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Effects of Hypoxia on the Behaviour, Mortality and Plasma Electrolyte Concentrations of Goldlined Seabream, *Rhabdosargus sarba*

Hamed M. Al-Gheilani*[1], Colin Waring[2], Abdulaziz Al-Kindi[3] and Shehla Amer[4]

[1]*Marine Science and Fisheries Centre, P.O. Box 227, PC 100, Muscat, Sultanate of Oman*
[2] *Marine Institute, Portsmouth University, UK*
[3]*Department of Biology, College of Science, Sultan Qaboos University, Sultanate of Oman*
[4]*Nizwa University, Sultanate of Oman*

تأثير نقص الأكسجين على سلوك ونسبة الوفيات وتركيز الايونات في بلازما الدم لأسماك القابض

حمد بن محمد الغيلاني ، كولن ويرنج، عبد العزيز بن يحيى الكندي وشهلا عامر

الخلاصة: تمت دراسة أثر نقص الأكسجين على سلوك ونسبة الوفيات وتركيز الايونات في بلازما الدم لأسماك القابض في المختبر باستخدام النسبة الطبيعية من الأكسجين (٨ مللي لتر/ لتر) وعند مستويات منخفضة من الأكسجين (١ و٢ مللي لتر/ لتر) في فترات زمنية مختلفة (٣ و٦ و٢٤ و ٤٨ ساعة). لوحظ من الدراسة زيادة في التنفس وانخفاضا في حركة بعض الأسماك لدى تعرضها لنقص الأكسجين في بعض الأسماك بينما زادت حركة البعض لدى تعرضها لنفس الكمية من الأكسجين. ولم توجد أية وفيات للأسماك عند تعرضها لنقص الأكسجين بعد ٣ و٦ و٢٤ ساعة بينما نفقت بعض الأسماك عند مستوى (١ مللي لتر/ لتر) بعد تعرضها إلى ٤٨ ساعة من نقص الأكسجين. الأسماك التي نفقت كانت اكبر حجما ومعظمها من الذكور. وزادت نسبة الكالسيوم عند الأسماك المعرضة لنقص الأكسجين (١ مللي لتر/ لتر : ٤٨ ساعة) بينما تتأثر الايونات الأخرى بنقص الأكسجين (الصوديوم، والمغنيسيوم والكلورايد). الدراسة أكدت أن لدى اسماك القابض في المياه العمانية القدرة على التأقلم مع انخفاض نسبة الأكسجين مقارنة بنفس النوع في المياه الأخرى. وقد يعود ذلك إلى النقص الطبيعي للأكسجين في المياه العمانية نتيجة ظاهرة التقليب والظواهر الأخرى المرتبطة بالتغيرات البيئية.

ABSTRACT: The behaviour, mortality rates and plasma electrolyte concentrations of goldlined seabream *Rhabdosargus sarba* challenged with low dissolved oxygen (DO) conditions was studied in an experimental setup, comprising a control (7.9 ml/l DO) and two hypoxic (2 ml/l and 1 ml/l DO) treatments. Increased ventilation rates and decreased swimming activity were observed in hypoxic treatments, but some fish exhibited strenuous avoidance actions. No mortalities were observed after 3 h, 6 h, or 24 h, but 50% of males and 18% of females died in the 48 h treatment at 1 ml/l DO. The mean size of surviving fish (305 ± 32.1 g total weight) was significantly smaller than those that died (425 ± 33.1 g). The plasma concentrations of Na^+, Cl^- and Mg^{2+} did not vary significantly relative to treatment, exposure time, fish size and gender, or interactions among treatment, time and gender. Ca^{2+} concentrations increased significantly after 48 h at 1 ml/l, but this result may be artificial because of the small sample size. The results suggest that *R. sarba* is comparatively tolerant of the low oxygen or hypoxic conditions that often occur in the coastal waters of Oman, where seasonal upwellings and high primary productivity have in the past caused mass mortalities of demersal fishes.

Keywords: Behaviour, mortality, hypoxia, electrolytes, goldlined seabream.

*Corresponding author. E-mail: asadalaqidah@hotmail.com

Introduction

Fish challenged with reduced levels of dissolved oxygen (DO), can respond by moving away (vertical or horizontal habitat changes) or by changing activity patterns to increase ventilation surfaces or decrease energy demands (Kramer, 1987; Dalla Via *et al.,* 1998). Increases in ventilation frequency have been reported in numerous species (Holeton and Randall, 1967; Soivio *et al.,* 1980; Soivio *et al.,* 1981; Woo and Wu, 1984; Thomas *et al.,* 1988; Brauner and Randall, 1998; Maxime *et al.,* 2000; Pichavant *et al.,* 2002; Timmerman and Chapman, 2004; Evans *et al.,* 2005), as have increases in ventilation volume (Smith and Jones, 1982; Randall, 1990). The result is an increased oxygen uptake and enhanced convective conditions for CO_2 removal (Brauner and Randall, 1998). Van Raaij *et al.,* (1996a) reported on behavioural strategies of surviving and non-surviving fish during confined hypoxia exposure. Non-surviving fish exhibited strenuous avoidance (or escape) reactions, and were not able to maintain homeostasis, as evidenced by elevated plasma ions, metabolic rate and stress hormones compared to the less active surviving fish. Elevations in plasma ion (electrolyte) levels in response to physical disturbances such as net confinement and transport have been documented for several marine teleosts (Fletcher, 1975; Pawson and Lockwood, 1980; Soivio *et al.,* 1980; Robenston *et al.,* 1987; Waring *et al.,* 1992; Waring *et al.,* 1996). Below a species-dependent critical oxygen threshold, aerobic energy production decreases and fish mainly resort to anaerobic metabolism (Dalla Via *et al.,* 1994) and sometimes metabolic depression (van Waversveld *et al.,* 1989). Most of these mechanisms are under hormonal control involving catecholamines and cortisol (Kinkead and Perry, 1991; Van Raaij *et al.,* 1996b; Pichavant *et al.,* 2002; Perry *et al.*, 2004).

Localized or extensive low oxygen or hypoxic conditions are common in the coastal waters of Oman (REF), where seasonal upwellings of nutrient-rich and oxygen-depleted waters are driven by the summer monsoon winds. These upwellings give rise to algal blooms in the photic zone bloom collapse, bacterial decomposition and settlement on the seafloor results in an oxygen-depleted bottom-water layer below the thermocline (Claereboudt *et al.,* 2001). Although generally beneficial to fisheries, phytoplankton blooms can trigger harmful algal blooms (HABs or red tides), and the latter have been implicated in massive fish mortalities in both the Gulf of Oman (Claereboudt *et al.,* 2001) and the Arabian Sea (Al-Busaidi *et al.,* this issue). These mortalities were attributed to asphyxia or toxins. A recent review of HAB occurrences between 1976 and 2004 showed 66 red tide events in the coastal waters of Oman, out of which 25 resulted in mass mortalities of fish and other organisms (Al-Gheilani *et al.,* to be submitted).

The importance of commercial fishing to Oman and increasing likelihood of low-oxygen conditions stimulated a recent PhD study on the physiology of goldlined seabream *Rhabdosargus sarba* confronted with hypoxic conditions (Al Gheilani, 2007). Goldlined seabream is a coastal species distributed throughout the Western Indian Ocean, including the Red Sea and Arabian Gulf (Randall, 1995). It is often encountered in small schools, reaches a maximum size of 60 cm, and feeds on bivalve molluscs, sand dollars, sea urchins and sand-dwelling crustaceans (Randall, 1995). It forms part of the demersal fish assemblage of Oman, which is heavily fished.

The aims of this study were to examine the effects of low oxygen conditions on the behaviour, mortality rates and electrolyte balance of *R. sarba* under controlled laboratory conditions. Particular attention was given to the influence of gender and body size on the above parameters.

Materials and Methods

Trap-caught goldlined seabream with an average weight of 245.9±8.6 g and length of 23.5±1.4 mm were purchased from a local fisherman in Muscat (24N˚ 58E˚). Fish were kept in oxygenated seawater while on board and transferred to well-aerated tanks on land where the water temperature and salinity were kept at 21-24°C and 20-25 psu. Fish were acclimatized for a total of 3 weeks during which they were fed once daily (Plante, *et al.,* 1998) with commercially-prepared fish pellets (Arasco, Saudi Arabia).

The continuous flow experimental setup consisted of three seawater reservoirs: an overhead 600 litre (l) tank, fully aerated 400 l fish acclimatization tank and a 400 l water circulation tank (see Fig. 1). The circulation tank was connected to 8 experimental tanks (30×60×40 cm; 45 l; glass with 2 ports), with flow rates of 1.5 $l.min^{-1}$ and water circulating through a biological filter and UV sterilizer (temperature, 22.9±0.1C˚; salinity 34.8±0.8 psu; ammonia, 2.01±0.6 µm/l; nitrite 0.23±0.04 µm/l; phosphate 0.5±0.01

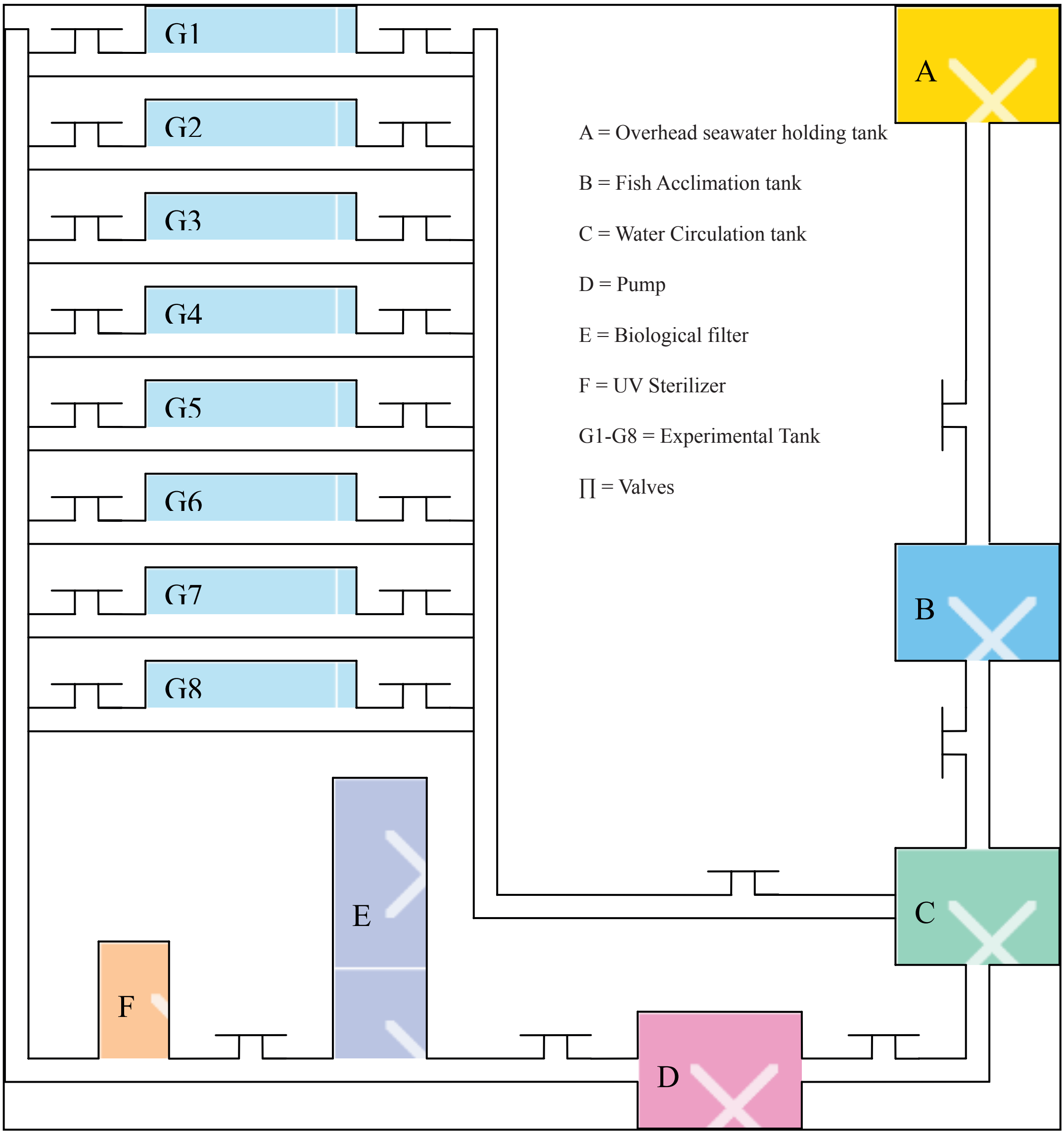

Figure 1. Arrangement of seawater holding and experiment tanks.

µm/l; and a 12L:12D photoperiod). The sides of the experimental tanks were covered with black paper to minimize disturbances to fish.

An Aqua Traul Oxygen Monitoring and Control System (Dryden Aqua, Scotland, UK.), fitted with 8 oxygen probes (Dryden Aqua, Scotland, U.K.) was connected to solenoid valves to regulate the oxygen and nitrogen input to the 8 experimental tanks. The Aqua Traul network communicates via RS 485 serial BUS protocol with a standard PC and was configured using Aqua Traul Software.

Feeding was stopped and fish transferred from the acclimatization to the experimental tanks (fully aerated seawater; 7.9±0.7 $ml.l^{-1}$ O_2 or 100% saturation) 24 h before low oxygen trials (see Lapner and Perry, 2001). Two levels of hypoxia, 2.0±0.9 $ml.l^{-1}$ O_2 (2.8mg/l or 25% saturation) and 1.1±0.2 $ml.l^{-1}$ (1.4 mg/l or 12.5% saturation) were selected for trials and control fish were maintained at 7.9±0.7 ml.l^{-1} O_2. Oxygen and nitrogen were purged from tanks by immersing flexible tygon tubing (ID 4 mm, OD 1.2 cm) attached to ceramic gas diffusers (Dryden Aqua, Scotland, U.K.), and oxygen levels adjusted manually and via the PC by bubbling pure nitrogen / oxygen into tanks from respective cylinders. The time required to adjust the DO level was 10-20 minutes. Once set up, the Aqua Traul units continued to monitor the system, automatically opening and closing the solenoid valves to regulate the flow of oxygen and nitrogen. Water samples (250 ml) were collected using Niskin bottles for analysis of ammonia, nitrite and phosphorus. Nutrients were measured using a 5-channel SKALAR Flow Access auto-analyzer (see Strickland and Parsons, 1972).

Fish behaviour during hypoxia exposure and time of death was monitored every 2–4 hours. After 3 h, 6 h, 24 h and 48 h individual fish in experimental tanks were netted, stunned by a blow to the head, and terminal blood samples taken. The sex, total weight (TW, g) and total length (TL, cm) were determined. The TW and TL of surviving fish were compared with those that died using Student's t-test.

Whole blood was allowed to clot at room temperature for 30 min and centrifuged at 11000 rpm for 5 min to obtain plasma (Hishida *et al.,* 1999). All plasma samples were immediately frozen at -80 C˚. The Beckman Synchron CX7 System (CX3 module) was used to determine plasma electrolytes. Sodium and chloride concentrations were determined by measuring electrolyte ion activity in solution. Magnesium concentrations were determined using the manufacturers reagent and a colourimetric timed-endpoint method. The calcium concentrations were determined by adding Arsenazo III calcium reagent and measuring the absorbance of the resulting coloured calcium-Arsenazo III complex at 650 nm and 700 nm.

The effects on plasma ion concentrations of the variables for gender, exposure time (3 h, 6 h, 24 h and 48 h), treatment (control, 1 ml/l or 2 ml/l DO), TL and TW, and the interactions of treatment×time, treatment×gender, time×gender and treatment×time×gender were analysed using a General Linear Model (GLM) with gender and body size (cm and g) as factors, accepting $P \leq 0.05$ as significant (REF). Statistical analysis was carried out using Minitab.

Results

All fish survived up to 48 h in the 2 ml/l DO trials. In the 1 ml/l DO trials, all fish exposed for 3 h, 6 h and 24 hours survived, but 50% of males (n = 12) and 18% of females (n = 17) died between 24 and 48 h exposure. The mortalities occurred after 26 h (3 fish), 28 h (1), 30 h (2), 36 h (2) and 40 h (1). The mean TW (305 ± 32.1 g) and TL (24.7 ± 1.0 cm) of surviving fish were significantly smaller ($P<0.05$) than that of the fish that died (425.1 ± 33.1 g; 28.7 ± 0.8 cm; see Table 1 and Fig. 2).

During the hypoxia trials two distinct behaviour patterns were observed. Fish that survived in the 1 ml/l

Table 1. The mean total length (TL, cm) and total weight (TW, g) of male and female *Rhabdosargus sarba* used in control and hypoxia treatments. Mean TL and TW of fish that died during the 48 h, 1 ml/l DO treatment are also shown. Sample sizes are in parenthesis.

	All fish		**Female survivors**		**Male survivors**		**Female mortalities**		**Male mortalities**	
	TW (g)	**TL (cm)**	**TW (g)**	**TL (cm)**	**TW (g)**	**TL (cm)**	**TW (g)**	**TL (cm)**	**TW (g)**	**TL (cm)**
Control	301.2 (16)	24.8 (16)	355.9 (10)	26.3 (10)	210.2 (6)	22.3 (6)	*	*	*	*
Hypoxia exposed	342.3 (29)	25.9 (29)	318.6 (14)	25.3 (14)	273.3 (6)	23.4 (6)	474.7 (3)	29.3 (3)	400.3 (6)	28.3 (6)

*No control; fish dead.

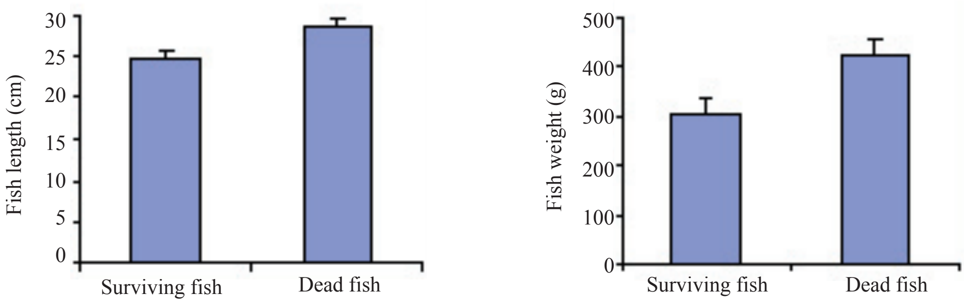

Figure 2. Comparisons of the TL and TW of surviving and non-surviving Rhabdosargus sarba kept at 1 ml/1 DO for 48 h. Means and standard errors are shown.

DO trials reduced their routine locomotor activity, and after approximately 20 h lay almost immobile at the bottom of the tanks, appearing to have increased their ventilation rates. The fish that eventually died swam upwards in the water column, sometimes at burst swimming movement, but thereafter lost their balance and sank to the bottom where they remained inactive until they died.

Plasma Na^+ concentrations ranged between 148 mmol/l in normoxic fish and a maximum of 176.6 mmol/l in control fish after 3 hours (Table 2). There were no statistically significant fluctuations in plasma Na^+ concentrations, irrespective of treatment, exposure time, gender, fish size, or the interactions (Table 3). Likewise, no significant trends could be observed in either Cl (range 136.8 – 160.8 mmol/l) or Mg^{2+} (0.07 – 0.25 mmol/l) (Tables 2 and 3). The Ca^{2+} concentrations were not examined at 6 h and at 24 h for the 1 ml/l DO treatment because not enough plasma was available for analysis. In the only trial with a positive result, the plasma Ca^{2+} concentrations were significantly higher in fish exposed to 1 and 2 ml/l DO for 48 h than their controls. However, given the small sample sizes used for the Ca^{2+} determinations, and the comparatively low value for the 48 h control measurement (0.47 mmol/l) relative to the other controls (0.57–0.65 mmol/l; see Table 2), the significant increase seen in Ca^{2+} after 48 h at 1 and 2 ml/l DO exposure may be artifactual. Therefore we concluded that none of the plasma electrolytes measured (Na^+, Cl^-, Mg^{2+} and Ca^{2+}) showed a significant effect relative to exposure of time, treatment, gender, TW or TL, or interactions between the boundaries tested.

Discussion

The effects of hypoxia on fish behaviour and mortalities have been studied for several species using a variety of DO levels and exposure times, and sensitivity to low oxygen appears to be species dependent, broadly ranging from 0.9 to 2.2 ml/l DO (see Table 4 and Itazawa, 1971; Gee *et al.,* 1978; Van den Thilart and Waarde, 1985). Woo and Wu (1984) found black seabream *Mylio macrocephalus* to be at the lower extreme of the sensitivity range (no mortalities at 0.7 ml/l DO in 7 h but some deaths at 0.4 ml/l DO; Wu and Woo, 1984). Conversely, Atlantic cod *Gadus morhua* and rainbow trout *Oncorhynchus mykiss* exhibited higher mortality rates over similar time spans at DO levels >0.7 ml/l (Plante *et al.,* 1998) (Table 4). In our study, no *R. sarba* died over a short time span of up to 24 h, even at 1 ml/l DO, and it therefore exhibits a relatively high tolerance to hypoxia.

Hypoxia elicits hyperventilation in a variety of marine teleosts (Holeton and Randall, 1967;; Soivio *et al.,* 1980; Soivio *et al.,* 1981; Woo and Wu, 1984; Thomas *et al.,* 1988; Brauner and Randall, 1998; Maxime *et al.,* 2000; Pichavant *et al.,* 2002; Evans *et al.,* 2005), and was also observed in *R. sarba*. The hyperventilation facilitates increased oxygen uptake and enhances convective conditions for CO_2 removal (Brauner and Randall, 1998). A reduction in swimming activity as an energy-saving strategy, as reported for flatfish *Solea solea* (Dalla Via *et al.,* 1998), was also observed for *R. sarba*. However, not all *R. sarba* reduced their swimming activity, with some individuals showing strenuous avoidance behaviour – the latter group with a higher mortality rate. Van Raaij *et al.* (1996a) reported a five-fold catecholamine elevation after strenuous avoidance behaviour of non-surviving *Oncorhynchus mykiss* – this information is unfortunately not available for *R. sarba*.

The *R. sarba* that died during the 48 h trial at 1 ml/l DO had a significantly larger mean size (both TL and TW) than those that survived. Smaller individuals of several other fish species were also found to be more

Table 2. Plasma concentrations of Na^+, Cl^-, Mg^{2+} and Ca^{2+} of *Rhabdosargus sarba* exposed to normoxia conditions (Norm) controls at 7.9 ml/l DO (C), 2 ml/l and 1 ml/l DO for 3 h, 6 h, 24 h and 48 h. Data represents mean values ± standard errors. Sample sizes are in parenthesis.

	Norm	Exposure											
		3 h			6 h			24 h			48 hr		
		C	2m/l	1ml/l	C	2ml/l	1ml/l	C	2ml/l	1ml/l	C	2ml/l	1ml/l
Na^+	148 ±2.7 (10)	176.6 ±2.8 (16)	173 ±2.4 (12)	169 ±3.1 (10)	172 ±1.7 (19)	167.3 ±2.5 (9)	175.7 ±4.4 (10)	171.6 ±2.6 (20)	174 ±3.6 (9)	176 ±2.6 (10)	168.7 ±3.8 (19)	171.7 ±5.0 (10)	170.3 ±3.7 (10)
Cl^-	136.8 ±2.5 (10)	160.8 ±3.1 (16)	153.3 ±2.0 (12)	155 ±2.4 (10)	153.5 ±2.7 (20)	147.3 ±2.0 (9)	149.9 ±1.3 (10)	148.6 ±2.1 (20)	156.9 ±3.9 (10)	146 ±1.3 (10)	149.9 ±1.2 (19)	152.6 ±1.64 (10)	153.2 ±3.59 (10)
Mg^{2+}	0.25 ±0.03 (13)	0.17 ±0.01 (16)	0.13 ±0.01 (12)	0.19 ±0.04 (10)	0.09 ±0.01 (19)	0.10 ±0.01 (9)	0.09 ±0.01 (8)	0.09 ±0.02 (18)	0.19 ±0.05 (10)	0.07 ±0.02 (9)	0.15 ±0.01 (18)	0.15 ±0.02 (10)	0.14 ±0.02 (10)
Ca^{2+}	0.65 ±0.07 (10)	0.60 ±0.03 (12)	0.60 ±0.05 (9)	0.61 ±0.02 (6)	nm	nm	nm	0.57 ±0.15 (2)	0.47 ±0.16 (3)	nm	0.47 ±0.02 (4)	0.59 ±0.09 (3)	0.59 ±0.09 (3)

nm - no measurements.

Table 3. The probability matrix (α = 0.05) of the effects of treatment (1 ml/l and 2 ml/l DO), exposure time (3 h, 6 h, 24 h and 48 h), gender, TW and TL, and the interactions time×treatment, time×gender, treatment×gender and time×treatment×gender on plasma electrolyte concentrations of *Rhabdosargus sarba*.

		TL/TW	Treat-ment	Time	Gender	Treat-ment* time	Treat-ment* Gender	Time* Gender	Treatment* Time* Gender
Na^+	TL	0.816	0.645	0.949	0.614	0.231	0.261	0.866	0.084
	TW	0.534	0.608	0.873	0.539	0.255	0.267	0.894	0.082
Cl^-	TL	0.373	0.228	0.707	0.096	0.050	0.566	0.908	0.926
	TW	0.594	0.222	0.456	0.075	0.049	0.591	0.912	0.944
Mg^{2+}	TL	0.749	0.522	0.816	0.505	0.866	0.553	0.749	0.893
	TW	0.857	0.857	0.531	0.846	0.846	0.534	0.761	0.900
Ca^{2+}	TL	0.051	0.023	0.066	0.231	0.020			
	TW	0.044	0.027	0.052	0.299	0.020			

tolerant of hypoxia than larger fish (Smale and Rabeni, 1995; Burleson *et al.,* 2001; Robb and Abrahams, 2003). The higher mortality rates of larger fish may be related to lower size-surface; body weight ratios in larger individuals.

Timmerman and Chapman (2004) studied the effect of hypoxia on behavioural and physiological responses of sailfin *Poecilia latipinna* and concluded that females were more tolerant to hypoxia than males. Overli *et al.* (2006) reported that male fish were more

Table 4. The effects of hypoxia on fish mortality rates from studies at a range of exposure times and DO levels.

Species	DO (ml/l)	Exposure time	Mortalities (%)	Reference
Solea solea	0.3 0.5	12 h 12 h	0 0	Dalla Via *et al.,* 1994
Scophthalmus maximus Dicentrarchus labrax	1.7	40 days	0	Pichavant *et al.,* 2003
Epinephelus akaara Mylio macrocephalus	0.7	7 h	0	Woo and Wu, 1984
Epinephelus akaara Mylio macrocephalus	0.4	7 h	Few	Wu and Woo, 1984
Gadus morhua	0.4 0.7 1.5	7 h 7 h 7 h	100 Most 0	Plante *et al.,* 1998
Scophthalmus maximus	1.3	6 h	0	Pichavant *et al,* 2002
Oncorhynchus mykiss	1.5	3 h	40	Van Raaij *et al.,* 1996a
Gadus morhua	1.3	6 h	21	Claireaux and Dutil, 1992

Table 5. The effects of hypoxia exposure on plasma electrolyte concentrations of selected fish species from the literature. No effect = 0; + = increase; – = decrease.

Species	DO ml/l)	Exp. time	Na^+	Cl^-	Ca^{2+}	Mg^{2+}	Reference
O. mykiss	1.5	12 h	0	0			(Van Raaij *et al.,* 1996b)
*Cyprinus carpio**	0.5	30 m	0	0			(Fuchs and Albers, 1988)
Acipenser baeri	0.4	30 m	0	0			(Maxime *et al.,* 1995)
Cyprinus carpio	1.5	24 h	0	0	0	+	(Kakuta *et al.,* 1992)
O. mykiss	4	3 h	+	–	–	–	(Soivio *et al.,* 1981)
Mylio macrocephalus	0.7	7 h	+		0		(Woo and Wu, 1984)
Scophthalmus maximus	2.5 3.5	45 days	0	0			(Pichavant *et al.,* 2000)

*Hypercapnic and hypoxia stress.

aggressive than females, and would presumably consume more oxygen. In the present study a larger proportion of males than females died in the 1 ml/l treatment for 48 h, and although the sample size was small (12 males and 17 females), we suggest that female *R. sarba* may be more tolerant to hypoxia than males.

The absence of significant fluctuations in plasma electrolytes (Na^+, Cl^-, Mg^{2+} and Ca^{2+}) of *R. sarba* during hypoxia exposure is in accordance with the results of several other studies on marine teleosts (see Table 5), where positive results were only sporadically found. Woo and Wu (1984) studied the effect of hypoxia on Ca^{2+} and Na^+ serum levels in *M. macrocephalus*, and found Ca^{2+} levels to be unchanged whilst Na^+ increased. They attributed the Na^+ elevation to impairment of branchial or renal functions. The decrease of Mg^{2+} reported by Kakuta *et al*. (1992) in *Cyprinus carpio* was attributed to a selective gain of ions entering the fish from a hyperionic environment. Most other studies could not, however, find a relationship between hypoxic conditions and fluctuations in plasma electrolytes (Table 5).

The effects of netting (or capture) stress, confinement, transport, exercise and air-exposure on marine teleost electrolyte balance have often been reported upon, and the causes for imbalances have been suggested in some cases. Railo *et al.,* (1985) reported rapid changes in the plasma electrolyte composition of even mildly stressed fish, which suggests that capture stress had profound effects on salt and water balance. Imbalances in plasma Na^+/Cl^- ratio may reflect disturbed acid-base regulation (McDonald and Wood, 1993; Mazon *et al.,* 2002), or increasing membrane permeability due to disruption of the membrane integrity of gill cells (Stagg and Shuttleworth, 1982; McDonald and Wood, 1993). Ionregulatory disruption induced by copper was related to inhibition of branchial Na^+- K^+-ATPase activity (Lauren and McDonald, 1985; Pelgrom *et al.,* 1995). Knudsen and Jensen (1998) reported on exercise-induced hyperkalaemia as a consequence of an efflux of K^+ from skeletal muscles during their depolarization and an insufficient reuptake. Farrell (1984) suggested that elevated plasma Ca^{2+} and catecholamine levels protect the teleostean heart from acidosis which might result from stress. Salm *et al.* (2006) found that the plasma Na^+ levels in *Pagrus pagrus* increased upon netting stress, but that other plasma ions remained unchanged, and suggested a selective gain of ions from a hyperionic environment. After 2 hours of netting stress, all plasma ion levels returned to, or dropped below basal control levels, suggesting that gill permeability had returned to normal and hydromineral balance restored.

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