Fish Physiology and Biochemistry vol. 13 no. 1 pp 1-11 (1994)
Kugler Publications, Amsterdam/New York

Physiology of seawater acclimation in the striped bass, *Morone saxatilis* (Walbaum)

Steffen S. Madsen[1], Stephen D. McCormick[2], Graham Young[3], Jeanette S. Endersen, Richard S. Nishioka and Howard A. Bern
Department of Integrative Biology, Cancer Research Laboratory and Bodega Marine Laboratory, University of California, Berkeley, California 94720, U.S.A.

Accepted: January 7, 1994

Keywords: striped bass, osmoregulation, Na^+,K^+-ATPase, chloride cell, intestinal water transport, cortisol, thyroxine

Abstract

Several experiments were performed to investigate the physiology of seawater acclimation in the striped bass, *Morone saxatilis*. Transfer of fish from fresh water (FW) to seawater (SW; 31–32 ppt) induced only a minimal disturbance of osmotic homeostasis. Ambient salinity did not affect plasma thyroxine, but plasma cortisol remained elevated for 24h after SW transfer. Gill and opercular membrane chloride cell density and Na^+,K^+-ATPase activity were relatively high and unaffected by salinity. Average chloride cell size, however, was slightly increased (16%) in SW-acclimated fish. Gill succinate dehydrogenase activity was higher in SW-acclimated fish than in FW fish. Kidney Na^+,K^+-ATPase activity was slightly lower (16%) in SW fish than in FW fish. Posterior intestinal Na^+,K^+-ATPase activity and water transport capacity (J_v) did not change upon SW transfer, whereas middle intestinal Na^+,K^+-ATPase activity increased 35% after transfer and was correlated with an increase in J_v (110%). As salinity induced only minor changes in the osmoregulatory organs examined, it is proposed that the intrinsic euryhalinity of the striped bass may be related to a high degree of "preparedness" for hypoosmoregulation that is uncommon among teleosts studied to data.

Introduction

The striped bass, *Morone saxatilis*, is a percichthyid teleost whose native range covers the east coast of North America (Raney 1952). The species was successfully introduced to the Pacific coast of North America between 1879 and 1900 – initially into the Sacramento River. Most naturally reproducing striped bass, including the Californian populations, follow an anadromous life cycle and their tolerance for brackish water and seawater (SW) shortly after hatching has been recognised (Doroshev 1970). Migration into SW can, however, occur at all stages, and is not a prerequisite for sexual maturation (see Specker *et al.* 1987). Furthermore, striped bass are capable of spawning and hatching in both fresh water (FW) and brackish water (Talbot 1966; Setzler *et al.* 1980). Naturally occurring non-anadromous populations that complete their lifecycle in FW are found along the coast of the Gulf of Mexico (Setzler *et al.* 1980), which represents the southern border of this species natural range.

The early development of SW tolerance (Doroshev 1970) makes the striped bass an excellent

Current addresses: [1]*Institute of Biology, Odense University, Campusvej 55, DK-5230 Odense M, Denmark*; [2]*Anadromous Fish Research Center, U.S. Fish and Wildlife Service, P.O. Box 796, Turners Falls, MA 01376, U.S.A.*; [3]*Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand.*

model for the study of euryhalinity. However, few studies have been concerned with the physiology of SW acclimation in this species. Chloride cells are present in the branchial epithelium and apparently undergo little ultrastructural change during SW acclimation (King and Hossler 1991). The aim of this study was to characterise the physiological and biochemical mechanisms involved in SW acclimation in the striped bass, and to determine how this species tolerates abrupt transfer from FW to full-strength SW. The time course of SW acclimation was studied, and FW- and SW-acclimated fish were compared with respect to several parameters in gill, opercular membrane, intestine and kidney.

Materials and methods

Experimental protocol

Striped bass, *Morone saxatilis*, used in experiments A and B were obtained from Central Valley Hatchery, Elk Grove, Sacramento, CA (California Department of Fish and Game) as one-two-year-old fish. They were reared in fresh water (FW; $[Na^+]$: 0.8 mM; $[Ca^{2+}]$: 0.3 mM), but were exposed to routine salt treatment (< 0.5% NaCl, < 12h) in the hatchery whenever handled or transported. Addition of salt has been shown to reduce the stress response and post-handling mortality in striped bass (Mazik *et al.* 1991).

Time course of seawater acclimation

A SW-transfer experiment was conducted in March-April 1990 with immature fish of both sexes weighing 262 ± 10 g (mean ± SEM, n = 104). The fish were previously kept in outdoor raceways for 1 month with flowthrough FW $[Na^+]$: 1.3 mM; $[Ca^{2+}]$: 0.9 mM; 10–12°C) at Bodega Marine Laboratory (BML) and fed Oregon Moist Pellets *ad libitum* once daily. Seawater (SW) transfer was accomplished by turning off the FW inflow and lowering the water level in the raceway to approximately 50%. SW supply was then turned on (time 0h) and 28 ppt was achieved within 1h. Full-strength SW (31–32 ppt, 12 ± 1°C) was attained after less than 6h. A group of control fish was treated similarly, but FW was used rather than SW. The experiment lasted for 21 days and subgroups of eight fish were sampled 0, 6 and 12h, and 1, 3, 7, and 21 days after transfer. Food was withheld 24h before sampling and SW transfer. Fish were killed by cranial concussion, blood was collected from the caudal vessels into heparinized syringes, and plasma was immediately separated by centrifugation and stored frozen until analysed. Filaments collected from the second gill arch were frozen on dry ice in sucrose-EDTA-imidazole buffer (SEI: 300 mM sucrose, 20 mM Na_2EDTA, 50 mM imidazole, pH 7.3), and stored at −80°C untilanalysed. Plasma osmolality, thyroxine and cortisol levels, and gill Na^+,K^+-ATPase activity were analysed as described below.

On day 21, second gill arches from FW and SW fish were stained using Champy-Maillet's fixative (McCormick 1990a), and chloride cells were counted and measured (see below).

Comparison of FW- and SW-acclimated fish

Hatchery reared fish (50–100 g) were held in either FW or SW raceways (12–14°C) at BML > 4 months before use and were fed as above. In October–December 1991, several experiments were performed in which opercular membranes, gills, kidney or intestine were sampled and analysed.

Second gill arches and the entire kidney were frozen in SEI buffer for measurement of enzyme activities. Opercular membranes were dissected and either stained immediately for chloride cell counts or frozen in SEI buffer for Na^+,K^+-ATPase analysis. Intestinal mucosa were scraped from musculature and stored frozen in SEI buffer for determination of Na^+,K^+-ATPase activity. In separate experiments, whole intestinal segments were used for measurement of water transport capacity (J_v).

Fish from a FW reservoir

Owing to the possible impact on osmoregulatory physiology of previous salt exposure in the hatch-

ery, hatchery-reared FW fish and wild FW fish were compared. The latter were electrofished in October 1991 in the New Hogan Reservoir, CA ($[Na^+]$: 0.2 mM; $[Ca^{2+}]$: 0.3 mM) with assistance from the California Department of Fish and Game. These fish were descendants of fish that had been isolated in the reservoir for generations, and thus had never been exposed to saline. After capture, the fish (200–600 g) were kept in an aerated holding tank (< 2h) and subsequently sampled for gills and opercular membranes. Gills were immediately frozen on dry ice in SEI buffer, and opercular membranes were stored in chilled Ringer's solution (140 mM NaCl, 25 mM $NaHCO_3$, 2.3 mM KCl, 2.1 mM $CaCl_2$, 1.4 mM $MgSO_4$, 1.3 mM KH_2PO_4, 10 mM D-glucose) oxygenated with 99:1 O_2:CO_2 until analysis (< 3h). These storage conditions did not affect the DASPEI staining capacity of the membranes (S.S. Madsen 1992, unpublished).

Analytical methods

Frozen samples were analysed within 3 months after sampling.

Plasma osmolality was determined with a micro vapour pressure osmometer (Wescor, Logan, UT).

Plasma cortisol and thyroxine were analysed by radioimmunoassay (Young 1986; Specker and Kobuke 1987) previously validated for use with striped bass plasma (Brown *et al.* 1987).

Opercular membrane chloride cell density was estimated using the DASPEI technique described by Foskett *et al.* (1981). DASPEI is a vital dye that specifically stains active mitochondria (Bereiter-Hahn 1976). Each membrane was incubated for 30–45 min in 2 µM DASPEI, rinsed and examined at 10 × magnification with a Zeiss epifluorescence microscope (100 W mercury illuminator, 450–490 nm excitation filter, 510-nm chromatic beam splitter, 520-nm longwave-pass filter). Thirty to fifty frames, covering a total area of 17–28 mm^2, were randomly chosen from each membrane and recorded onto an optical disc (Panasonic OMDR, Tokyo) *via* a CCD video camera (MTI, Boston, MA). Using playback and a computerised image-analysing system (Image-1, Universal Imaging, West Chester, PA), chloride cell density (cells/cm^2) was measured on each frame and calculated for each fish.

Gill chloride cell density was measured in 5 µm sections of Champy-Maillet fixed specimens (stains phospholipids of the extensive tubular system; Garcia-Romeau and Masoni 1970). Interlamellar chloride cell density was measured blindly in coded slides by counting the number of chloride cells in a 470 µm diameter field (40 × objective) and dividing by the number of lamellae. At least twelve sections were chosen at random for each individual.

Gill chloride cell size was also measured in the above sections by obtaining a digital image with a CCD camera on a Nikon Diaphot microscope and analysing with the Image-1 program. The outline of chloride cells was obtained by thresholding the image of each section individually (converting gray levels above and below a certain threshold into a binary image). Threshold levels varied < 10%. Cell area (μm^2) was calculated using a stage micrometer as external standard.

Na^+,K^+-ATPase activity was measured at 25°C in homogenates of gill, kidney, opercular membrane and intestinal scrapings using a NADH-coupled assay as described by McCormick and Bern (1989). The intestine was roughly divided into middle and posterior segments by a cut through the ileorectal valve. Initially, the requirement of gill Na^+,K^+-ATPase for Na^+, K^+ and Mg^{2+} was investigated in FW fish and SW-acclimated fish in a series of optimisation assays (Fig. 5). In these assays, the concentrations of two cations were held constant while the third ionic species was varied. Optimal salt conditions, used routinely in all other ATPase assays reported, were found to be the same as those used as routine conditions by McCormick and Bern (1989) (45 mM Na^+, 10 mM K^+ and 2.5 mM Mg^{2+}). Optimal ATP (Na_2ATP, vanadate free, Sigma, St. Louis, MO) concentration was found to be 0.5 mM. Protein content of tissue homogenates was analysed according to Lowry *et al.* (1951), and the results were expressed as µmol ADP/mg protein/h.

Succinic dehydrogenase (SDH) activity was determined in gill homogenates according to Clark and Porteous (1964) as the rate of reduction of 0.07% (w/v) iodonitrotetrazolium violet (INT) to

formazan. Gills were homogenised (300 mM sucrose, 100 mM imidazole, 10 mM Na_2EDTA, 10 mM mercaptoethanol, pH 7.2) and centrifuged at 500 × g for 30 sec. An aliquot of the supernatant was then incubated for 20 min under the following conditions: 0.25 mg/ml homogenate protein in 50 mM sodium succinate, 50 mM imidazole, 70 mM sucrose, 2 mM Na_2EDTA, 2 mM mercaptoethanol, pH 7.2, 20°C. The reaction was linear over this time period, and was terminated by adding chilled trichloracetic acid (final concentration 3% w/v). Formazan was extracted with ethyl acetate and measured spectrophotometrically at 490 nm. The specificity of the assay for succinate was tested by addition of 50 mM malonate, which completely inhibited the succinate-dependent formation of formazan (data not shown). Protein content was analysed according to Lowry *et al.* (1951), and results were expressed in nmol formazan/mg protein/h.

Intestinal water transport capacity (J_v) was measured in fish that were non-fed for 3–4 days prior to sampling. The following method for measuring J_v was modified from Collie and Bern (1982). The fish were killed and the part of the intestine extending from approximately 1 cm posterior to the attachment of the pyloric caeca to the anus was excised. Perivisceral fat and large blood vessels were dissected away, and the intestine was divided into middle and posterior segments by a transverse cut through the ileorectal valve. Each segment was then rinsed with fish Ringer's solution (140 mM NaCl, 15 mM $NaHCO_3$, 1.5 mM $CaCl_2$, 1.0 mM KH_2PO_4, 0.8 mM $MgSO_4$, 2.5 mM KCl, 10 mM D-glucose, 5 mM N-2-hydroxyethyl-piperazine propanesulfonic acid, pH 7.8) and tied on to the flared end of a 2-cm piece of polyethylene tubing. To avoid air bubbles, Ringer was slowly flushed through the segment as the other end was tied to form a noneverted gut sac. The sac was filled with Ringer and closed by inserting a plastic plug into the tubing. The sacs were preincubated for 1–2h in Ringer gassed with 99:1 O_2:CO_2 at 16°C, after which the contents were replaced with fresh Ringer. The sacs were then incubated in Ringer, and for the next 3 hours weighed to the nearest 0.001 g at 20- to 30-min intervals. They were gently blotted before each weighing, and the net mucosa-to-serosa water flux was calculated as the slope of the regression line for sac weight loss as a function of time. By weighing the empty, blotted sac after the experiment, water flux was normalised to wet weight and expressed as µl/g/h.

Statistics

Significant differences among groups were tested by one- or two-way ANOVA, Student t-test or Student-Newman-Keuls multiple comparison test, as appropriate. Results were considered significantly different when $p < 0.05$.

Results

Time course of SW acclimation

Plasma osmolality remained relatively constant in fish transferred to SW (Fig. 1), and was within 10 mOsm/kg of FW controls throughout the experiment. Two-way ANOVA revealed an overall effect of salinity ($p < 0.005$) on plasma osmolality; however, neither time nor time-salinity interaction had an effect. Only at 7 days was plasma osmolality higher after FW-SW transfer than after FW-FW transfer ($p < 0.05$).

Except for a minor peak in the FW-FW group one day after transfer ($p < 0.01$), there was no obvious pattern of change in plasma thyroxine (Fig. 1). Mean values remained within the range of 3 to 8 ng/ml. Time and time-salinity ($p < 0.001$) affected plasma thyroxine levels, whereas salinity by itself had no effect.

Plasma cortisol increased 20-fold within 6h of transfer to SW, and was higher than FW values at 6 and 12h ($p < 0.01$, Fig. 1). There was a return to basal levels within 3 days. A nonsignificant peak was observed in the FW-FW group 12h after transfer. Both salinity, time and the interaction of time and salinity strongly influenced plasma cortisol levels ($p < 0.0001$).

Gill Na^+,K^+-ATPase activity (Fig. 1) was not influenced by salinity, but there was an overall effect of time ($p < 0.0001$), with levels increasing gradually over the 21-day experimental period.

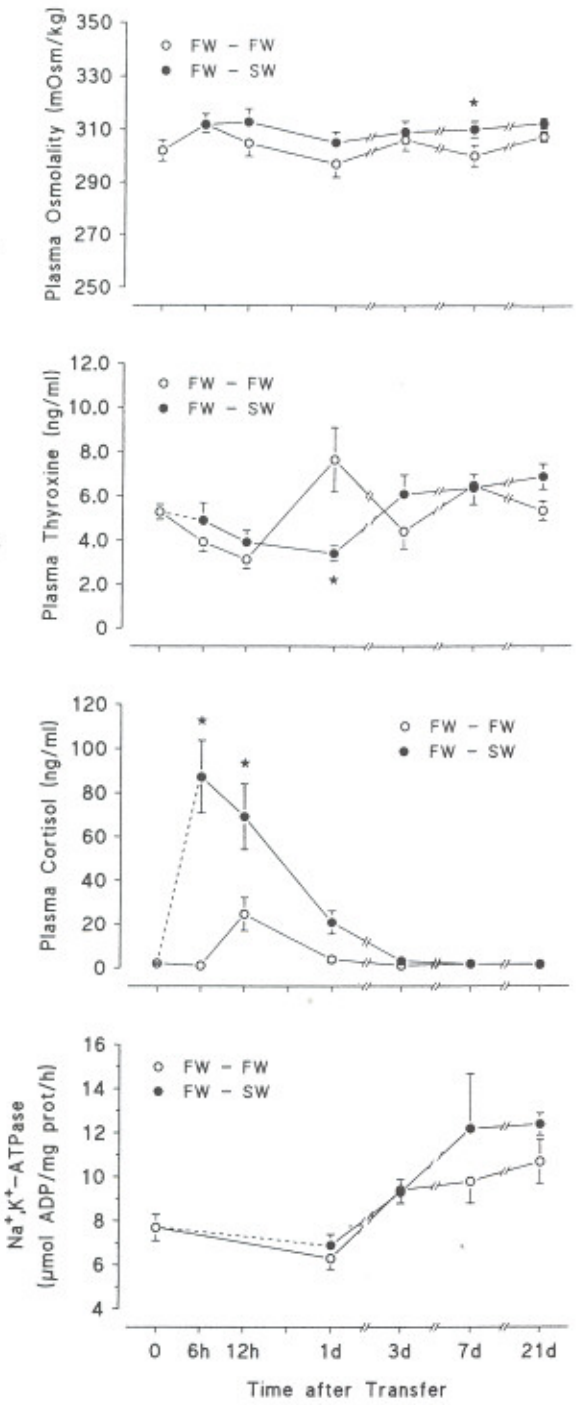

Fig. 1. Changes in plasma osmolality, thyroxine, cortisol and gill Na^+,K^+-ATPase activity in *M. saxatilis* transferred from FW to FW (○) or SW (●). Values are means ± SEM (n = 8). *$p < 0.05$, different from FW-FW value.

Gill chloride cells were present throughout the interlamellar space but were most numerous near the trailing edge of the primary filament (Fig 2). Secondary lamellae chloride cells made up < 0.2% of all chloride cells. Chloride cell density and distribution pattern were unaffected by salinity but cell size was increased 16% ($p < 0.0001$) after 21 days in SW (Table 1, Fig. 2).

Comparison of FW fish and SW-acclimated fish

Kidney Na^+,K^+-ATPase activity was slightly lower and middle intestinal Na^+,K^+-ATPase activity higher in SW-acclimated fish than in FW fish ($p < 0.05$, Fig. 3). Gill and posterior intestinal Na^+,K^+-ATPase activities were unaffected by acclimation to SW (Fig. 3).

Opercular membrane chloride cell density and Na^+,K^+-ATPase activity were unaffected by acclimation to SW (Table 2). Branchial SDH activity, however, was 60% higher in SW-acclimated than in FW fish ($p < 0.05$, Table 2).

Water transport capacity (J_v) of the middle intestine was increased in fish exposed to SW ($p < 0.05$). In contrast, J_v in the posterior region was already high in FW and remained unchanged upon SW exposure (Fig. 4).

Salinity had no effect on gill Na^+,K^+-ATPase apparent affinities for Na^+, K^+ or Mg^{2+} (Fig. 5). This further validates the method for measurement of gill Na^+,K^+-ATPase in fish from both FW and SW.

Fish from a FW reservoir

Fish caught in the New Hogan Reservoir (FW) had chloride cell numbers and gill Na^+,K^+-ATPase activities in the same range as hatchery-reared FW fish and SW-acclimated fish (Table 2).

Discussion

Acclimation of anadromous and euryhaline teleosts to SW has been the subject of a large number of

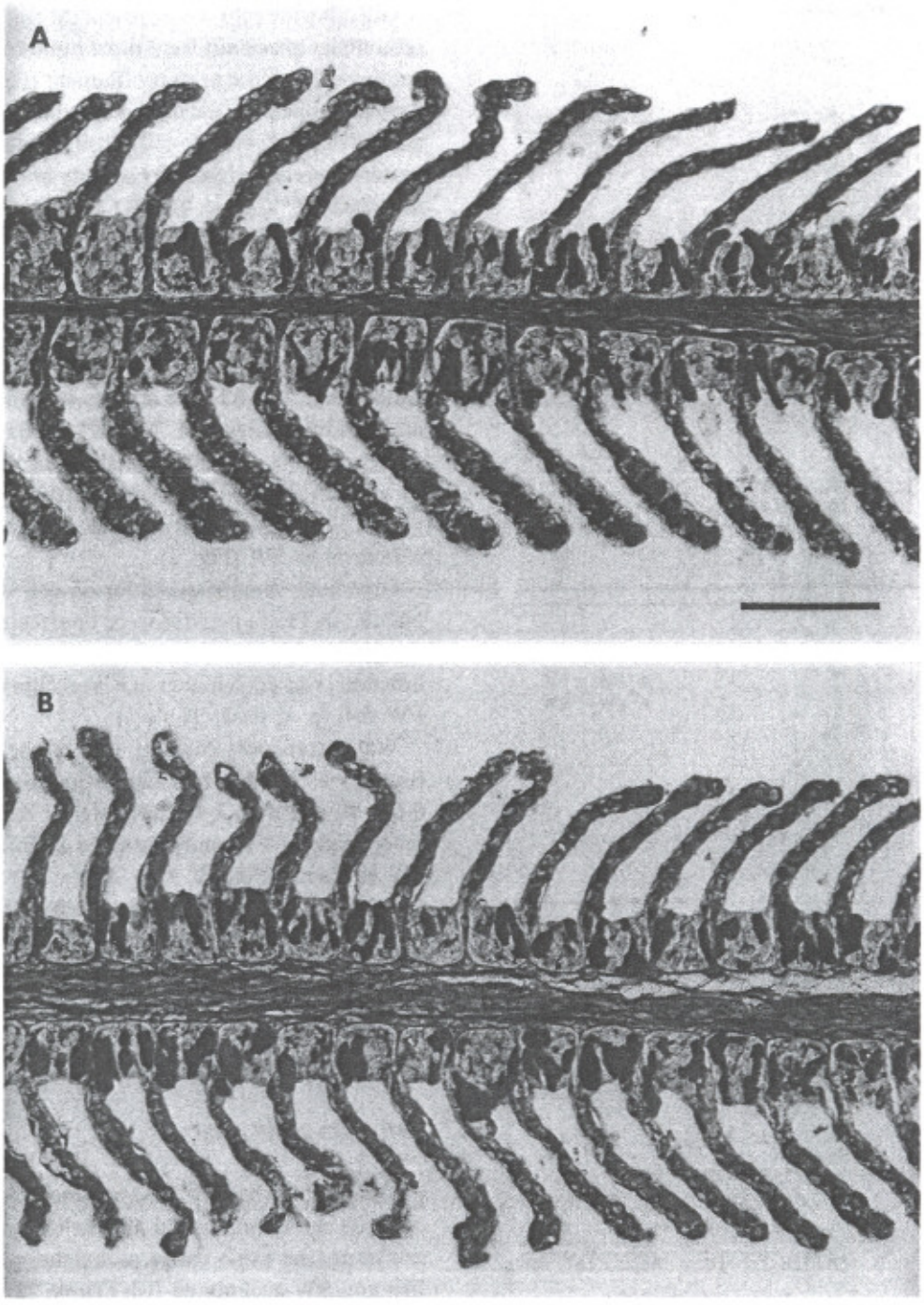

Fig. 2. Sections of a gill filament from FW (A) and SW (B) acclimated fish. Chloride cells were stained black with Champy-Maillet's fixative. The tissue was cut in 5 µm sections parallel to the long axes of the primary filament and perpendicular to the secondary lamellae. Bar = 40 µm.

Table 1. Chloride cell density and cell size in *M. saxatilis* in FW or acclimated to SW for 21 days. Cell counts were made from at least 15 sections from 4 individuals at each salinity (> 3000 cells in each group). Cell size was measured for > 100 cells from each of 4 fish at each salinity

	Chloride cell density (# cells/lamella)	Chloride cell size (μm^2)
Freshwater	3.7 ± 0.3[a]	78.6 ± 1.6
Seawater	3.3 ± 0.3	91.4 ± 2.1*

[a]mean ± SEM; *p < 0.0001, different from FW value.

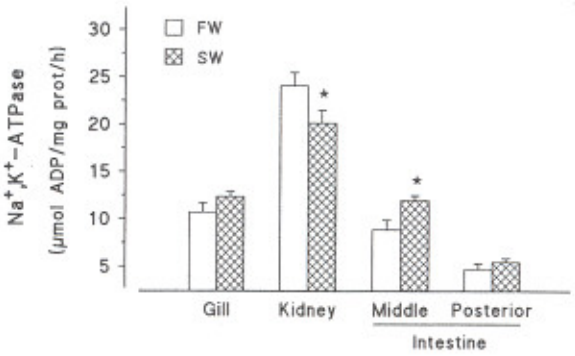

Fig. 3. Na^+,K^+-ATPase activity in various tissues in *M. saxatilis* reared and sampled in FW or acclimated to SW for several months. Values are means ± SEM (n = 10). *p < 0.05, different from FW value.

studies. The strategy of acclimation has been described for many species, most of which seem to undergo similar osmoregulatory adjustments upon entry into high salinity water. The general model emphasises the proliferation of the gill chloride cell system with its associated Na^+,K^+-ATPase in order to excrete excess salts derived from induced drinking and passive diffusion. This is often viewed as the rate limiting process and requires more than 5 days for acclimation from FW to full strength SW. A few marine species make an exception to this model, however, in that enzyme activity does not change (*Platichthyes flesus*: Stagg and Shuttleworth 1982) or increases (*Dicentrarchus labrax*, *Crenimugil labrosus*: Lassere 1971) upon reverse acclimation to FW.

The present investigation reveals that the striped bass lacks the "classic" acclimation pattern with regard to development of gill and opercular membrane chloride cells and Na^+,K^+-ATPase activity. Only a small increase in cell size was found (Table 1), which may indicate altered cell activity. However, the degree of hypertrophy is much smaller than found in other species exposed to a similar change in environment (*Oreochromis mossambicus*: Foskett *et al.* 1983; *Gillichthys mirabilis*: Yoshikawa *et al.* 1993). The DASPEI-positive cells in the opercular membrane of FW and SW striped bass also stained well with Champy-Maillet's fixative and with anthroylouabain (McCormick 1990b;

Table 2. Plasma osmolality, gill Na^+,K^+-ATPase and succinic dehydrogenase (SDH) activity, operculum membrane chloride cell density (CCD) and opercular membrane Na^+,K^+-ATPase activity in *M. saxatilis*. Fish were either hatchery reared and acclimated to FW or SW or caught in New Hogan Reservoir (FW)

	Hatchery reared		New Hogan Reservoir (FW)
	FW-adapted	SW-adapted	
Plasma osmolality (mOsm/kg)	339.0 ± 2.0 (8)[a]	344.0 ± 3.5 (8)	–
Gill Na^+,K^+-ATPase (μmol ADP/mg prot/h)	11.1 ± 0.5 (8)	12.4 ± 0.6 (8)	12.1 ± 1.5 (5)
Gill SDH (nmol/mg prot/h)	135.9 ± 11.2 (8)	218.9 ± 15.7 (8)*	–
Operculum CCD ($cells/cm^2$)	9,645 ± 854 (10)	11,140 ± 778 (10)	12,426 ± 1,352 (5)*
Operculum Na^+,K^+-ATPase (μmol ADP/mg prot/h)	1.90 ± 0.16 (8)	1.61 ± 0.17 (8)	–

[a]mean ± SEM (n); *p < 0.05, different from hatchery reared FW value.

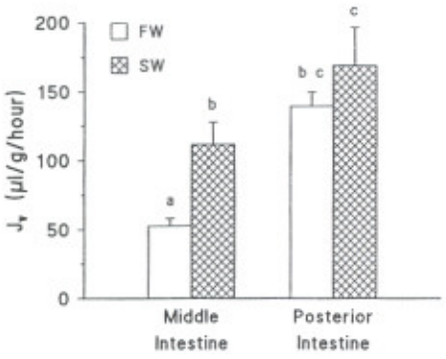

Fig. 4. Water transport capacity (J_v) in middle and posterior intestinal segments in *M. saxatilis* reared and sampled in FW or acclimated to SW for several months. Values are means ± SEM (n = 10). Values with shared symbols are not significantly different ($p > 0.05$).

S.S. Madsen 1992, unpublished), indicating that these cells are indeed chloride cells. The possibility that previous salt treatment to reduce handling stress might be responsible for the development of these cells was eliminated, inasmuch as similar numbers of DASPEI-positive cells occurred in landlocked specimens from a FW reservoirs (Table 2). Our analyses do not attempt to differentiate between different structural types of chloride cells (reviewed by Pisam and Rambourg 1991), and we cannot exclude transitions from one type to another that may facilitate osmotic acclimation. However, King and Hossler (1991) showed that striped bass branchial chloride cells undergo only minimal ultrastructural modification during SW acclimation compared with other species, and become active in salt extrusion after 1.5h in SW.

As shown by Foskett and Scheffy (1982), the chloride cell of the opercular membrane actively extrudes Cl^- in SW-acclimated tilapia (*O. mossambicus*). In tilapia and other species, fewer and less differentiated chloride cells appear in the opercular membrane of FW-acclimated fish. SW acclimation is characterised by increased density, size and complexity of chloride cells and their junctional connections with accessory cells, another mitochondrion-rich cell type (Laurent and Dunel 1980; Karnaky 1986). There is yet no direct evidence of active ion transport by FW chloride cells; however, recent correlative evidence indicates a possible role as

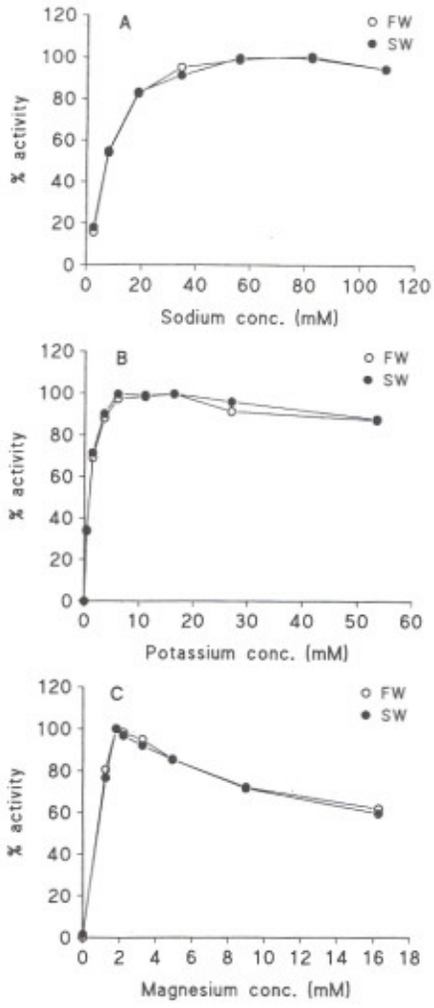

Fig. 5. Effect of varying concentrations of Na^+ (A), K^+ (B) and Mg^{2+} (C) on Na^+,K^+-ATPase acitivity in gill homogenates from FW (o) or SW-adapted (•) *M. saxatilis*. Values are means of 4 fish. Apparent K_m values, calculated from Lineweaver-Burk plots were for FW and SW acclimated fish respectively (in mM): Na^+: 10.4, 10.3; K^+: 0.83, 0.83; Mg^{2+}: 0.93, 1.12.

the site of active Na^+ (Perry and Laurent 1989) and Ca^{2+} uptake in FW (Perry and Wood 1985; McCormick *et al.* 1992). A role in FW ion uptake does not rule out the possibility that these cells are also latent salt secreting cells.

In the present study, a relatively large number of chloride cells and Na^+,K^+-ATPase activity even in landlocked FW striped bass, suggest this system may have a physiological function in FW. Ion uptake remains a speculative role of the FW

"chloride" cell in striped bass opercular membrane as ion flux measurements do not indicate such capacity (C.A. Loretz, S.S. Madsen, R.S. Nishioka and H.A. Bern 1992, unpublished). Rather, it seems likely that the FW chloride cell population is inhibited or quiescent, awaiting increased external salinity to induce its function. The lack of an adaptive increase in branchial and opercular membrane Na^+,K^+-ATPase activity and the similarity in cation affinities of branchial Na^+,K^+-ATPase from FW- and SW-acclimated specimens also support the idea that FW striped bass are equipped with latent salt-excreting mechanisms that become rapidly activated upon SW exposure.

The unexpected variation in gill Na^+,K^+-ATPase (Fig. 1) and plasma osmolality cannot be fully accounted for. However, both parameters may be influenced by environmental cues other than salinity. Tisa *et al.* (1983) reported a large variation in plasma osmolality in both wild caught and laboratory held FW striped bass (321–381 mOsm/kg) and emphasised this to be within the range of healthy SW striped bass.

Although plasma osmolality only changes slightly after SW transfer, the major peak in plasma cortisol seems to be induced by SW (Fig. 1). Cortisol and environmental NaCl have both been proposed as direct activators of salt-excreting mechanisms (Foskett *et al.* 1983), and the role of cortisol in SW acclimation is well established in several teleosts (Bern and Madsen 1992). On the other hand, there is no convincing evidence that thyroxine is directly involved in SW acclimation in the striped bass or yet in any other species. Triiodothyronine may be required for SW-acclimation in trout (Lebel and Leloup 1992).

Our observations in the striped bass are similar to recent findings by Yoshikawa *et al.* (1993) in the mudsucker, *G. mirabilis*. Even though FW acclimation was not reported, this euryhaline marine gobiid does not show changes in chloride cell numbers or in Na^+,K^+-ATPase activity when acclimated to 1.5 ppt, thereby maintaining its "readiness" to reenter SW. Only cell size correlates with salinity. The authors argued that this strategy might be a common feature of euryhaline teleosts of marine origin. The striped bass, however, is of FW origin, and anadromous as well as non-anadromous FW populations exist naturally (Rulisfon *et al.* 1982). From an evolutionary point of view, there must be at least no major disadvantages in maintaining a hypoosmoregulatory system that remains latent for extended periods of time.

Among the mechanisms we investigated, gill SDH activity and middle intestinal J_v increased in response to SW exposure (Table 2, Fig. 4). The time course of these responses was not investigated, and we do not know whether these particular changes are rate limiting in the acclimation process. Posterior intestinal J_v was generally higher than middle J_v (Fig. 4) but unresponsive to salinity. Similar regional differences were reported in *Oncorhynchus kisutch* (Collie and Bern 1982) and *O. mossambicus* (Mainoya 1982). An increase in intestinal J_v also followed SW acclimation in *Anguilla japonica* (Oide and Utida 1967), *O. mossambicus* (Rowdon and Cornish 1973), *O. kisutch* (Collie and Bern 1982) and *Salmo salar* (Usher *et al.* 1991), and is of similar magnitude as that observed in the striped bass (100% increase). Increased J_v normally accompanies increased drinking rate (Shehadeh and Gordon 1969; Hirano 1974; Skadhauge 1976; Evans 1979), and in our study, it correlates with an increased Na^+,K^+-ATPase activity in the same intestinal segment (Fig. 3). This agrees well with the situation in *A. rostrata* (Jampol and Epstein 1970). Kidney Na^+,K^+-ATPase was slightly higher in FW than in SW striped bass, possibly indicating reduced fluid-handling by the kidney in SW. A similar change in kidney Na^+,K^+-ATPase was found following FW acclimation of two marine teleosts, *C. labrosus* and *D. labrax* (Lassere 1971), and of *Fundulus heteroclitus* (Epstein *et al.* 1969); however, enzyme activity remained unchanged under similar circumstances in *A. rostrata* (Jampol and Epstein 1970), *O. mykiss* (Jürss *et al.* 1985) and *S. salar* (McCormick *et al.* 1989). Interestingly, kidney Na^+,K^+-ATPase was unaffected by salinity in another percichthyid teleost, *Macquaria novemaculeata* Langdon 1987).

Branchial SDH is a mitochondrial enzyme and thus particularly abundant in chloride cells (Sargent *et al.* 1975). The present increase in activity in SW (Table 2) may indicate a modification of the

chloride cell function, which is further indicated by the increase in chloride cell size (Table 1). There are few reports of branchial SDH in euryhaline teleosts, all of which show increased activity after SW acclimation (*A. anguilla*: Sargent *et al.* 1975; *S. salar*: Langdon and Thorpe 1984); however these are much larger (2–2.5 fold) than we observed in the striped bass. Although chloride cell mitochondrial density is unaffected by salinity in the striped bass (King and Hossler 1991), the small (16%) increase in chloride cell area would result in a proportionately larger increase in cell volume and total mitochondria.

In conclusion, the high SW tolerance of striped bass may be attributed to a high degree of "preparedness" of its hypoosmoregulatory system. This strategy is different from that used by other diadromous teleosts studied so far, and seems unrelated to salt exposure earlier in development. The ontogeny and endocrinology of this salt tolerance deserves further attention.

Acknowledgements

S.S.M. was a postdoctoral fellow of the Carlsberg Foundation (Denmark) during this study. We are grateful to Alberto Corrales and Brian Williams for assistance. We also thank California Department of Fish and Game and its Striped Bass Stamp Program and Zenyaku Kogyo Co. of Tokyo for supporting this research. This work was sponsored in part by the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA89AA-D-SG-138, project number R/F-145, through the California Sea Grant College, and in part by the California State Resources Agency. The U.S. Government is authorised to reproduce and distribute for governmental purposes.

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