied by a necessary increase in ingestion of SW. [Smith \(1932\)](#) and [Keys \(1933\)](#) demonstrated this by preventing water ingestion by blocking the esophagus with a surgically implanted balloon. This led to uncontrolled water loss in SW. [Maetz and Skadhague \(1968\)](#) later demonstrated that FW-acclimated eels ingested water as well, but at lower rates than in SW. As in other teleosts, ingested SW is desalinated, followed by further dilution in the

stomach before the water reaches the intestine. In the intestine the bulk of water uptake is driven by the lower osmolality of the fluid, further facilitated by  $\text{Cl}^-$  uptake via intestinal NKCC and CFTR (Cutler and Cramb, 2002b; Ando et al., 2003). Although mRNA AQP3 is located in the esophagus and gut, expression does not change between FW and SW (Cutler et al., 2007) and is not immunolocalized to enterocytes as would be expected if it were involved in water uptake (Lignot et al., 2002). It is more likely that water is taken up paracellularly, between adjacent enterocytes, as it is in mammals (Cutler et al., 2007). While Cutler and colleagues have examined the underlying endocrine basis of AQP regulation (e.g. Martinez-Alvarez et al., 2005; Cutler et al., 2007), control of drinking behavior and osmoregulatory capacity of the digestive tract remain poorly characterized.

Silvering is probably cued by changes in photoperiod and lunar cycles (Tsukamoto et al., 2003), as mediated by changes in endocrine status. The endocrine control of silvering is somewhat analogous to smoltification in salmonids (van Ginneken et al., 2007a; also see McCormick, 2013, Chapter 5, this volume). In yellow European eel, silvering may be initiated by  $\text{T}_4$ , which peaks in the spring and rises modestly in late summer prior to silvering (van Ginneken et al., 2007a). Similar findings, along with parallel increases in the  $\beta$ -subunit of thyroid-stimulating hormone (TSH) mRNA, were reported in Japanese eel (Han et al., 2004). However, Aroua et al. (2005) did not observe similar variation in  $\text{T}_4$  profiles, and chronic  $\text{T}_4$  administration to yellow eels did not induce silvering.

Elevated plasma cortisol and GH act in a dual manner to increase NKA activity and SW ionocyte number in smolting salmonids (McCormick, 2001), but the actions of these hormones in silvering eels is less clear-cut. Plasma GH concentrations, at least in female eels, show no distinct temporal variation in the months preceding silvering (van Ginneken et al., 2007a). It also seems unlikely that GH plays a significant role in osmoregulation because hypophysectomy has no effect on FW or SW tolerance in eels (Olivereau and Ball, 1970). However, there is a two-fold increase in plasma cortisol in silver compared to yellow European eel (van Ginneken et al., 2007a). This increase may be causal to increases in ionocyte size and number as well as increased NKA activity in the gill (Epstein et al., 1971; Wong and Chan, 2001) and intestine (Epstein et al., 1971). These shifts during silvering result in the higher salt excretory capacity (Mayer et al., 1967). Increased cortisol may also promote the mobilization of energy stores needed for migration (van Ginneken et al., 2007b).

Cortisol also produces an upregulation of AQP1 in the esophagus and intestine of SW-acclimating European eel (Martinez-Alvarez et al., 2005). This suggests that in addition to salt extrusion, cortisol plays an important role in water desalination and water uptake from ingested SW (Hirano and

Utida, 1968, 1971). It is unlikely that changes in cortisol alone are sufficient to trigger increased water uptake by the eel digestive tract, and it is still unclear whether such changes precede SW entry as preparatory adaptations. Other hormones have been implicated in osmoregulatory processes, including atrial natriuretic peptide and somatostatin (reviewed by Ando et al., 2003; Rankin, 2009), but their roles are unclear. The advent of high-throughput genomic techniques such as microarray analysis (Kalujnaia et al., 2007) should yield additional clues about the physiological and hormonal processes that prepare the temperate eels for seaward migration.

### 5.2.2. MUGILIDS

The catadromous mullets (Mugilidae) spawn in offshore SW waters, and the newly hatched larvae drift shoreward into saltmarshes and estuaries where they develop into juveniles (Moore, 1974; McDowall, 1988; Nordlie, 2000). Striped mullet (*Mugil cephalus*) larvae and small juveniles are not capable of osmoregulating in FW until they are least 40 mm in length (Nordlie et al., 1982; Ciccotti et al., 1995), but survive and grow in 17 ppt to full SW. While larger juveniles are tolerant of salinities from FW to SW, they generally remain in elevated salinities (Nordlie, 2000; Cardona, 2006), where growth is enhanced (Nordlie, 2000; Cardona, 2006). This may be because the energetic costs of osmoregulation are lowered when the animals are in oligomesohaline (brackish) waters nearer the osmolality of their own tissues (Murashige et al., 1991; Cardona, 2006).

The mullets also apparently maintain a state of physiological “preparedness” for a wide range of salinities. FW ionocytes are found on the gill filament, the interlamellar space, and the lamellae, and increase in density in response to low salinity (Cicotti et al., 1994; Khodabandeh et al., 2009). Entry into FW is marked by pronounced increases in gill NKA activity (Gallis and Bourdichon, 1976; Cicotti et al., 1994), which is localized to gill ionocytes (Cicotti et al., 1994; Khodabandeh et al., 2009).

SW ionocytes dominate the interlamellar space in SW-acclimated animals. Like the ionocytes of other euryhaline fishes, these cells are characterized by an elongated shape and a pronounced apical crypt (Cicotti et al., 1994). Given the increasing scarcity of temperate eels, and the ability to rear large numbers of mullet in hatcheries (Lee and Ostrowski, 2001), it is conceivable that this fish could serve as an important model to further our understanding of the physiological drivers and basis for catadromy.

### 5.3. Amphidromous Fishes

Because amphidromous fishes migrate seaward soon after hatching, early development of SW tolerance is necessitated. The fundamental mechanisms of

osmoregulation in the amphidromous fishes are probably the same as in their diadromous counterparts (e.g. [McCormick et al., 2003](#)). FW ionocytes play a more dominant role in FW adults, but SW ionocytes are likely to be more important in the larvae as they passively drift from FW, through estuaries, and on to SW. Studies on the amphidromous ayu (*Plecoglossus altivelis*) of Japan suggest that increased temperature and salinity lead to more rapid yolk depletion and impaired growth in larvae ([Iguchi and Takeshima, 2011](#)). The gills probably take on added importance after the yolk sac is resorbed ([Rombough, 1988](#)), as described in the juvenile Hawaiian goby (*Stenogobius hawaiiensis*) ([McCormick et al., 2003](#)). These metamorphosed juveniles captured in FW have ionocytes found on both the gill filament and the lamellae. Following acclimation to SW (20 and 30 ppt), the ionocytes increase in size and number. This increase is accompanied by a modest increase in the abundance of basolateral NKCC and NKA proteins, and NKA activity. Immunopositive staining for CFTR increases markedly in SW, and the protein is restricted to the apical crypts of the SW ionocytes. Thus, these amphidromous gobies retain their ability to osmoregulate in SW for some time after FW entry. This is similar to the pattern noted earlier in the striped bass, but also the estuarine mummichog ([Marshall, 2013](#), Chapter 8, this volume).

Preparatory adaptation is probably essential for larval amphidromous fishes. In the Antillian rock-climbing goby (*Sicydium punctatum*), early larvae (0–5 d posthatch) select salinities less than 10 ppt, but within a week volitionally occupy increasing salinities. Exposure to elevated salinities is associated with an early cessation of migratory behaviors ([Bell and Brown, 1995](#)). [Yada et al. \(2010\)](#) used a salinity gradient that allowed larval ayu to spontaneously move from FW to SW. Their study revealed that a marked downregulation of prolactin mRNA takes place within 10 days of hatching, coinciding with movement into SW. Similar reductions in GH are also observed, although slightly delayed. Whole-body water and Na<sup>+</sup> content are similar in SW-selecting and FW-selecting fishes, but these metrics are perturbed in larvae abruptly transferred into SW. It is therefore tempting to speculate that reduced prolactin secretion precedes SW entry in these (and perhaps other) amphidromous fishes.

Metamorphosis in the amphidromous goby (*Sicyopterus lagocephalus*) appears to be triggered by a rise in both T<sub>3</sub> and T<sub>4</sub> ([Taillebois et al., 2011](#)). Given the importance that these hormones have in osmoregulation and development in other diadromous fishes, they are likely to influence osmoregulation following this species' return to FW. While this work begins to prove the endocrine control of FW entry, the role of T<sub>3</sub> and T<sub>4</sub> in the preparatory adaptation for SW entry as larvae remains a conspicuous gap in our knowledge. Very little is known of the relationship between osmotic tolerances and development in amphidromous fishes.

#### 5.4. Freshwater-Linked and Seawater-Linked Fishes

FW-linked organisms face the challenge of possibly having to hypoosmoregulate in saline waters, and the current evidence suggests that this is achieved through the modulation of FW and SW gill ionocyte abundance and distribution, and corresponding increases in NKA activity (Morgan et al., 1997; Varsamos et al., 2005; Tseng and Hwang, 2008). Drinking also increases in FW-linked fishes such as the Mozambique tilapia following the FW to SW transition, along with decreases in urinary output (Varsamos et al., 2005). Although the Mozambique tilapia can withstand full-strength SW, many other FW-linked fishes that facultatively use the estuary have upper tolerance levels well below full-strength SW. For instance, Sr:Ca otolith data suggest that wild largemouth bass (*M. salmoides*) can withstand salinities approaching 10 ppt in estuaries along the US Atlantic coast, but tend to avoid higher salinities, probably due to physiological constraints (Lowe et al., 2009). The bulk of evidence generated so far would seem to suggest that the FW-linked fishes respond to more saline waters, rather than making any preparatory physiological adjustments before entering higher salinities. However, this working hypothesis could change as more work is done on these estuarine fishes.

Preparatory adaptation is also important in SW-linked fishes such as the flounder (*P. dentatus*) and gilthead sea bream (*S. aurata*), which hatch at sea in full-strength SW and drift into the estuary (Schreiber and Specker, 2000; Bodinier et al., 2010). In the summer flounder, thyroid hormone is critical for triggering metamorphosis, and it probably triggers a shift from larval ionocytes that function in the dilute salinities of the estuary to juvenile ionocytes better suited to ion excretion in SW (Schreiber and Specker, 2000). In the sea bream, osmotic tolerance is dependent upon increased ionocytes in the integument and the gills, reflecting the variable salinity these fish experience (Bodinier et al., 2010). More work is needed, however, to determine whether changes to the osmoregulatory apparatus are initiated before entry into SW.

The use of the estuary may also be facultative. For instance, SW-linked juvenile sea bass (*Dicentrarchus labrax*) reproduce and hatch in saltwater, with some juveniles entering more dilute BW (Nebel et al., 2005). However, survival is highly variable in the more dilute waters of the estuary and rivers up which some animals are known to migrate (Lemaire et al., 2000; Varsamos, 2002). The underlying physiological basis for the inability of some fish to cope with more dilute waters appears to be related to the lack of renal tubules, which makes it impossible for the fish to produce the copious amounts of dilute (hypoosmotic) urine needed to counteract water uptake in more dilute waters (Nebel et al., 2005). While these differences may be

genetically predetermined (Nebel et al., 2005), these findings also suggest that sea bass may have a narrow window of opportunity to take advantage of the estuary, before ontogenetically determined changes more suited to life in SW environments become irreversible. Ultimately, a better understanding of the underlying physiological mechanisms, and the endogenous (endocrine signals, genetic preprogramming) and exogenous signals (e.g. photoperiod, temperature) that regulate these processes, is needed to more fully understand habitat use by FW-linked and SW-linked fishes.

## 6. GROWTH AND OSMOREGULATION

Osmoregulating fish in FW or SW must actively transport ions, necessitating energy expenditures associated with standard metabolic rate. Assuming hypoosmoregulation and hyperosmoregulation both require active energy inputs, an isosmotic environment of approximately 12 ppt should be least taxing (Potts, 1954; Watanabe et al., 1989; Wootton, 1990; Gaumet et al., 1995; Imsland et al., 2001; Rocha et al., 2005), as demonstrated for Mozambique tilapia (*Oreochromis mossambicus*) (Febry and Lutz, 1987; Morgan et al., 1997; Chang et al., 2007). Observed patterns diverge from this construct, varying with species, ontogeny, and season (Gutt, 1985; Morgan and Iwama, 1991; Lambert et al., 1994; Deacon and Hecht, 1999). The energy cost of osmoregulation in different salinities may be relatively modest in teleosts (Boeuf and Payan, 2001) but can be significant when salinity shifts rapidly (Du Preez et al., 1990; Morgan et al., 1997; Morgan and Iwama, 1999). Salinity effects can be acute. If unable to offset the mass actions of the surrounding environment, disruption of ion balance occurs in advance of metabolic failure and mortality (Woo and Fung, 1981). An expanded examination of the energetics of osmoregulation can be found in Chapter 9 of this volume (Brauner et al., 2013).

Salinity may impact metabolism directly (increasing standard metabolic rate) or indirectly through food conversion efficiency, endocrine shifts associated with acclimation, or changing feeding behavior (Boeuf and Payan, 2001). Direct metabolic costs of osmoregulation in SW have been reported to be as low as approximately 10% in recent studies (e.g. Kidder et al., 2006) but as much as 50% in others (Boeuf and Payan, 2001). Because endocrine factors that affect osmoregulation are also important for growth (e.g. IGF-I and GH) (McCormick, 1996; Mancera and McCormick, 1998), the impact of salinity may transcend a simple energetic cost. Because drinking is an active part of the osmoregulatory process in SW, the scope for growth in SW may be influenced by the increased ATP demands that SW

ingestion could place on the enterocytes (absorptive cells) of the gastrointestinal tract. As a result, energy partitioning could influence the external and internal milieu of the gastrointestinal tract, influencing digestion and food conversion efficiency (DeSilva and Perera, 1976; MacLeod, 1977; Ferraris et al., 1986). For many fish, salinity does influence growth and this optimum can be empirically assessed.

Many FW spawners (FW-linked, anadromous, and amphidromous fishes) have higher growth rates in salinities at or below isosmotic (0–12 ppt). Even some stenohaline FW species exhibit increased growth at low salinities, below 2 ppt, by increasing their food conversion rate (Boeuf and Payan, 2001), perhaps by offsetting the costs of ion uptake in FW (e.g. the FW catfish *Mystus vittatus*) (Arunachalam and Reddy, 1979). As the environment becomes more saline, growth scope declines (Britz and Hecht, 1989; Morgan and Iwama, 1991; Brown et al., 1992). For green sturgeon there is no difference in metabolic rate in FW or SW, but osmotic perturbations in SW may prevent entry into SW or confer a growth disadvantage (Allen and Cech, 2007). Lower growth rates in SW have been observed in other sturgeon juveniles (e.g. shortnose sturgeon) (Jarvis and Ballantyne, 2003). Some species have fairly defined optima, e.g. approximately 7 ppt for striped bass (Brown et al., 1992). For some amphidromous fishes, the early growth phase may be optimized in BW. For the ayu high salinity results in the acceleration of yolk depletion and reduced growth (Iguchi and Takeshima, 2011). The distribution of ayu larvae near shore through the yolk-sac and larval stage (Tago, 2002; Yagi et al., 2006) suggests the significance of low-salinity BW in their survival.

Conversely, many SW-linked and catadromous fishes generally have increasing growth near or above isosmotic (usually 5–18 ppt; Boeuf and Payan, 2001; Morrison and Secour, 2003; Jessop et al., 2008; Acou et al., 2003; Melia et al., 2006). While the estuary may be viewed as an environment to which many SW fishes are not adapted, many species exhibit greater growth at lower salinities, e.g. European flounder (*Platichthys flesus*) (Gutt, 1985) and Atlantic cod (*Gadus morhua*) (Lambert et al., 1994). Increased growth rate may not necessarily indicate the lowest cost of osmoregulation, but an integration of processes. Cod grown at 7 ppt had higher growth than at 28 ppt owing to greater food conversion efficiency (Boeuf and Payan, 2001), and feeding can decrease in juvenile cod at higher salinities (Lambert et al., 1994). Changing conditions can change feeding dynamics (Le Bail and Boeuf, 1997). For turbot (*Scophthalmus maximus*), greater growth at or near isosmotic salinity was linked to increased food ingestion (Gaumet et al., 1995; Imsland et al., 2001).

It should be noted that assessment of metabolic costs and growth is usually accomplished in a static setting and does not incorporate costs of

movements through varying salinity environments. Swimming studies on tilapia (*Oreochromis niloticus*) (Farmer and Beamish, 1969) and *O. mossambicus* (Febry and Lutz, 1987) indicated that oxygen consumption at 12 ppt was lower than in full FW or SW, yet growth studies at near isotonic conditions provide less clear results (Morgan and Iwama, 1991; Boeuf and Payan, 2001). Such apparent differences may be associated with the multiple functions of the gill for respiration and osmoregulation. Across a steep osmotic gradient, there is a theoretical diminishing return on increased gill perfusion due to the cost of ion transport (Boeuf and Payan, 2001) leading to an osmoregulatory compromise (Nilsson, 1986).

Growth and metabolism are effective physiological assessments not only of salinity influence, but also of the optimal environmental conditions of a fish (Cech, 1990). Modeling of environmental parameters in an ecological framework has provided valuable insight into the role of osmoregulation in bluegill (*Lepomis macrochirus*) (Neill et al., 2004), red drum (*Sciaenops ocellatus*) (Fontaine et al., 2007), and juvenile sole (*Solea solea*) (Fonseca et al., 2010). For many fish in the estuary, salinity in conjunction with temperature and oxygen can define suitable habitat (Imsland et al., 2001). For example, white perch have reduced feeding and increased metabolic costs associated with salinities greater than 16 ppt (Hanks and Secor, 2011) and these fish are seldom observed in salinities that exceed this level (Setzler-Hamilton, 1991; Nemerson and Able, 2004). Juvenile white perch exhibit the greatest growth rates in salinities from 4 to 8 ppt (Kerr and Secor, 2009), but this benefit is not independent of temperature and dissolved oxygen. The interaction of these environmental factors has been characterized as a “habitat squeeze” (Coutant and Benson, 1990; Niklitschek and Secor, 2005; Hanks and Secor, 2011) where temperature increases escalate basal metabolic demands (Guderley and Pörtner, 2010), further perturbing the osmorepiratory compromise. In addition to increased metabolic rates under hypoxic conditions, food consumption decreases (Hanks and Secor, 2011). These three environmental factors therefore limit rearing areas for juvenile white perch through their impact on growth and, probably, performance (Miltner et al., 1995; Lankford et al., 2001; Harrison and Whitfield, 2006). It is not unreasonable to assume that other fishes would be similarly limited.

## 7. CONCLUSIONS AND PERSPECTIVES

Over the past few decades advances in a suite of technologies have informed both the “where” and “how” of diadromous migrations.

Telemetry has long been used for direct tracking of large species (e.g. sturgeon) (Taverny et al., 2002; Kelly et al., 2007) but technological advances have allowed effective tracking even for moderately sized juveniles such as salmon smolts (e.g. Holbrook et al., 2011). The advent of Sr:Ca microchemical analysis of otoliths, and the correlation with salinity, changed the playing field in the study of migrating fishes (Kalish, 1990; Secor, 1992; Secor et al., 1995; de Pontual et al., 2003). This approach has advanced our understanding of migratory patterns on one hand while blurring the lines of stereotyped life history variants on the other. The use of stable isotopes has also revealed complexities in movement patterns. Isotope signatures can reflect integration of diet over several weeks, allowing spatial feeding patterns to be inferred over a brief timescale (Hesslein et al., 1993; Barnes and Jennings, 2007). In addition to using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measures,  $\delta^{34}\text{S}$  has likewise emerged as an important tool for assessing movement in estuarine fishes (Hoffman et al., 2007; Fry and Chumchal, 2011). Less technical approaches have also been informative. Trnski (2002) physically followed the larvae of estuary-dependent coastal spawners using scuba gear. Together, these efforts have revealed the degree to which many fish that migrate between FW and SW are facultative in their use of the estuary (Gerking, 1994; Blaber, 1997; Wootton, 1999; Elliott and Hemingway, 2002; Elliott et al., 2007). The construct of “contingent behaviors” as described by Kerr and Secor (2010) is useful in describing variations in migratory patterns.

Understanding dynamic habitat shifts of the estuary and their importance to euryhaline fishes will be critical as estuarine waters become more highly impacted by human activity (Able, 1999; Hoss et al., 1999; Quinlan and Crowder, 1999). The recruitment of ecologically important species like the anchovy (*Engraulis encrasicolus*) is strongly linked to river inflow (Chícharo et al., 2001; Drake et al., 2007) such that impoundments would be likely to compromise anchovy success (Morais et al., 2009; Morais et al., 2010). Degradation of estuarine conditions has been linked to lower survival rates in salmonine species (Magnusson and Hilborn, 2003), and there is no reason to suspect that these effects would be restricted to salmonines in the reduction of life history and species diversity. Longer term stressors due to factors such as climate change may influence settlement habitats (Able et al., 2006). A northward creep of distributions of euryhaline fishes has already begun to reshape temperate estuaries (Nicolas et al., 2010). Flow regimens into estuarine systems impact the suitability of the estuary as a rearing habitat through their influence on salinity, temperature, and oxygen (Chícharo et al., 2006; Lassalle and Rochard, 2009). Hanks and Secor (2011) speculate that this “habitat squeeze” would be exacerbated by climate change scenarios (e.g. Najjar et al., 2010) as regions of hypoxia are

more likely to persist during the summer months of temperate estuaries (Breitburg et al., 2009). Industrial, agricultural, and municipal contaminants and reduced FW input could also have additive or synergistic impacts on available habitat (Cooper and Brush, 1991; Najjar et al., 2000; Niklitschek and Secor, 2005).

The estuarine environment is also likely to be a frontline for many invasive species. Salinity tolerance will probably define the speed and extent of expansions of invasives (e.g. armored catfish) (Capps et al., 2011) which may opportunistically use fluctuations in river plumes as a means of dispersal (Brown and St. Pierre, 2001; Bringolf et al., 2005; Scott et al., 2008). Non-native piscivores such as the largemouth bass (*M. salmoides*) may threaten estuary-dependent SW species along the Atlantic seaboard (Weyl and Lewis, 2006; Wasserman and Strydom, 2011; Peer et al., 2006; Norris et al., 2010). Invasives may also influence native euryhaline fishes through direct interaction, such as through competition between juveniles of SW-spawned and non-native fish species (Wathen et al., 2011; Wathen et al., 2012) or through diet overlap (Skelton, 1993; Mansfield and McCardle, 1998).

These ecological challenges are inextricably linked to the physiological abilities and ontogenic requirements of migrating species. Efforts to characterize the physiological adjustments that precede or accompany the FW to SW transition will inform measures to counter the inevitable challenges that these euryhaline fishes face. Although the past decade has seen an explosion of research on osmoregulation in migratory euryhaline species, much of the field remains open territory. However, several themes are emerging. There are notable commonalities between salmonine smoltification and many of the preparatory adaptations of other species described in this chapter. Like smolting salmonines, sea lamprey, alosines, and catadromous eels exhibit increases in NKA abundance and activity, as well as in branchial ionocytes, prior to seaward migration. In advance of SW entry (and/or upon SW entry) there is a shift from predominantly FW ionocytes to SW ionocytes. While preparatory adaptation may be obligatory, some fishes are quite plastic. Other species (e.g. alewife and striped bass) or other life stages (e.g. yellow eels) exhibit an impressive capacity to move between FW and SW. These fishes remain in a state of readiness, perhaps mediated by rapid control of ionocyte function.

Cortisol is a critical endocrine factor that mediates the changes in gill ionocyte structure and function in anticipation of SW entry. As in salmonines, thyroid hormone probably plays an important role by promoting corticosteroid receptor proliferation. The critical role played by  $T_4$  and  $T_3$  in initiating metamorphosis (e.g. in lampreys, flounders, and at least one species of ampipriform goby) appears to be directly tied to the

preparatory adaptation process. It also appears likely, as in salmonids, that cortisol acts in concert with GH to initiate SW ionocyte proliferation (McCormick, 2001; Evans et al., 2005). Our understanding of ion and water transport processes in the digestive tract has advanced substantially (Ando et al., 2003; Grosell, 2011) but research on the endocrine control of preparatory changes is limited. Less is known about the preparative changes of the kidneys, as they shift from the role of “bilge pump” to an organ of water conservation and divalent ion excretion. Although research is now beginning to shed light on cell-sensing and intracellular signaling pathways, particularly the interactions between IGF-I and EGF, and the MAP kinases in sensing cell volume, much more work is needed in this area.

A great deal more integrative research is therefore needed to learn how environmental, somatic, temporal, and physiological factors interact to allow fish to undergo the dramatic and critical transition from FW to SW. With the advent and development of more sophisticated techniques (e.g. cell isolation, morpholino, immunohistochemistry) and continual advances in genomics and proteomics, the tools are currently available to address the data gaps identified here. We are in a period of great discovery and of great potential. Integrative research approaches can not only inform our understanding of fish physiology, but also provide fisheries managers with the information they need to protect these fascinating and vulnerable species.

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