

2013

# The dorsal organ: what is it and what is it for?

Robertson, S.

Roberston, S. (2013) 'The dorsal organ: what is it and what is it for?', The Plymouth Student Scientist, 6(1), p. 412-433.

<http://hdl.handle.net/10026.1/14025>

---

The Plymouth Student Scientist  
University of Plymouth

---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.*

# The dorsal organ: what is it and what is it for?

Stuart Robertson

*Project Advisor:* [John Spicer](#), School of Biomedical & Biological Sciences, Plymouth University, Drake Circus, Plymouth, PL4 8AA

## Introduction

Scientific literature concerning the development of arthropods, in particular crustaceans, is littered with references to structures that have been given the name 'dorsal organ'. However, the majority of these structures although homologous in name seem to differ, to varying degrees, in their structure or function. The two main references to a dorsal organ concern either the cuticular or sensory dorsal organ found externally on post-embryonic crustaceans, predominantly worked on by Laverack (1988, 1990, 1992), or the embryonic dorsal organ (Fioroni, 1980) particularly well documented in the Peracarida (Strömberg, 1972; Meschenmoser, 1989; Martin & Laverack, 1992) but also documented within the Hexapoda (Tiegs, 1942; Jura, 1967). There has been much speculation regarding the probable function of these two structures (e.g. Fioroni, 1980; Martin & Laverack, 1992; Aladin & Potts, 1995). However, despite this there has been no single study that has been able to state conclusively the entire function of these organs. This review will focus on the embryonic form and aims to, through accumulated evidence from studies concerning either the embryonic dorsal organ directly or studies closely related to its probable functions, condense the most important information and conclusions. This will aid clarification of the current understanding of the embryonic dorsal organ, in relation primarily to its function. I believe this is necessary in order to further understand the ontogeny of homeostatic control in crustaceans. While the focus will be on the embryonic dorsal organ a clear distinction is needed between the two structures, as confusion in the literature may have arisen.

Initially in this review the cuticular or sensory dorsal organ shall be referred to only as the cuticular dorsal organ as this infers only its location and does not concern its morphology or function. Although the potential homology between the two dorsal organs has been discussed in the literature (Hosfeld, 1999) basic clear distinctions can be made. The embryonic dorsal organ appears during the development of many Crustacea and some Hexapoda. Apart from its appearance during the embryonic phase of development, another important factor that separates it from Laverack's cuticular dorsal organ is the fact that it is transitory (Fioroni, 1980). The embryonic dorsal organ is a site of cellular degeneration in arthropod embryos. In amphipods it seems to begin to form during the development of the germ layers (Turquin, 1967),

with the timing of its degeneration differing between species (Meschenmoser, 1989). The cuticular dorsal organ, on the other hand, is found exclusively on larval or adult forms (post-embryonic) (Martin & Laverack, 1992), never during embryonic development. Although Martin and Laverack (1992) do mention the idea, due to its position and possible function, that there is a degree of homology between the two dorsal organs and the possibility that in some species the cuticular dorsal organ is in fact merely a remnant of the embryonic form, they think it is unlikely.

Knowledge of the cuticular dorsal organ reaches back to at least 1851 when Leydig described it within the larval stages of the anostracans *Branchipus stagnalis* and *Artemia salina* (Martin & Laverack, 1992). Since then the literature well documents an organ found on the dorsal region of many post-embryonic crustaceans. Here it is referred to as the cuticular organ but it has been described using a number of different names: dorsal organ, nackenorgan, neck or nucal organ, salt gland, integumental window, lattice organ, cephalic dorsal hump and hafptorgan covers the majority of descriptions (Elofsson & Hessler, 2008); some of these names have also been given to the embryonic dorsal organ. The internal and external morphology of the cuticular dorsal organ, along with its distribution amongst the Crustacea, is documented by Martin and Laverack (1992). This same piece of work also mentions the possible function of the organ in question; however, the diversity of the name alone is a good indicator of the range of ideas about its function. Early ideas about the anostracans by Weisz (1947) and Benesch (1969) thought the organ was involved in little more than anchoring the antennal and mandibular muscles. However, an array of work carried out in the latter half of the 20<sup>th</sup> century led to the cuticular dorsal organ of anostracans being widely demonstrated to function in salt or chloride regulation (Conte *et al.*, 1972, 1973; Hootman *et al.*, 1972; Criel, 1991). This, along with Croghan's work (1958) on osmotic and ionic regulation in *Artemia salina*, gave rise to the notion of a salt gland involved in salt transport. Along with ion regulation the other main function, of the cuticular dorsal organ, described is that of a sensory role. Highlighted by Horridge (1965) by the discovery of a nerve cord connected to the organ (Martin & Laverack, 1992). There have since been many descriptions of the cuticular dorsal organ functioning either in some form of ion regulation, for example Hofeld and Schminke's work on integumental windows of harpacticoid copepods (1997), or as a sensory organ as found in two taxa of malacostracan decapods, (*Crangon crangon*) and syncarids (*Anaspides tasmaniae*) (Laverack *et al.*, 1996).

The level of ambiguity surrounding the embryonic dorsal organ is not as great as that of the cuticular, however an amount of uncertainty exists and clarity is needed. Much of what is known about the embryonic dorsal organ, particularly its ultrastructure, comes from work on the Peracarida, mainly the Amphipoda and Isopoda. However, some of the earliest work concerning the embryonic dorsal organ was described using Collembolan embryos (Tiegs, 1942). Nevertheless the focus of this review will be on the Crustacea.

The embryonic dorsal organ, like cuticular, gains its name from its location and similarly to the cuticular it is found predominantly on the exterior of the developing arthropod, while still within the outermost membrane.

### **Function of the embryonic dorsal organ**

Much of the work concerning the embryonic dorsal organ has been on crustaceans. However, it has not exclusively been studied on crustaceans and its existence in other groups has been documented (Jura, 1967), although a strict homology has not been discovered. This knowledge base being grounded in work on crustaceans, particularly marine and brackish species, strengthens some of the main ideas as to its function; a role in embryonic osmoregulation, as highlighted by many authors (e.g. Meschenmoser, 1989; Charmantier & Charmantier-Daures, 2001; Seneviratna & Taylor, 2006).

#### *The ontogeny of embryonic osmoregulation*

Salinity acts as a strong selection pressure on aquatic organisms. The capacity for an organism to live in an aquatic environment depends on its ability to adapt. In many aquatic environments salinity is variable, to different degrees. Some habitats may fluctuate only very slightly in salinity where as others may vary from almost fresh water to full strength sea water and back to fresh water in a matter of hours. It is an organism's ability to tolerate these conditions that allows them to inhabit an area. Therefore a physiological ability to osmoregulate, as found in crustaceans, is viewed as an adaptive function (Charmantier & Charmantier-Daures, 2001). There has been a large amount of work carried out on adult crustacean's osmoregulatory processes (reviews by Mantel & Farmer, 1983; Pequeux, 1995). However as Burggren (1992) stated; natural selection acts on all stages of development and therefore knowledge of osmoregulation during development must not be ignored. Many of the studies on development focus on the larval and post-larval stages (Charmantier, 1998), while there are far fewer studies that centre on the embryonic stages of development (e.g. Morrill & Spicer, 1995).

Charmantier (1998) identified three major patterns of ontogenic osmoregulation in crustaceans. In the first group the larvae either osmoconform or weakly osmoregulate. The second show an osmoconforming pattern at the larval stage or in some larvae hyper-osmoconforming. The third group of crustaceans show an ability to osmoregulate during the embryonic phase (Charmantier & Charmantier-Daures, 2001). It is this ability that is frequently linked with the appearance of specific transitory embryonic structures not present in adults (Taylor & Seneviratna, 2005) i.e. the embryonic dorsal organ. This organ is attributed in many studies (e.g. Morrill & Spicer, 1995; Seneviratna & Taylor, 2006) to this extraordinary early ability to osmoregulate during embryogenesis. However, in order to understand better how this organ might achieve this it would be beneficial to look at its morphology and ultrastructure.

#### *Morphology and ultrastructure*

As mentioned above and alluded to by its name, the embryonic dorsal organ is situated on the dorsal side of the embryo, behind the developing head in the 'neck' region. In crustaceans, it provides the only direct connection between the embryo and chorion or embryonic envelope (Strömberg, 1972; Meschenmoser, 1989). In amphipods the organ begins to appear during the development of the germ layers (Turquin, 1967) and it begins to disappear at slightly different times, depending on the species, but always during the later stages of development. Remnants of the embryonic dorsal organ have even been observed in newly hatched juveniles

(Meschenmoser, 1989; unpublished observations on *Gammarus chevreuxi* by Robertson & Truebano, 2011).

There have not been many studies on the ultrastructure of the embryonic dorsal organ of arthropods (Tammarelle, 1975, 1981; Dorn, 1978) but the best and most recent is that by Meschenmoser (1989) on *Orchestia cavimana*. Meschenmoser describes the morphology of the organ as hemispherical in shape and consisting of approximately 50 bottle-shaped cells, each about 80µm in length. These are arranged radially around a centre, which is formed of different types of extracellular material. A similar morphological description of the organ in an isopod can be found in Strömberg's work (1972). During Meschenmoser's description of the ultrastructure of the cells within the embryonic dorsal organ he highlights four different regions: apical, neck, nuclear and basal. The nuclear region contains numerous mitochondria. Along with this Meschenmoser found evidence of chloride in the dorsal organ. Precipitates of silver chloride were observed in all stages that were investigated.

With the knowledge gained from Meschenmoser (1989), when comparing the dorsal organ to cells, cell-groups, epithelia and organs involved with the transport of ions and water many similarities can be drawn. 'The cup-shaped cavity of the intercellular space and the central cone, both filled with extracellular material, are connected and can be compared with the spaces in other systems...Also common to cells which are involved in active transport (Bradley, 1984), is the enlargement of the apical surfaces and the numerous mitochondria, which are associated with the membrane' (Meschenmoser, 1989). There are a few dissimilarities but taking everything into account, including the fact that the organ is the only direct connection between the embryo and the surrounding marsupial fluid (Meschenmoser, 1989) it is fair to accept Meschenmoser's conclusion that transport activity is one function of the embryonic dorsal organ, and that ions, in particular chloride ions, are one of the substances being transported.

#### *A key embryonic osmoregulatory organ?*

Evidence has been presented by Mechenmoser (1989, 1996) for secondary functions of the embryonic dorsal organ; functioning in the utilisation of yolk and also having a role in the embryonic moult. However, it is ion transport that has been attributed as the main role of the embryonic dorsal organ throughout much of the literature (e.g. Surbida & Wright 2001; Elofsson & Hessler, 2008). Nevertheless, before recent work by Wright and O'Donnell (2010) no attempt had been made to record actual ion fluxes across the eggs of peracarid crustaceans. Much of what came before this was attained from staining and ultrastructure studies (Meschenmoser, 1989; Surbida & Wright, 2001). Although Wright and O'Donnell's work was carried out on a terrestrial isopod it is still very comparable; the species studied (*Armadillidium vulgare*) does develop a transitory dorsal organ, seemingly homologous to the aforementioned embryonic dorsal organ. It is also a member of only a few terrestrial groups that have retained thin-walled lecithotrophic eggs during development (Wright & O'Donnell, 2010). These eggs are brooded in a fluid-filled marsupium. The osmolality of this fluid can change during this time and therefore a 'capacity for independent osmotic and ionic regulation by the extraembryonic membranes of the egg would...provide for tighter homeostatic control of the embryonic environment' (Wright & O'Donnell, 2010). Wright and O'Donnell (2010)

concluded that the embryonic dorsal organ in *A. vulgare* was vitally important in the function of ion regulation, further confirming much of the previous work and many hypotheses. An example of such work is the study by Morritt and Spicer (1995) on the osmoregulation of the brackish water amphipod *Gammarus duebeni* during development. They found that during embryonic development there were changes in osmoregulatory function. Perhaps counter-intuitively the organism's most 'complicated' pattern of osmoregulation was found during this embryonic phase and not in its most 'complex' (adult) stage (Morritt & Spicer, 1995). It was reported that the regulation of the periembrionic fluid occurred before the appearance of the coxal gills, the presumed primary osmoregulatory organ in the adult phase (Morritt & Spicer, 1995). They do strongly suggest the idea that the dorsal organ is causing these patterns in the absence of the coxal gills but cannot be certain as much of their information comes from previous ultrastructure and staining studies. However, with the knowledge of the developmental timings of such organs and the osmoregulatory curves coupled with this new information from Wright and O'Donnell (2010), about the dorsal organ controlling ion transport, these ideas and many like them concerning the function of the embryonic dorsal organ (Meschenmoser, 1989) can be strengthened further.

The osmoregulatory capacity of embryonic decapods has not been as closely linked to the embryonic dorsal organ until recently, relative to the Peracarida. Instead the limited work on osmoregulation in decapod embryos has been linked to the permeability of the egg membrane. Work by Bas and Spivak (2000) on two grapsid crabs, *Chasmagnathus granulatus* and *Cyrtograpsus angulatus*, found that embryos of the two species could tolerate a wide range of salinities for up to three days and they attributed this to a decrease in the permeability of the egg membranes. Similarly Susanto and Charmantier (2000, 2001) reported that the evident embryonic tolerance of the freshwater crayfish *Astacus leptodactylus* was due to a similar protective nature of the egg membrane. There is however very little quantitative data on the permeability of the membranes of crustacean embryos (Taylor & Seneviratna, 2005). In fact measurements of ion content, changes in volume and embryonic respiration of decapods (Pandian, 1970; Wear, 1974; Taylor & Leelapiyanart, 2001 respectively) suggest a moderate permeability to gases, water and salts (Taylor & Seneviratna, 2005). Taylor and Seneviratna (2005) strongly refute many of these hypotheses (Charmantier & Aiken, 1987; Charmantier & Charmantier-Daures, 2001; Susanto & Charmantier, 2001) about tolerance to variable salinities in embryos coming from a decrease in the permeability of the egg membrane. They state that in principle osmotic protection in this way could be provided but it would result in implausibly low permeabilities of the membrane to water and other molecules. Particularly when it is known that crabs have high metabolic rates (Taylor & Leelapiyanart, 2001; Seneviratna, 2003) which in turn require high rates of oxygen, carbon dioxide, ammonium and other ions (Taylor & Seneviratna, 2005). Instead the hyper-osmotic regulation of the periembrionic fluid found by Taylor and Seneviratna (2005) in the two species of grapsid crab, and also found in other decapod species (Susanto & Charmantier, 2000, 2001), more likely requires the embryos to actively uptake salts directly from the external medium; the presumed function of the embryonic dorsal organ in many other crustaceans. A transitory embryonic dorsal organ has been described in decapods (Anderson, 1973; Fioroni, 1980) but a potential role in osmoregulation had not been investigated. Not until Seneviratna and Taylor (2006) conducted a follow up study exploring the ontogeny of osmoregulation

in embryos of intertidal crabs, using one of the same species and one closely related (*Hemigrapsus sexdentatus* and *H. crenulatus*) but this time focusing on the possible vital involvement of the embryonic dorsal organ. Their findings were, by this point perhaps unsurprising but nevertheless, key in the understanding of the embryonic dorsal organ. It is strongly suggested that the embryonic dorsal organ of *Hemigrapsus sexdentatus* and *H. crenulatus* is a site for chloride extrusion (Seneviratna & Taylor, 2006). As a result of their work Seneviratna and Taylor (2006) put forward a model for post-gastrula decapod embryos, part of which is that 'osmotic uptake of water is balanced by excretion of water and salts via the dorsal organ'.

### **Homology between dorsal organs**

Many ideas have arisen regarding the different functions and ontogeny of the two dorsal organs, cuticular and embryonic, discussed in this review. However, although the notion that there may be some homology between the two has been highlighted (e.g. Martin & Laverack, 1992) it is often dismissed. This dismissal has perhaps been too quick in the past. Despite their differences there are many similarities between the two; similarities in location but also in function and timing during development (Hosfeld, 1999). Although the embryonic dorsal organ shows no signs of any of the sensory functions shown in some of the cuticular dorsal organs (Martin & Laverack, 1992) both forms show signs of ion transport (Hosfeld, 1999; Wright & O'Donnell, 2010). Similarities can also be observed in developmental timing. The cuticular dorsal organ of harpacticoid copepods is present from the first nauplius (Hosfeld, 1999). This is identical in timing to the embryonic dorsal organ of many Peracarida described by Meschenmoser (1996). However, as the Peracarida develop directly with no free larval stages (Gruner, 1993) Meschenmoser did not use the terms nauplius or metanauplius to describe their development. Yet the Peracarida go through all the larval stages in the egg (Hosfeld, 1999).

There are many more examples of these 'coincidences' between the two dorsal organs. Despite this there is no strict homology between the two. Yet there is also no strict homology that can encompass either one of these dorsal organs wholly, including morphology, function and ultrastructure. It is more likely that these organs evolved convergently or, as suggested by Fioroni (1980), over many multiple evolutionary events, and their differences come from varying needs caused by ontogenic or environmental conditions. This idea reinforces Elofsson and Hessler's (2008) thought that all crustacean structures named dorsal organ, or similarly, fall into two distinct categories; those with a sensory function and those involved with ion transport. This led to the proposal of the re-naming of these two types of organ to: 'dorsal sensory pit organs' and 'dorsal ion-transporting complexes' (Elofsson & Hessler, 2008). In this review the cuticular dorsal organ falls into the first category and the embryonic dorsal organ the latter.

### **Conclusions**

1. From the cumulative information it is fair to conclude that the embryonic dorsal organ, found during the development of many crustaceans, is involved in the transport of ions across the chorion. It is this ion movement that results in hyper-, hypo-, or in some cases hyper-hypo-osmoregulation that allows the embryo to survive in euryhaline conditions. It is therefore vital in the

adaptation of many crustaceans to new habitats, one of their many tools that have allowed them to penetrate into many ecosystems across the natural world.

2. The osmoregulatory patterns observed in embryonic crustaceans, such as the hyper-hypo-regulation in late amphipod embryos, can be explained by an osmoregulatory function of the embryonic dorsal organ.
3. The majority of the literature focuses on the crustaceans. There is evidence for an embryonic dorsal organ within the Hexapoda. However, the homology between the two, whilst evident, is vague.
4. Although the primary function of the embryonic dorsal organ seems evident it may also have secondary functions; such as a role in the utilisation of yolk and also having a function in the embryonic moult.
5. I believe the terms cuticular, sensory and embryonic dorsal organ, along with the varying names for the same structures, should be discarded. There are many names for the same or very similar structures, this has led to much confusion. As no strict homology has been observed it seems that each time a slight difference is found, in a dorsal organ, it is given a whole new name. I think that due to their possible evolutionary history these, potentially convergent, organs should be placed into broader categories. Elofsson and Hessler (2008) have successfully created such categories: 'dorsal sensory pit organs' and 'dorsal ion-transporting complexes'. I suggest a slight amendment to the second of these; when referring to the previously named embryonic dorsal organ it should be called an 'embryonic dorsal ion-transporting complex', in order to separate it from the non-transitory dorsal ion-transporting complexes found on many post-embryonic crustaceans.
6. These conclusions are drawn from work on many studies including those on ultrastructure, staining, developmental timings, osmoregulatory curves and ion fluxes, to name a few. However, more work is needed that draws on all of these within one study, and also across a variety of groups.

## References

- Aladin, N.V. & Potts, W.T.W. (1995). Osmoregulatory capacity of the Cladocera. *Journal of Comparative Physiology B* 164: 671-683.
- Anderson, D.T. (1973). Embryology and phylogeny in annelids and arthropods. In *International Series of Monographs in Pure and Applied Biology, Zoology Division* (ed. G.A. KERKUT), pp. 1-22. Pergamon Press, Oxford.
- Bas, C.C. & Spivak, E.D. (2000). Effect of salinity on embryos of two southwestern Atlantic estuarine grapsid crab species cultured in vitro. *Journal of Crustacean Biology* 20: 647-656.



- Benesch, R. (1969). Zur ontogenie und morphologie von *Artemia salina* L. *Zoologische Jahrbücher Anatomie* 86: 307-458.
- Bradley, T.J. (1984). Mitochondrial placement and function in insect ion-transporting cells. *American Zoology* 24: 157-167.
- Burggren, W.W. (1992). The importance of an ontogenic perspective in physiological studies; Amphibian cardiology as a case study. In *Strategies of Physiological Adaptation, Respiration, Circulation and Metabolism* (ed. S.C. Wood., R. Weber., A. Hargens. & R. Millard), pp. 235-253.
- Charmantier, G. & Aiken, D.E. (1987). Osmotic regulation in late embryos and prelarvae of the American lobster *Homarus americanus* H. Milne-Edwards, 1837 (Crustacea, Decapoda). *Journal of Experimental Marine Biology and Ecology* 109: 101-108.
- Charmantier, G. (1998). Ontogeny of osmoregulation in crustaceans: a review. *Invertebrate Reproduction and Development* 33: 177-190.
- Charmantier, G. & Charmantier-Daures, M. (2001). Ontogeny of osmoregulation in crustaceans: the embryonic phase. *American Zoology* 41: 1078-1089.
- Conte, F.P., Hootman, S.R. & Harris, P.J. (1972). Neck organ of *Artemia salina* nauplii. *Journal of Comparative Physiology* 80: 239-246.
- Conte, F.P., Peterson, G.K. & Ewing, R.D. (1973). Larval salt gland of *Artemia salina* nauplii. Regulation of protein synthesis by environmental salinity. *Journal of Comparative Physiology* 82: 277-289.
- Criel, G.R.J. (1991). Ontogeny of *Artemia*. In *Artemia Biology* (R.A. Browne., P.A. Sorgeloos. & C.N.A. Trotman), pp. 155-185.
- Croghan, P.C. (1958). The osmotic and ionic regulation of *Artemia salina* (L.). *Journal of Experimental Biology* 35: 219-233.
- Dorn, A. (1978). Ultrastructure of the embryonic envelopes and integument of *Oncopeltus fasciatus* (Insecta heteroptera) II. Secondary dorsal organ. *Zoomorphology* 89(1): 57-72.
- Elofsson, R. & Hessler, R.R. (2008). Two microvillar organs, new to Crustacea, in the Mystacocarida. *Arthropod Structure & Development* 37: 522-534.
- Fioroni, P. (1980). The dorsal organ of arthropods with special reference to Crustacea Malacostraca-a comparative survey. *Zoologische Jahrbücher Anatomie* 104: 425-465.
- Gruner, H.E. (1993). Crustacea. In *Lehrbuch der Speziellen Zoologie, Vol 1: Wirbellose Tiere, Part 4: Arthropoda (ohne Insecta)* (ed. H.E. Gruner), pp. 448-1030. Gustav Fischer Verlag, Jena.

Hootman, S.R., Harris, P.J. & Conte, F.P. (1972). Surface specialization of the larval salt gland in *Artemia salina* nauplii. *Journal of Comparative Physiology* 79: 97-104.

Horridge, G.A. (1965). Arthropoda: details of the groups. In *Structure and Function in the Nervous Systems of Invertebrates* (ed. T.H. Bullock. & G.A. Horridge), pp. 1165-1270.

Hosfeld, B. & Schminke, H.K. (1997). The ultrastructure of ionocytes from osmoregulatory integumental windows of *Parastenocaris vicesima* (Crustacea, Copepoda, Harpacticoida). *Archives für Hydrobiologie* 139: 389-400.

Hosfeld, B. (1999). Ultrastructure of ionocytes from osmoregulatory integumental windows of *Tachidius discipes* and *Bryocamptus pygmaeus* (Crustacea, Copepoda, Harpacticoida) with remarks on the homology of nonsensory dorsal organs of crustaceans. *Acta Zoologica* 80: 61-74.

Jura, Cz. (1967). The significance and function of the primary dorsal organ in embryonic development of *Tetrodontophora bielanensis* (Waga) (*Collembola*). *Acta Biologica Cracoviensia* X: 301-311.

Laverack, M.S. (1988). Larval locomotion, sensors, growth and their implications for the nervous system. In *Aspects of Decapod Crustacean Biology* (ed. A.A. Fincham. & P.S. Rainbow), pp. 103-122.

Laverack, M.S. (1990). External sensors and the dorsal organ of Crustacea. In *Frontiers in Crustacean Neurobiology* (ed. K. Wiese., W-D. Krenz., J. Tautz., H. Reichert. & B. Mulloney), pp. 90-96.

Laverack, M.S., Macmillan, D.L., Ritchie, G. & Sandow, S.L. (1996). The ultrastructure of the sensory dorsal organ of crustacea. *Crustaceana* 69: 636-651.

Leydig, F. (1851). Über *Artemia salina* und *Branchipus stagnalis*. *Zeitschrift für Wissenschaftliche Zoologie* 3: 280-358.

Mantel, L.H. & Farmer, L.L. (1983). Osmotic and ionic regulation. In *The Biology of Crustacea, Internal Anatomy and Physiological Regulation* (ed. L.H. Mantel), pp. 53-161. Academic Press, New York, USA.

Martin, J.W. & Laverack, M.S. (1992). On the distribution of the crustacean dorsal organ. *Acta Zoologica* 73: 357-368.

Meschenmoser, M. (1989). Ultrastructure of the embryonic dorsal organ of *Orchestia cavimana* (Crustacea, Amphipoda); with a note on localization of chloride and on the change in calcium-deposition before the embryonic moult. *Tissue Cell* 21: 431-442.

Meschenmoser, M. (1996). Dorsal- und Lateralorgane in der Embryonalentwicklung Von Peracariden (Crustacea, Malacostraca). Göttingen: Cuvillier-Verlag.

- Morritt, D. & Spicer, J.I. (1995). Changes in the pattern of osmoregulation in the brackish water amphipod *Gammarus duebeni* Lilljeborg (Crustacea) during embryonic development. *The Journal of Experimental Zoology* 273: 271-281.
- Pandian, T.J. (1970). Ecophysiological studies on the developing eggs and embryos of the European lobster *Homarus gammarus*. *Marine Biology* 5: 154-167.
- Péqueux, A. (1995). Osmotic regulation in crustaceans. *Journal of Crustacean Biology*. 15: 1–60.
- Seneviratna, D. & Taylor, H.H. (2006). Ontogeny of osmoregulation in embryos of intertidal crabs (*Hemigrapsus sexdentatus* and *H. crenulatus*, Grapsidae, Brachyura): putative involvement of the embryonic dorsal organ. *The Journal of Experimental Biology* 209: 1487- 1501.
- Seneviratna, D. (2003). Ontogeny of osmoregulation of the embryos of two intertidal crabs *Hemigrapsus edwardsii* and *Hemigrapsus crenulatus*. Ph.D. Thesis, University of Canterbury, New Zealand.
- Strömberg, J.O. (1972). *Cyathura polita* (Crustacea, Isopoda), some embryological notes. *Bulletin of Marine Science* 22: 463-482.
- Surbida, K.L. & Wright, J.C. (2001). Embryo tolerance and maternal control of the marsupial environment in *Armadillidium vulgare* (Isopoda: Oniscidea). *Physiological and Biochemical Zoology* 74: 894-906.
- Susanto, G.N. & Charmantier, G. (2000). Ontogeny of osmoregulation in the crayfish *Astacus leptodactylus*. *Physiological and Biochemical Zoology* 73: 169-176.
- Susanto, G.N. & Charmantier, G. (2001). Crayfish freshwater adaptation starts in eggs ontogeny of osmoregulation in embryos of *Astacus leptodactylus*. *Journal of Experimental Zoology* 289: 433-440.
- Tamarelle, M. (1975). Nouvelles observations ultrastructurales sur l'organe dorsal Collemboles. Mise en évidence d'un type de différenciation 'en cocarde' chez *Proisotoma minuta*. *Comptes Rendus de l'Académie des Sciences Paris* 280 D: 1147-1150.
- Tamarelle, M. (1981). La formation et l'évolution d'organe dorsal chez les embryons de cinq Collemboles (Insecta: Apterygota). *International Journal of Insect Morphology and Embryology* 10: 203-224.
- Taylor, H.H. & Leelapiyanart, N. (2001). Oxygen uptake by embryos and ovigerous females of two intertidal crabs, *Heterozius rotundifrons* (Bellidae) and *Cyclograpsus lavauxi* (Grapsidae): scaling and the metabolic costs of reproduction. *Journal of Experimental Biology* 204: 1083-1097.

Taylor, H.H. & Seneviratna, D. (2005). Ontogeny of salinity tolerance and hyperosmoregulation by embryos of the intertidal crabs *Hemigrapsus edwardsii* and *Hemigrapsus crenulatus* (Decapoda, Grapsidae): survival of acute hyposaline exposure. *Comparative Biochemistry and Physiology* 140: 495-505.

Tiegs, O.W. (1942). The "dorsal organ" of collembolan embryos. *Quarterly Journal of Microscopical Science* 83: 153-169.

Turquin, M.J. (1967). L'organe dorsal de *Niphargus virei* (Crustacé, Amphipode hypogé). *Memories de Fédération Française de Spéléologie*, 305-312.

Wear, R.G. (1974). Incubation in British decapod Crustacea and the effects of temperature on the rate and success of embryonic development. *Journal of the Marine Biological Association U.K.*54: 745-762.

Weisz, P.B. (1947). The historical pattern of metameric development in *Artemia salina*. *Journal of Morphology* 81: 45-89.

Wright, J.C. & O'Donnell, M.J. (2010). In vivo ion fluxes across the eggs of *Armadillidium vulgare* (Oniscidea: Isopoda): the role of the dorsal organ. *Physiological and Biochemical Zoology* 83: 587-596.