Zoological Studies
a SpringerOpen Journal

RESEARCH Open Access

Concentrations of osmotically related constituents in plasma and urine of finless porpoise (*Neophocaena asiaeorientalis*): implications for osmoregulatory strategies for marine mammals living in freshwater

Aihuan Guo[1,2], Yujiang Hao[1*], Jingzhen Wang[1,2], Qingzhong Zhao[1] and Ding Wang[1*]

Abstract

Background: Most cetaceans inhabit the hyperosmotic marine environment with only a few species living in freshwater habitats. The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) is the only freshwater subspecies of the genus. Our aim was to study whether the osmoregulation mechanism of the Yangtze finless porpoise is different from the marine subspecies, the East Asian finless porpoise (*Neophocaena asiaeorientalis sunameri*). We assayed and compared the concentrations of the constituents involved in osmoregulation in the blood and urine in the Yangtze finless porpoise and the East Asian finless porpoise. We also compared the corresponding urine constituents of the porpoises with existing data on fin whales (*Balaenoptera physalus*) and bottlenose dolphins (*Tursiops truncatus*).

Results: The mean plasma osmolality of Yangtze finless porpoise was significantly lower than that of the marine subspecies ($P < 0.01$). Similarly, the urine osmolality of Yangtze finless porpoise was also significantly lower than that of its marine counterpart ($P < 0.05$). However, the urine sodium concentration of freshwater finless porpoise was significantly lower than that in the marine subspecies ($P < 0.01$), even though their serum sodium has no significant difference. Moreover, the freshwater porpoise has significantly lower urine urea concentration but much higher serum urea than in the marine finless porpoise ($P < 0.05$).

Conclusions: These results suggest that the freshwater finless porpoise does have different osmoregulatory mechanism from marine cetaceans. Conserving sodium by excreting urine with low ion levels may be an essential strategy to maintain the serum electrolyte balance for the freshwater subspecies that also appears to be more susceptible to hyponatremia.

Keywords: Finless porpoise; Osmoregulation; Plasma; Urine

Background

Based on fossil and genetic evidence, cetaceans have undergone dramatic changes during their evolutionary transformation from four-legged land animals to mammals adapted to aquatic life (Thewissen et al. 1996; Gatesy and O'Leary 2001; Gingerich et al. 2001). Today, most cetaceans inhabit the oceans, and they are well adapted to the hyperosmotic environment. Pfeiffer (1997) reported that extant cetaceans do not appear to possess extra renal organs for salt excretion and have only a small number of anatomical modifications in the kidney. Therefore, it is likely that the aquatic ancestors of modern cetaceans relied mainly on physiological mechanisms to maintain water and electrolyte homeostasis in seawater, which is essential for the marine mammals to avoid dehydration (Ortiz 2001; Janech et al. 2002).

* Correspondence: hao.yj@ihb.ac.cn; wangd@ihb.ac.cn
[1]Key Laboratory of Aquatic Biodiversity and Conservation, Institute of Hydrobiology, Chinese Academy of Sciences, 7th South Donghu Road, Wuchang District, Wuhan, Hubei 430072, People's Republic of China
Full list of author information is available at the end of the article

Clinical examination of serum and urine can reflect the body status and health condition of the animal and may also provide essential information on their water and electrolyte homeostasis (Kjeld 2001). Blood and urine composition has been investigated in several marine cetacean species. Birukawa et al. (2005) assayed the osmoregulatory constituents in plasma and urine from common minke whales (*Balaenoptera acutorostrata*), sei whales (*Balaenoptera borealis*), Bryde's whales (*Balaenoptera brydei*), and sperm whales (*Physeter macrocephalus*), and Kjeld (2001) reported that the concentrations of various constituents in the blood and urine of fin whales (*Balaenoptera physalus*) related to osmoregulation. Much research has also been conducted on bottlenose dolphins (*Tursiops truncatus*) (Fetcher and Fetcher 1942; Malvin and Rayner 1968; Ortiz 2001; Ortiz et al. 2010; Ridgway and Venn-Watson 2010). Most of the results suggest that marine cetaceans may have the ability, by excreting hypertonic urine, to maintain their plasma electrolyte homeostasis to adapt to the hypertonic marine environment (Birukawa et al. 2005). However, the existing studies on cetacean osmoregulation are fairly limited, and the mechanism by which cetaceans maintain water and solute homeostasis is only partially understood (Janech et al. 2002).

Marine mammals are not normally exposed to freshwater; however, each taxonomic order of marine mammal has at least one species that exists solely in a freshwater environment (Ortiz et al. 2002). Although adapting to freshwater habitats may appear beneficial because conserving freshwater is no longer a problem, the aquatic mammals that adapt to such habitats are confronted with a different osmotic challenges. Living in a freshwater environment may require appropriate physiological mechanisms to conserve electrolytes (Ortiz 2001). The narrow-ridged finless porpoise (*Neophocaena asiaeorientalis*) has two subspecies in Chinese waters. The Yangtze finless porpoise (YFP, *N. asiaeorientalis asiaeorientalis*) is the sole freshwater subspecies and only inhabits the middle and lower reaches of the Yangtze River and its appended lakes (Wang 2009). The other subspecies is the East Asian finless porpoise (*Neophocaena asiaeorientalis sunameri*), which is widely distributed in the coastal areas of the Yellow/Bohai Seas and the northern part of the East China Sea (Jefferson and Wang 2011). Previous research suggests that the Yangtze finless porpoise originated from the marine finless porpoise (Yang et al. 2008; Zheng et al. 2005). Living in the hypotonic freshwater environment, YFP is confronted with different but equally challenging problems compared with its marine counterpart, the East Asian finless porpoise. The adaptation of two closely related subspecies to such divergent habitats provides an ideal model to understand the mechanisms of cetacean osmoregulation.

Therefore, this work aims to (1) compare the differences in osmoregulation-related constituents in the plasma and urine of freshwater and marine finless porpoise, (2) compare the freshwater and marine finless porpoise to previously published data on other cetacean species, and (3) identify the major challenges confronted by YFP and their adaptation strategies for living in the freshwater environment.

Methods

Blood and urine sample collection

We obtained 22 blood samples from 22 free-ranging YFP in the Tian-e-Zhou Reserve (E 112° 31′ to 112° 31′, N 29° 46′ to 29° 51′) in October 2010. This reserve is the only *ex situ* conservation area for cetacean species in the world. It was established in 1992, and there are currently approximately 40 animals living in the reserve. In total, 22 blood samples of marine finless porpoise were collected from 15 animals represented by the Bohai Sea population (BFP), including 17 samples from 10 marine finless porpoise in Penglai Sea World, Shandong province, and 5 blood samples from 5 marine finless porpoise in Shanhaiguan Happy Ocean Park, Hebei province, China. These animals were captured accidentally by the local fisherman in the Bohai Sea and were successfully rescued and are kept in captivity by Penglai Sea World and Shanhaiguan Happy Ocean Park.

All of the animals were captured and transferred with care to a holding area for physical examination. Briefly, a 10-ml blood sample was collected from the central vein of the tail fluke using a 10-ml disposable syringe. Out of this sample, 4 ml was placed in a pre-chilled EDTA-treated tube; the sample was then centrifuged for 15 min at 3,000 × *g*, and the plasma was transferred to cryovials and frozen at −20°C for later analysis. The remaining blood was placed in an untreated tube for 30 min and then centrifuged for 15 min at 3,000 × *g*. Finally, the serum was transferred to cryovials and frozen at −20°C for future analysis.

The YFP urine samples were collected from three captive adults in Baiji Dolphinarium, Wuhan, China. These porpoises had been trained to flip onto their back and urinate voluntarily. They were mainly fed a diet of crucian carps (*Carassius auratus*) four times a day. The BFP urine samples were collected postmortem by direct needle aspiration from the urinary bladder of animals killed accidentally as fishing bycatch. The urine samples were transferred to cryovials and frozen at −20°C for later analysis. In total, 16 YFP and 4 BFP urine samples were obtained. The study was licensed under the Regulations on the Management of Laboratory Animals, issued by the Ministry of Science and Technology of the People's Republic of China. All animal procedures were approved under the China's wild animal protective law.

Blood and urine analysis

Plasma and urine osmolality were measured by Micro-osmometer Model 3300 (Advanced Instrument Inc., Norwood, MA, USA). Serum and urine electrolytes, urea, creatinine, and glucose concentrations were measured with a clinical autoanalyzer (Abbott Aeroset System Laboratories, Abbott Park, IL, USA) in Zhongnan Hospital of Wuhan University. The analyzer was calibrated with a Randox quality control product (350/2 and 223VE/1; Antrim, Northern Ireland, UK) before each assay.

The concentrations of corresponding constituents in the urine of fin whales and bottlenose dolphins were obtained from literature (Kjeld 2001; Suzuki et al. 2008) and compared with those of the freshwater and marine finless porpoise.

Statistical analysis

The serum and urine constituent data were analyzed using the descriptive statistics (mean ± SD and range) in the SPSS 13.0 software (SPSS 13.0, SPSS Inc., Chicago, IL, USA). The Mann–Whitney *U* test was used for difference analysis between YFP and BFP. Because the raw data for the other cetacean species was not available in the published literature, only the mean value and standard deviation (SD) were used for comparison with the finless porpoise.

Results

The plasma osmolality and osmoregulation-related serum constituent concentrations of freshwater and marine finless porpoise are shown in Table 1. There was no significant difference in the serum Na^+ observed between YFP and BFP. However, the YFP serum Cl^- concentration was significantly lower than that in the BFP ($P < 0.01$). Furthermore, the serum P^{3+} and Mg^{2+} concentrations were also higher in BFP than in YFP, but no discernible difference was detected in serum K^+ and Ca^{2+} concentrations between the two subspecies. There was also no significant change in the levels of serum creatinine and glucose between YFP and BFP, while the serum urea ($P < 0.05$) and uric acid ($P < 0.01$) concentrations were significantly higher in YFP. The plasma osmolality of the YFP was much lower than that of the BFP ($P < 0.01$).

The urine osmolality and related constituents in the freshwater and marine finless porpoises are presented in Table 2. The corresponding values for fin whales and bottlenose dolphins from published research are also listed in the table for comparison. The levels of the corresponding constituents in freshwater and seawater are also presented for reference.

The concentrations of urine Na^+ and Cl^- in YFP were significantly lower than those in BFP or the other marine cetacean species. YFP also had urinary urea concentrations significantly lower than BFP ($P < 0.05$), fin whales, or bottlenose dolphins. The urine K^+, Mg^{2+}, and Ca^{2+} concentrations were quite similar in those of the two finless porpoise populations but showed slight difference compared with those of the other marine cetaceans. There was no significant difference in the urinary creatinine concentration between YFP and BFP. The urine osmolality of the YFP was significantly lower than that of the BFP ($P < 0.05$) and that of the other two marine cetacean species.

Discussion

Inorganic ions

The concentrations of serum Na^+ and Cl^- of toothed cetaceans are in general within a narrow range. For instance, the concentrations of serum Na^+ and Cl^- were 156.6 and 114.3 mmol/l in harbor porpoise (*Phocoena*

Table 1 Plasma osmolality, serum electrolytes, and concentrations of other constituents in the Yangtze and Bohai finless porpoise

Constituents	Yangtze population				Bohai population			
	N (*n*)	Mean ± SD	Range	CV%	*N* (*n*)	Mean ± SD	Range	CV%
Osmolality mosmol/kg	21 (21)	329.24 ± 7.06	317.0 to 342.0	2.14	8 (8)	361.5 ± 15.2**	342.0 to 387.0	4.20
Na^+ mmol/L	22 (22)	153.4 ± 1.71	149.1 to 156.4	1.11	15 (22)	156.24 ± 8.11	147.0 to 175.4	5.19
K^+ mmol/L	22 (22)	4.5 ± 0.79	3.64 to 7.29	17.56	15 (22)	4.28 ± 0.85	3.4 to 7.3	19.86
Cl^- mmol/L	22 (22)	107.9 ± 3.41	96.80 to 111.70	3.16	15 (22)	117.29 ± 7.63**	106.0 to 131.70	6.50
Ca^{2+} mmol/L	21 (21)	2.62 ± 0.07	2.47 to 2.77	2.67	15 (22)	2.53 ± 0.25	2.1 to 3.11	9.88
Mg^{2+} mmol/L	21 (21)	0.7 ± 0.11	0.54 to 1.01	15.71	15 (15)	0.87 ± 0.15**	0.6 to 1.1	17.24
P^{3+} mmol/L	22 (22)	1.26 ± 0.26	0.89 to 1.93	20.0	15 (15)	1.86 ± 0.61**	0.3 to 3.0	32.80
Creatinine umol/L	22 (22)	81.2 ± 11.67	64.00 to 106.70	14.37	15 (22)	72.48 ± 24.02	41.0 to 125.2	33.14
Urea mmol/L	20 (20)	16.75 ± 3.19*	9.35 to 22.56	19.04	15 (22)	14.35 ± 3.11	9.3 to 18.6	21.67
Glucose mmol/L	20 (20)	7.73 ± 1.17	5.85 to 10.37	15.14	15 (15)	8.31 ± 2.27	3.9 to 11.5	27.32
Uric acid umol/L	22 (22)	44.6 ± 17.14**	22.80 to 84.20	38.43	15 (22)	12.94 ± 7.98	4.3 to 36.0	61.67

Significant differences between the finless porpoises are indicated by *$P < 0.05$ and **$P < 0.01$. N, individual number; n, sample number.

Table 2 Osmolality and other constituent values in urine of finless porpoise compared with other cetacean species

Constituents	Fin whale[a]	Bottlenose dolphin[b]	Freshwater[c]	Seawater[d]	Yangtze population		Bohai sea population	
					N (*n*)	Mean ± SD	*N* (*n*)	Mean ± SD
Na^+ mmol/L	303.0 ± 56.6	490.1 ± 87.9	0.35	470	3 (15)	20.07 ± 8.13	4 (4)	156.95 ± 77.33**
Cl^- mmol/L	306.0 ± 57.5	402.7 ± 79.6	0.23	548	3 (15)	13.0 ± 5.38	4 (4)	194.15 ± 76.92**
K^+ mmol/L	60.9 ± 21.3	80.7 ± 25.8	0.08	10	3 (16)	65.5 ± 12.14	4 (4)	60.55 ± 12.49
Ca^{2+} mmol/L	-	-	0.75	10	3 (16)	2.4 ± 0.72	4 (4)	3.35 ± 2.16
Mg^{2+} mmol/L	19.4 ± 6.2	-	0.21	54	3 (16)	2.2 ± 0.62	4 (4)	2.21 ± 1.64
Creatinine mmol/L	4.3 ± 3.07	8.5 ± 5.0	-	-	3 (16)	2.6 ± 0.89	4 (4)	3.2 ± 1.79
Urea mmol/L	419.0 ± 186.0	703.5 ± 253.9	-	-	3 (4)	40.7 ± 15.78	4 (4)	74.96 ± 20.06*
Osmolality mosmol/kg	1040 ± 211.0	1715.7 ± 279.4	-	1,000[b]	3 (14)	934.6 ± 149.99	4 (4)	1223.75 ± 341.84*

[a]Kjeld 2001; [b]Suzuki et al. 2008; [c]Hill et al. 1989; [d]Kjeld 2003. Significant differences between the finless porpoise are indicated by *$P < 0.05$ and **$P < 0.01$. N, individual number; n, sample number.

phocoena) (Koopman et al. 1995) and 156 and 113 mmol/l in Atlantic bottlenose dolphins (*T. truncatus*) (Fair et al. 2006), respectively. This implies that these serum electrolytes play an important role in maintaining the homeostasis of body fluid and physiological functions. However, serum electrolyte levels may be affected by diet and habitat. It is thought that marine mammals obtain water and electrolytes mainly from their food (Costa 2002). When bottlenose dolphins were exposed to seawater and high-protein meals, their serum sodium, chloride, and potassium levels were temporarily elevated (Ridgway and Venn-Watson 2010). Furthermore, captive and wild West Indian manatees (*Trichechus manatus*) living in freshwater were found to have significantly lower plasma Na^+, K^+, and Cl^- levels than wild manatees living in brackish and saltwater (Ortiz et al. 1998). Similarly, the Amazon River dolphin (*Inia geoffrensis*) was also reported to have lower Na^+, Cl^-, and K^+ values than marine cetaceans (Ridgway et al. 1970). Therefore, based on these previous studies, it would be expected that the relatively low serum Cl^-, Mg^{2+}, and P^{3+} concentrations found in YFP, compared with BFP, were caused by their environmental and dietary differences. However, interestingly, no significant difference in serum Na^+ levels was found between YFP and BFP, even though their osmotic environment is entirely different, which suggests the importance of the relatively stable serum natrium in the freshwater porpoise.

There are no exocrine glands in the skin of cetaceans to excrete electrolytes (Ridgway 1972). Therefore, the urinary electrolyte levels are likely to reflect their food intake from their prey to a large extent (Kjeld 2001). The urine Na^+ and Cl^- concentrations in YFP were much lower than those in BFP, fin whales or bottlenose dolphins. The YFP, living in freshwater and feeding on small freshwater fish species, is exposed to less salt than the marine mammals. This makes YFP, and especially the captive animals, more susceptible to hyponatremia than their marine counterparts. The extremely low Na^+ and Cl^- in the urine samples of the captive YFP may imply that it is important for the animals inhabiting freshwater to conserve their sodium to keep their blood sodium balance. In fact, this has also been reported in some pinnipeds kept in freshwater facilities (Geraci 1972).

Organic solutes

Urea is a product of nitrogen compound proteins and amino acids and plays a key role in the urine-concentrating mechanism in mammals (Sands 2002). As a small molecular product of protein metabolism production, urea is easily dissolved in water, which makes it a water-conserving nitrous product excreted in urine (Knepper and Mindell 2009). This may be particularly significant for the marine cetaceans, considering the saline environment they inhabit.

The urea concentration of urine is considered to be related to high-protein food. For example, ingesting a high protein and fat diet may increase the urea concentration of urine in bottlenose dolphins (Ridgway and Venn-Watson 2010). Similar results were also found in harbor seals (*Phoca vitulina*) (Schmidt-Nielsen et al. 1959). Interestingly, YFP had higher serum urea but much lower urine urea than the marine finless porpoise. Since both freshwater and marine porpoise are mainly fed on fish, this cannot be ascribed to dietary differences, even though they may prey on different species of fish. The significantly lower urine and higher serum urea in YFP, compared with BFP and other marine cetaceans, may indicate that freshwater porpoise need to retain the urea in their body fluid. This suggests that serum urea may have a function in regulating the osmotic pressure of blood.

Previous research has shown that baleen whales have significantly higher concentrations of urea in plasma and urine than the terrestrial cattle, which suggests that urea may be used to maintain the body fluid of cetaceans (Birukawa et al. 2005). Other studies have also suggested that cetaceans can maintain their body fluid osmotic

pressure by reabsorbing urea through their kidney (Birukawa et al. 2008; Janech et al. 2002), the main organ regulating urea excretion. Approximately 25% to 40% of filtered urea is reabsorbed in the renal tubules (Bossart et al. 2001), which may be regulated by changes in the urea transporter types and the functions of cetacean kidneys (Janech et al. 2002). The significant difference in serum and urine urea levels between the freshwater and marine finless porpoise may indicate different osmoregulation mechanisms in the two distinct porpoise subspecies. Therefore, this warrants further comparative investigation of urea reabsorption in the kidneys of the YFP and BFP to further understand the osmoregulatory divergence of the two finless porpoise subspecies.

Uric acid is a product of purine metabolism (Ridgway et al. 1970). In this study, the freshwater porpoise had higher serum uric acid levels compared to the marine subspecies ($P < 0.05$). The serum uric acid in Amazon River dolphin (about 600 μmol/L) was also found to be higher than those of some small marine odontocetes (Ridgway et al. 1970). However, the serum uric acid can be influenced by stress, high dietary purine, and renal disease (Daniels 2003). More research is therefore needed to be able to conclude whether the serum uric acid concentration plays a role in osmoregulation in freshwater cetaceans.

Osmotic pressure balance

The plasma osmolalities in YFP and BFP both kept in relatively narrow range with pretty low CVs (2.14% and 4.2% for freshwater and marine captive finless porpoise, respectively), which may indicate the importance of osmotic homeostasis for their body fluid. Bottlenose dolphins can maintain their plasma osmotic homeostasis by excreting urine with variable osmolalities (Ridgway and Venn-Watson 2010). This has also been demonstrated in other cetacean species (Malvin and Rayner 1968). Moreover, West Indian manatees can also regulate their plasma osmolalities in relatively narrow range over a broad range of environmental salinities (Ortiz et al. 1998). The distinct but relatively stable plasma osmolalities in the respective finless porpoise subspecies is much likely to be a result of adaptation to their different osmotic environments. Moreover, the plasma osmolality of bottlenose dolphin can so be changed in a certain range when they were fed with different types of fish species (Skog and Folkow 1994; Ortiz 2001). Therefore, the significantly high plasma osmolality in marine finless porpoise than in the Yangtze finless porpoise may be also partly due to their diet difference in captivity, which definitely needs further detailed investigations.

The urine osmolality of YFP was found to be statistically lower than that of the BFP and that of the other cetaceans, which may be an important strategy for the freshwater porpoise to conserve electrolytes and for the marine subspecies to conserve their body water content. In fact, based on previous findings, it is not surprising to see that marine cetaceans produce concentrated urine to preserve water and maintain osmotic balance in their body fluid (Ortiz 2001; Birukawa et al. 2005). However, the osmotic pressure of some YFP urine samples can reach higher than 1,000 mosM (Table 2), which indicates that YFP can also excrete highly concentrated urine but, interestingly, without much higher Na^+ and Cl^- concentrations. Unlike the other freshwater vertebrates, such as teleost fish, lampreys, and frogs, it seems that it is not necessary for YFP to deliberately produce super hypoosmotic urine to void excess water (Hill et al. 1989). Drinking water does not appear to be a common way for cetaceans and pinnipeds to obtain water (Fetcher and Fetcher 1942; Ortiz 2001), and similarly, YFP may also mainly acquire water from their food and via their metabolism. Therefore, YFP may not have as much of a need to excrete excess water as the other lower aquatic vertebrates. Because the major urine electrolyte concentrations in YFP are generally much lower compared with those in the marine subspecies, the significant osmolality variation in the urine of freshwater porpoise may be determined mainly by the organic constituents and influenced by their diet.

Conclusions

YFP and BFP are two porpoise subspecies living in osmotically distinct environments. Their differences in serum electrolyte and osmotic blood homeostasis suggest that they may have divergent osmoregulation strategies to adapt to their distinct environments. Based on our findings, conserving serum sodium appears to be essential for the freshwater porpoise. Conversely, excreting highly concentrated urine with much higher sodium and chloride content is the major strategy for the marine porpoise to release their hypertonic burden. Furthermore, serum urea appears to play an important role in maintaining the blood osmolality homeostasis in the freshwater finless porpoise. They have much higher serum urea but much lower urine urea than their marine counterpart. This study helps to shed light on the adaptation divergence of the finless porpoise in osmotically different habitats. It also suggests that further morphological and physiological investigation is needed on the osmoregulation adaptation mechanisms in these two ecologically different subspecies of finless porpoise.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

YH and DW designed and conceived the experiment. QZ, YH, and AG carried out all the sampling. AG and YH performed the data analysis. AG, YH, and JW wrote the paper. All authors read and approved the final manuscript.

Acknowledgments
We are grateful to the staff of the Tian-e-Zhou Reserve, Director Liang-Hui Hu, and Dao-Bin Gao for facilitating the capture of Yangtze finless porpoise and the staff of our research group for the sample collection. We also thank the staff of Penglai Sea World and Shanhaiguan Happy Ocean Park for collecting the samples of marine finless porpoise. We also express our sincere gratitude to the Zhongnan Hospital for the sample assay. This work was funded by the Knowledge Innovation Program of the Chinese Academy of Sciences (No. KSCX2-EW-Z-4).

Author details
[1]Key Laboratory of Aquatic Biodiversity and Conservation, Institute of Hydrobiology, Chinese Academy of Sciences, 7th South Donghu Road, Wuchang District, Wuhan, Hubei 430072, People's Republic of China. [2]University of Chinese Academy of Sciences, Beijing 100864, China.

Received: 3 September 2013 Accepted: 6 February 2014
Published: 12 February 2014

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doi:10.1186/1810-522X-53-10
Cite this article as: Guo *et al.*: Concentrations of osmotically related constituents in plasma and urine of finless porpoise (*Neophocaena asiaeorientalis*): implications for osmoregulatory strategies for marine mammals living in freshwater. *Zoological Studies* 2014 **53**:10.