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Review Artiicle

Biological Mechanism of Osmoregulatory Stress in Penaeid Shrimp, *Penaeus Indicus*

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ABSTRACT

Osmoregulation in several crustaceans is an adaptive function to carry out different important physiological roles and processes during their entire life cycle. Most of the penaeid shrimp during their entire life span, spend part of their life in deeper marine waters and rest in brackish waters. For breeding and spawning, they migrate in high saline waters and for the purpose of growth particularly during the early phases of development; they migrate towards a brackish water environment. This kind of anadromous and catadromous migratory behaviour of the animals requires a lot of energy to meet the physiological stresses and successful adaptations to adjust to new changing environments frequently. The mechanism of homeostasis plays an important role in all these animals to maintain internal salt and ionic concentration of the body fluids always higher than the surrounding medium. Several workers have tried to reveal physiological mechanisms underlying osmoregulatory adaptations in a number of crustaceans including shrimp. Besides the role of organic constituents, several studies also mentioned about the role of hormones and endocrine glands in osmoregulation. In recent times due to advancements in molecular tools in molecular biology and genomics, efforts are being made to find out the gene responsible for controlling salt and ions in body fluids. In the present paper, efforts have been made to discuss intracellular and extracellular osmotic adaptations and also neuroendocrine control of Osmotic and Ionic Regulation. With the advent of development in the field of molecular biology and genomics in recent years, future perspectives of research directions are also mentioned to reveal mechanisms of osmoregulatory adaptations at the genome level.

Keywords: Osmoregulation; Body fluids; *Penaeus indicus*

INTRODUCTION

Crustaceans show a greater variety of osmotic behaviour than any other animal group. A considerable amount of information available on the physiology of osmoregulation in crustaceans has been reviewed from d time to time in earlier years and the mechanism of osmotic regulation has been studied from various points of view. The adaptations of marine animals to brackish and freshwater are closely dependent on the development of osmoregulatory powers. Body fluids of most marine invertebrates generally have the same osmotic pressure as the surrounding seawater, but when they migrate to brackish waters, they have to maintain their body fluids at levels higher than that of a diluted medium. The dilution of the body fluids by osmotic inflow is counteracted by active processes. The extent of the higher range to which the animals could regulate their body fluids is a variable factor amongst species belonging to a group, but the osmotic curve of an individual species is a distinct physiological criterion. The degree of hypertonicity that these animals can maintain is an index of their salinity tolerance [1].

LITERATURE REVIEW

The osmoregulatory capacity is essential for the littoral shrimp of the genus Penaeus for successful completion of their life history in the wide differing aqua-regions-the sea and the estuary. The highly fecund females liberate the fertilized eggs demersally in the offshore continental shelf waters [2,3]. After 3-4 weeks of larval existence, the post-larvae migrate and settle in the shallow inshore waters and open estuaries. As the growth process continues juvenile shrimp tend to move into deeper waters and sexual maturity is attained in waters of oceanic salinity. Paniker

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has suggested that it is the decreased osmoregulatory capability which necessitates the migration of adult shrimp back to sea. But Castille and Lawrence [4], pointed out that this migration behaviour is not directly necessitated by osmotic regulation since the adult animals are still capable of hyper osmotic regulation at salinities below the isosmotic points. However, the adult migration to higher salinity waters may be necessary for ovarian development [5] and for embryonic and larval development [6,7]. Chong-Robles et al. [8] carried out studies on osmoregulatory mechanisms and salinity tolerance in shrimp Leptopenaeus vannamei during post-embryonic development. From their studies, it was concluded that L. vannamei is a highly euryhaline species during juvenile and adult stages exhibiting hyper and hypo osmoregulatory behaviour and they can tolerate a wide range of salinity fluctuations. Further, it was also observed that during the early phases of the life cycle, shrimp exhibited more hyper and hypo osmoregulatory patterns whereas they developed more tolerance to the changing salinity as they grow from larval to adult stages showing increased efficiency of osmoregulatory mechanisms. Antony et al. [9] carried out studies on growth, survival and osmoregulatory adaptation in juvenile shrimp *P. Indicus* reared in low salinity amended inland saline groundwater and seawater. From their studies, it was observed that the osmoregulatory capacity of juveniles did not vary much between amended inland saline groundwater and seawater of identical salinities. Iso-osmotic points of shrimp reared in both types of water bodies were almost similar. It was concluded that shrimp *P. indicus* juveniles are efficient osmoregulators and exhibit typical euryhaline behaviour with identical growth parameters over a wide range of salinity. Several studies have been carried out on similar lines earlier and almost identical results have been reported by the number of workers [6,9]. It is now evident that the osmoregulatory pattern changes with advanced stages of growth in shrimp and is influenced by many biotic and abiotic factors. Therefore, the osmoregulatory ability is not onto-genic but purely an adaptive feature in crustaceans that may change markedly during the development according to environmental needs.

Literature on osmoregulation in penaeid shrimp has been very general and most of the works related it to the influence of environmental factors. Paniker and Viswanathan [10] gave an account of chloride regulation in Metapenaeus monoceros. William et al. [11] has described the influence of temperature on osmotic regulation in two species of penaeids, *Penaeus aztecus* and *P.duorarum*. A brief mention on osmotic and ionic behaviour has been made by McFarland and Lee [5] on *P. aztecus* and Trachy-penaeus similes and by Bursey and Lane et al. [12] on *P. durarum*. Castille and Lawrence described the salinity effects on osmotic concentration in *Penaeus setiferus*, *P.duorarum*, *Penaeus vannamei* and *Penaeus stylirostris*. A comparative account of ionic regulation of four species of penaeids has been given by Dall and Smith et al. [13]. Certain aspects of the osmoregulatory capabilities of some penaeid shrimp have been documented [14].

In osmotic adaptive mechanisms, besides an isosmotic extracellular regulation which mainly involves ion exchange between blood and external medium, there is another isosmotic intracellular mechanism where the body's amino acids are catabolized or synthesized for the same purpose. Duchateau and his associates in 1955 were the first to analyse the free amino acids in the tissues of crustacean animals subjected to osmotic shock and mentioned their role in osmotic adjustment. Subsequently, this has been confirmed by many other workers, particularly in penaeid shrimp like *P. kerathurus* [13], *P. japonicus* [14] and M. *monoceros*. But information with regard to protein variation and its relation to the amino acid pool in response to osmotic variations still appears to lack unanimity. In conjunction with osmotic responses, significant changes in ammonia (NH_4+-N) excretion rate also has been reported for many crustaceans. However, salinity effects on other nitrogenous excretory products generally depend on species and its particular osmoregulatory capability.

While dealing with the neuroendocrine control over osmoregulation in crustaceans several workers have demonstrated the effect of the eyestalk neuroendocrine complex on sodium, chloride and ammonia regulation. Although substantial evidence of neuroendocrine control in hydromineral regulation has been reported they lack consistency. Further, there is no information pertaining to changes occurring in neurosecretory cells in response to salinity variations.

The present paper on osmoregulation covers information on the osmotic capability of shrimp at juvenile and adult stages, intracellular adaptive mechanisms to osmotic stress and the neuroendocrine control of osmotic and ionic regulation [15]. Alterations in the neurosecretory cell structure in response to osmotic stress are also described. Perspectives and challenges in this particular niche area have also been discussed considering the advancement of knowledge in molecular biology and genomics.

DISCUSSION

Extracellular osmotic adjustment

The shrimp Penaeus indicus is a good osmoregulator. In both at juvenile and adult phases, hyperosmotic behaviour is predominant in lower salinities (15%) and hypo osmotic behaviour in higher salinities [16]. The adult shrimp are more tolerant to higher salinities because of their rapid osmolarity adjustment (48 hrs) and higher isoosmotic points. Whereas the juvenile shrimp are less tolerant to extreme variations in the salinities. At the juvenile stage also though shrimp show rapid changing salinity media, their isosmotic points are lower than the adults. Therefore, higher iso-osmotic point in adults and lower in juvenile shrimp is a clear indication that the P.indicus prefers lower saline media in the early phase of its growth. In the adult shrimp, the capacity to osmoregulate both at low and high salinities is extremely good. Dall et al. [17] mentioned that most of the penaeid species are able to adapt extremely well to very low salinities during their early juvenile life but this ability reduces in the adult stage. Diwan and Laxminarayana [18] found that the juvenile *P. indicus* osmoregulated well between 3%-26% S for 24 and 48 h duration with isosmotic points ≈ S 18‰ and ≈ S 14% respectively. Adults also they have reported to have good osmoregulatory capability between 5-30‰ S with isosmotic points ≈ S 21‰ and ≈ S 17‰ for 24 and 48 h duration respectively. A duration of 48 h is essential for shrimp to adjust to the new medium.

Generally, when the shrimp are acutely transferred to different salinities, there is a rapid change in the osmolal concentration of haemolymph and to reach a steady state equilibrium the animal requires time. In the case of *P. indicus*, both juveniles and adults require at least 48 hrs for exhibiting stability in the haemolymph osmolar concentration to the changes in the ambient medium. Bursey and Lane [12] reported a period of 24 hrs to establish new steady state equilibrium for shrimp *P. duorarum* while Castille and Lawrence [19] reported 3-4 days for *P. setiferus*. Pillai and Diwan while studying the osmoregulatory adaptation of the shrimp *Metapenaeus monoceros* in the estuarine environment found that the sub-adults of this species revealed a cyclic variation in mean haemolymph osmolality concentration, with higher values recorded for pre-monsoon periods, and its significant positive relationship with salinity and temperature and a weak negative relationship with pH of the environment. The shrimps showed a hyperosmotic regulation in salinities lower than the iso-osmotic values (450-480 mOsm/kg) and hypo-osmotic regulation in those above. The osmoregulatory curve was more or less flat over the salinity range encountered in the study (1.2-32.5‰) indicating that M. monoceros is one of the most efficient osmoregulatory among penaeids. While comparing osmoregulatory capabilities of *P. indicus*. Diwan et.al. [20] found that the adult *Penaeus monodon* osmoregulated well between salinities 3 and 45‰ for 24 48-hour duration with isosmotic points around ≈ S 18.5 ‰ and ≈ S 23.5‰ respectively. Duration of 48 hr is essential for prawns to adjust to the new medium. Lin et al. [21] worked on osmoregulation in relation to the turbidity of water on the survival of juvenile shrimp *P. japonicus*. From their experimental results, it was observed that high turbidity in water was less tolerant to changes in surrounding salinity and showed higher mortality among shrimp. However, in young juveniles, osmoregulatory capacity was not affected by turbidity but in late juvenile stages it was significantly reduced. Reduced osmoregulatory capacity resulted from impaired regulation of Na+ and Cl- concentration. Gill Na + and K+, ATPase activity of exposed late juveniles increased with turbidity, apparently as compensating reaction to disruption of osmotic and ionic balance. There are also reports regarding adaptations to osmoregulatory capacity in shrimp when they are cultured in low saline waters. Molina et al. [22] while working on osmoregulation in shrimp L. vannamei reported that the culture of shrimp in low saline water leads to a series of challenges such as management of deficiency of certain minerals, recirculation system and higher densities of stocking of animals. In order to compensate for mineral deficiencies, a special shrimp feed was designed to meet animals' requirements for these conditions. The deficiencies of main ions particularly potassium K^+ and magnesium Mg^+ are compensated by the addition of salt of these minerals. For good growth of shrimp in low saline waters, ionic levels and proportions of the specific ions (Na^+, K^+, Mg^+, Ca^+ etc.) have to be maintained which is almost similar to the seawater.

Intracellular osmotic adjustment

In intracellular osmotic adaptation, the general assumption is that there is a cellular breakdown or synthesis of organic constituents particularly protein and certain amino acids depending on the surrounding low or high saline environment respectively. The role of free amino acids in the control of cell volume or water volume regulation has been experimentally proved many times in whole animals as well as isolated tissues and nerves in crustaceans and fishes. In *P.indicus* low saline environment imposes a decrease in the levels of protein and free amino acids in muscle and hepatopancreatic tissues as well as in haemolymph which may probably be an indication of degradation of these organic constituents while adjusting to the new environment. Catabolization of free amino acids (oxidative deamination) is also very much evident due to the high rate of ammonia excretion [23]. Spaargaren and his associates stated that in euryhaline shrimp ammonia excretion rate is inversely related to the salinity of the medium. They emphasized the role of ammonia in maintaining alkali reserves of the animal at hypo-osmotic stress. On the contrary in *P. indicus* in the high saline medium the protein and free amino acids content in muscle, hepatopancreas and haemolymph are always more than normal and there is a subsequent decrease in ammonia excretion rate also, which may perhaps reflect the decrease in oxidative deamination process of amino acids leading to conservation or/ synthesis of more proteins in tissues. But in high saline conditions due to a uniform increase in the levels of both protein and free amino acids in tissues and blood, a relation between these two organic constituents could not be established which otherwise would have reflected clearly on the anabolic/ synthetic process [24].

Neuroendocrine control of osmotic and ionic regulation

Neuroendocrine control of osmolal and ionic concentration of haemolymph in the case of *P. indicus* has been proved mainly through eyestalk surgery and injection therapy techniques of suspected endocrine centres. Eyestalk removal in P.indicus generally leads to a significant fall in the levels of osmolal concentration of haemolymph while the levels in eye ablated animals administered with extract of the eyestalk, brain and thoracic ganglion do not result in a decrease but remain on par with values of normal ones (Table 1).

A fall in the levels of osmolal concentration in eyestalk ablated prawns is considered to be due to a loss of hormonal factors related to osmotic control. Recouping of normal values of osmolality in eye-ablated or/administered with hormonal extract also occur and is considered to be due to the release of osmotic stimulating factor present in the brain and thoracic ganglia. But the response of haemolymph osmolarity to various neuroendocrine elements generally depends on the ionic concentration of the surrounding medium. In *P. indicus* eyestalk removal causes a substantial increase in sodium (Na^+), Chloride (Cl^-) and Potassium (K^+) ions in the haemolymph. The

Hours after operation	Normal shrimp	Sham operated control	Bilateral eyestalk surgery+sea water injection	Bilateral eyestalk surgery+injection of eyestalk extract	Bilateral eyestalk surgery+injectionof cerebral ganglion extract	Bilateral eyestalk surgery+injection of thoracic ganglion extract
0	975 ± 3	1132 ± 6	905 ± 7	1307 ± 10	9251 ± 3	1075 ± 8
1	889 ± 4	934 ± 3	895 ± 8	878 ± 2	979 ± 12	904 ± 7
2	889 ± 5	992 ± 5	946 ± 5	927 ± 10	876 ± 4	856 ± 16
4	872 ± 18	874 ± 8	836 ± 3	852 ± 4	876 ± 4	846 ± 7
8	859 ± 5	864 ± 10	801 ± 3	877 ± 3	881 ± 9	877 ± 4
12	855 ± 4	870 ± 8	826 ± 7	868 ± 2	837 ± 12	874 ± 38
18	838 ± 17	873 ± 7	823 ± 10	8783 ± 3	869 ± 5	856 ± 6
24	847 ± 27	861 ± 6	780 ± 4	908 ± 25	939 ± 53	8954 ± 6
48	883 ± 7	883 ± 11	708 ± 2	856 ± 6	876 ± 4	899 ± 9
72	879 ± 36	875 ± 15	820 ± 5	838 ± 5	854 ± 19	896 ± 5

Table 1: Neuroendocrine control of osmolal concentration of haemolymph in the shrimp *P. indicus* (mOsm/kg).

rise in the level is due to the active uptake of ions from the ambient medium. In ablated prawns administered with eyestalk extract, the elevated ionic levels come down and sometimes reach a level lower than normal prawns. Thus the eyestalk neuroendocrine factors help in maintaining or regulating haemolymph ionic concentration. No exact reliable information is available about the mechanism of eyestalk hormones in the control of ionic or osmolal regulation. The current explanation is that the respective ion controlling hormone may be acting on the body surface, and the excretory organs. At the body surface it would decrease the outward permeability of the epithelial cells while at the same time promoting active uptake of ions across the gills by stimulating Na^+, Cl^- and K^+ activated ATP-as enzymes. Ion retention may also be taking place in the excretory organs. Further investigation on these lines is warranted to show how the hormones deploy the ion regulating system [25,26]. Diwan and Laxminarayana [18] studied the influence of various neuroendocrine centres on the osmolal concentration of haemolymph. In eyestalk, ablated shrimp osmolal concentration decreased with time and reached its lowest after 48 h. Eyestalk ablated shrimp injected with extracts of the eyestalk, brain and thoracic ganglia did not show any decrease in the values with time but remained on par with the values of normal ones.

In attempting to derive the concept of hormonal control of osmoregulation in crustaceans, every time ganglionic portions of the central nervous system which are suspected to be the sites of hormonal production are either removed from the animals or extracts of the same implanted to confirm the regulatory process. Unfortunately, no attempts have ever been made so far to look into the histological changes taking place in neurosecretory cells in response to varying salinities in any of the crustaceans except for a singular report by Bosch et al. [27] on Artemia. The occurrence of five types of neurosecretory cells in the whole of the neuroendocrine system of *P.indicus* has been already described in the Chapter on Neuroendocrine system. Major changes take place in the histological structure of only giant and A-type neurosecretory cells in response to osmotic stress. In the changing environment from high saline to diluted seawater, neurosecretory cells exhibit very distinct secretory activity. Such cells develop a large number of vacuoles with less accumulation of granules in the cytoplasm, enlargement of nuclei with many nucleoli in each of them and much disturbance in cellular profile. On the other hand, neurosecretory cells do not exhibit much secretory activity in the prawns exposed to low to high saline conditions. In the non-secretory phase, the cytoplasm of giant and A-cells becomes granular with few vacuoles and a distinct nucleus with or without nucleoli. The cellular profile in general is less disturbed in a high saline environment. Hence such alterations in histological structure in neurosecretory cells strongly suggest their possible involvement in the osmoregulatory process of P.indicus and further substantiates the evidence of neuroendocrine control of osmolality concentration in this species obtained through surgical techniques [28].

Osmoregulation and genomic perspectives

With the advent of knowledge in molecular biology and genome analysis, efforts are being made to investigate the role of any specific genes in the control of osmoregulatory mechanisms. The genomic basis of osmoregulation mostly involves gene expression patterns of specific genes which are related to the control of ionic balance under different adaptations to salinities. Rahi et al. [29] in their review paper extensively covered information regarding the involvement of genes related to the osmoregulation process. They could identify 32 candidate genes which are having important functional roles in maintaining ionic balance across decapod crustaceans. They have classified different groups of genes for several broad functional roles in osmoregulation. The different categories of genes they reported are gene controlling sensing of osmotic stress, then signal transduction, osmotic stress tolerance, ion transportation, active ion exchange and regulation of cell volume [30]. Further, it is mentioned that most of the genes explored were related to a better understanding of the osmoregulation process and other genes responsible for different functions remain highly unexplored.

CONCLUSION

Members of the genus Penaeus are distributed over a wide range of salinities and cultured under a wide variety of conditions in many tropical and sub-tropical parts of the world. During their life cycle, many penaeid shrimp have a common migratory behaviour of returning to more saline conditions for maturation and spawning. After spawning young ones enter the estuaries and move to shallow brackish nursery grounds to continue their growth. Such a migratory pattern would reflect the osmoregulatory capabilities of the species in question. Juveniles and adults *P.indicus* are good osmoregulators with different iso-osmotic points being lower for juveniles and higher for adults. Their tolerance capacity in wide ranging salinity media also differs to some extent. The shrimp require at least 48 hrs duration to adjust to the new medium.

The role of organic molecules in the osmoregulation seems to have more influence on metabolism. In intracellular osmotic adjustment, some of the metabolites like protein and free amino acids play a very important role in cell volume regulation. In *P. indicus* under hypo-osmotic stress protein constituents particularly free amino acids undergo a catabolic process and thus lead to a high rate of ammonia excretion. In hyperosmotic stress, the reverse process may also be true but requires confirmation through extensive research. There is also an urgent need to explore the possibility of involvement of the types of amino acids involved in active water regulation, the role of lipid and carbohydrates and the energy budget.

Evidence of neuroendocrine control in hydromineral regulation in decapod crustaceans has been proved from time to time. In *P. indicus*, eyestalk, brain and thoracic ganglia have hormonal factors which influences not only the osmolal concentration of haemolymph but also individual ions like Na^+, Cl^- and K^+. Distinct histological changes that occur in the neurosecretory cells in response to osmotic variations further strengthen the evidence of hormonal control of osmoregulation in P.indicus. More research studies are required to unravel the details of the physiological mechanism in regulating the osmoregulatory process of this species. In recent years with advancement in the knowledge of molecular biology and genomics, efforts being made to find out the involvement of genes in controlling ions in body fluids.

In recent years efforts have been made to find out gene involvement in ionic regulation. It has been reported that there are specific gene groups in most of the crustacean animals including shrimp which control different functions of osmoregulatory mechanisms. At present literature is available only on those genes which control osmoregulation process. However, other gene groups involved in various physiological mechanisms of osmoregulation need to be explored.

CONFLICT OF INTEREST

There is no conflict of interest among authors.

DATA AVAILABILITY STATEMENT

Data sharing not applicable-no new data generated.

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