

ONTOGENETIC SHIFTS IN CARAPACE PATTERNING AND/OR COLOURATION IN INTERTIDAL AND SUBTIDAL BRACHYURAN CRABS

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ABSTRACT. – Some juvenile intertidal and subtidal crabs are known to exhibit carapace polymorphism, crypsis, or disruptive colours which are lost as the crabs mature, i.e. they undergo ontogenetic shifts in patterning and/or colouration. These patterns and colours are thought to protect young crabs from visual predators. The transformation is often dramatic and most likely reflects a critical life-stage that is possibly unique to marine arthropods. Two main hypotheses have been proposed to explain changes in colouration as crabs grow: they no longer need such a defense as they become bigger and stronger or, they migrate from nursery habitats to areas where such patterns and colours do not confer protection. To identify the extent of ontogenetic shifts in intertidal and subtidal crab patterning and/or colouration, a database was assembled from the literature (primary and grey); from expert scientific opinions (via personal interviews and email correspondence); and website-derived observations from non-professionals worldwide.

KEY WORDS. – Camouflage, crypsis, disruptive colouration, polymorphism, visual predator.

INTRODUCTION

Camouflage is a predator evasion strategy employed by many animals (Endler, 1978, 1984; Ruxton et al., 2004). Several forms have been described, including crypsis (background matching) where an organism possesses colouration or markings that are similar to the substrates they are found on (Endler, 1978, 1984), and disruptive colouration, where the outline of the body is broken up, making it difficult for a visual predator to detect its true form (Cott, 1940; Cuthill et al., 2005). Disruptive colouration has been observed in an array of organisms ranging from molluscs, crustaceans and insects to snakes, birds and mammals (Ruxton et al., 2004) and has been shown experimentally to successfully reduce predation (Cuthill et al., 2005, 2006; Stevens et al., 2006).

It has been well-documented that juvenile shore crabs, *Carcinus maenas* (Linnaeus, 1758), possess carapace patterns that are lost as they mature (Crothers, 1968; Hogarth, 1975, 1978; Bedini, 2002; Palma et al., 2003; Todd et al., 2005, 2006). Todd et al. (2005) noted that age-specific habitat shifts could be an underlying cause for this change in carapace patterning. The larvae of shore crabs settle on nursery grounds such as seagrass (Hovel & Lipcius, 2002) and mussel beds (Thiel & Dornedde, 1994). These habitats tend to be polychromatic and complex compared to the more homogeneous background of sand, macroalgae and rock that the adults generally inhabit. Two, non-mutually exclusive,

hypotheses have been proposed to explain ontogenetic shifts in colouration as *C. maenas* grow: that they no longer need defensive camouflage as they become bigger and stronger; or they migrate from nursery habitats to areas where carapace patterns no longer confer protection (Hogarth, 1978; Palma et al., 2003; Todd et al., 2006).

Carapace polymorphism can also protect juvenile crabs from predation, although it has been studied less in the Brachyura compared to other marine invertebrates (Palma et al., 2003). A population exhibiting a variety of morphs makes it more difficult for a visual predator to create a search image (e.g. Pietrewicz & Kamil 1979). For example, the bivalve *Donax faba* is relatively conspicuous on its usual sandy habitat, but its polymorphism appears to protect it from predation (Smith, 1975). The protective effect of polymorphism has also been proposed to explain the range of colour and pattern morphs found in *Littorina saxatilis* (Ekendahl & Johannesson, 1997), *Donacilla cornea* (Whiteley et al., 1997) and *Cepea* sp. (Jones et al., 1977; Goodhart, 1987). The morphs in polymorphic populations are often also cryptic, especially on polychromatic backgrounds (Jones et al., 1977; Goodhart, 1987; Palma & Steneck, 2001; Parsonage & Hughes, 2002; Wente & Phillips, 2003). Using predator exclusion experiments, Palma & Steneck (2001) found that polymorphic rock crabs (*Cancer irroratus* Say, 1817) were harder to find against a background of cobblestones and sand than one made of grey plastic. Thus,

polymorphism in juvenile crabs may also be associated with living among the complex substrates that are often characteristic of their nursery grounds.

The hypothesis that patterned adult *C. maenas* are rare because they are preferentially preyed upon when young was dismissed by Hogarth (1978) based on the fact that, if the absence of patterned adults was due to predation pressure on juveniles, then the genes for patterning would be removed from the population over time and therefore no such crabs would exist at any life stage. But the inverse is true, with a high number of juvenile patterned shore crabs identified by Hogarth (1975) and, 30 years later, by Todd et al. (2005, 2006). The same argument can be used for age-dependent changes from polymorphic to monomorphic populations and, throughout this paper, we assume that the species listed in Table 1 undergo ontogenetic shifts as opposed to juveniles being preferentially preyed upon.

In the species that are known to change from patterned and/or polymorphic to monochromatic with maturity; the transformation is dramatic and most likely reflects a critical life-stage that is possibly unique to marine arthropods (Palma & Steneck, 2001). Palma et al. (2003) identified eight species of near-shore brachyuran crabs in central Chile that are polymorphic, and often cryptically coloured, as juveniles but not as adults. In this study, we build on Palma et al.'s (2003) work by determining the prevalence of these ontogenetic shifts in intertidal and subtidal crabs worldwide. Data were gathered from primary and grey literature (including website searches) and via direct correspondence with crustacean biologists around the globe. We aim to establish whether the juvenile-to-adult change in carapace patterning observed in *C. maenas* is representative of a wider predator-avoidance strategy among crab species that live in intertidal and subtidal habitats.

MATERIALS AND METHODS

The database of subtidal and intertidal crabs that are known to shift from patterned to unpatterned and/or from polymorphic to monomorphic populations was assembled from a variety of sources: 1) primary literature via the online resources Web of Science and JSTOR using combinations of approximately 20 key words; 2) primary and grey literature via electronic and manual searches of the National University of Singapore library, the Raffles Museum of Biodiversity library and Prof. Peter Ng's personal collections; 3) primary literature, grey literature, and website searches via Google and Google Scholar using combinations of approximately 20 key words; 4) via expert scientific opinions, through personal interviews, email correspondence and a general query posted on CRUST-L (a mailing list for crustacean biologists). Whenever possible, differences in juvenile and adult habitats, and their geographical distribution, were noted.

To examine the spread among superfamilies, families and sub-families for taxa that display different juvenile and

adult patterning and/or colouration, all species in the final database were mapped onto a taxonomic tree based on the nomenclature and systematics described in Ng et al. (2008).

RESULTS

A total of 21 species that undergo ontogenetic shifts in patterning and/or colouration were described in published literature. Sixteen species are polymorphic and/or patterned as juveniles and become monochromatic or much plainer as they mature (Table 1). Two species, *Atergatis floridus* (Linnaeus, 1767) and *A. integerrimus* (Lamarck, 1818) are patterned as both juveniles and adults, but the patterns change. One species, *Pugettia producta* (Randall, 1840), changes from one monomorphic colour (red) to another (amber). The remaining two species, *Chiromantes haematocheir* (De Haan, 1833) and (male) *Portunus pelagicus* (Linnaeus, 1758) have more complex colour patterns as adults than as juveniles.

The 29 species, including the eight described by Palma et al. (2003), span nine Eubrachyura superfamilies (Fig. 1) and represent a worldwide distribution (Table 1). The Xanthinae contain six species of crabs that undergo ontogenetic shifts in patterning and/or colouration. Cancridae contains five species, Portunidae contains four species, Epialtidae three, Menippidae and Hymenosomatidae two each, and the families Platyxanthidae, Pilumnidae, Pilumnoididae, Pseudoziidae, Sesarmidae, Varunidae and Ocypodidae all contain one species that change colour with age.

Numerous other species were proposed by scientists contacted by email as undergoing shifts in patterns and/or colours that could not be confirmed in the literature, including: *Glebocarcinus amphioetus* (Rathbun, 1898), *Chasmagnathus convexus* (De Haan, 1835), *Eriphia sebana* (Shaw & Nodder, 1803), *Eriphia smithii* (Shaw & Nodder, 1803), *Gaetice depressus* (De Haan, 1835), *Leucosia anatum* (Herbst, 1783), *Leptodius exaratus* (H. Milne Edwards, 1834), *Ocypode stimpsoni* Ortmann, 1897, *Pseudozius caystrus* (Adams & White, 1849), *Uca crassipes* (White, 1847), and *Uca tetragonon* (Herbst, 1790).

We have not included the eight species listed by Palma et al. (2003) in Table 1 as there is too little information regarding their preferred habitats; however, they have been mapped onto the taxonomic tree in Fig. 1.

DISCUSSION

Through a combination of literature searches and anecdotal observations we have established that at least 21 species of subtidal and intertidal crabs undergo ontogenetic shifts in carapace patterning and/or colouration. Together with the eight identified by Palma et al. (2003), the list now totals 29 species. This number is likely to be an underestimate as, for many species, information on juvenile carapace

Table 1. Species that exhibit ontogenetic shifts in carapace patterning and /or colouration. Geographical distributions from the Integrated Taxonomic Information System (2008).

Species name	Juvenile habitat	Adult habitat	Juvenile carapace	Adult carapace	Distribution	References
1 <i>Atergatis floridus</i> (Linnaeus, 1767)	–	Intertidal to subtidal	Purple with white spots	Greenish blue/ brown with patterns	Western Pacific, Southeast Asia	Ng & Davie (2007)
2 <i>Atergatis integerrimus</i> (Lamarck, 1818)	–	Coral reefs, under rocks or in crevices	Red with white margin around carapace	Red with white spots	Southwest Pacific, South China Sea	Tan & Ng (1988)
3 <i>Cancer irroratus</i> Say, 1817	Either sand or cobble; mid to low intertidal	Highest survival on cobble; mid and low intertidal to shallow subtidal	Colour polymorphism, e.g. white, brown, tan, dark, yellow	Mostly brown, the remainder dark	Northwest Atlantic	Haefner (1976); Palma et al. (1998); Palma & Steneck (2001)
4 <i>Cancer pagurus</i> Linnaeus, 1758	Under boulders, coarse or muddy ground; intertidal zone	Under boulders, coarse or muddy ground; shallow subtidal	White or purple-brown with white patches	Reddish-brown	Northeast Atlantic	Bennett (1995)
5 <i>Cancer productus</i> Randall, 1840	Kelp and eelgrass beds	Sheltered areas with rocky outcrops and sandy or gravel bottoms	Polymorphic, e.g. red, white, orange, brown. Can also be patterned.	Homogeneously dull brick red	Northeast Pacific	Meinkoth (1981)
6 <i>Carcinus maenas</i> Linnaeus, 1758)	Musselbeds, when available	Rocky shore and seaweed beds.	Juveniles are polymorphic and often dull with white, and occasionally red, markings	Generally a dull green/grey/brown	East and Indo-west Pacific, east and west Atlantic	Crothers (1968); Hogarth (1975; 1978) Todd et al. (2005; 2006)
7 <i>Callinectes arcuatus</i> Ordway, 1863	–	Bays and estuaries; sandy, muddy or shell bottoms	More variable in colour; camouflaged as sand or shell hash	Olive grey-green	Northeast Pacific	Wicksten (2008)
8 <i>Chironantes haematocheir</i> (De Haan, 1833)	Coastal Bays	Back mangroves seasonal marshes, streams, river banks	Dull grey	Red	Japan to Hong Kong	Ades et al. (2006)
9 <i>Echinoecus pentagonus</i> (A. Milne Edwards, 1879)	Shallow-subtidal	Shallow-subtidal	Dark red-brown with a white band across anterior portion of carapace	Females tend to lose their white band and become dull maroon	Hawaii to Australia	Chia et al. (1999) Castro (Pers. comm.)
10 <i>Hallicarcinus innominatus</i> Richardson, 1949	Intertidal (especially lower intertidal)	Intertidal (especially lower intertidal)	Pale yellow carapace flecked with black, orange and white	Brown with green or black tints.	Southwest Pacific	McLay (1988)
11 <i>Hemigrapsus oregonensis</i> (Dana, 1851)	Intertidal (under rocks)	Intertidal (under rocks)	White or mottled patterns are common	Dark or grey-green	Northeast Pacific	Jensen (1995)
12 <i>Leptodius exaratus</i> (H. Milne Edwards, 1834)	Pebble beaches	Rocky and cobble shores	Some dark patches	No patches	Red Sea to Japan and Queensland, Australia	Simoes et al. (2001)
13 <i>Liocarcinus depurator</i> (Linnaeus, 1758)	–	Subtidal; fine muddy sand or gravel	Polymorphic with patterned comprising white patches	Pale reddish-brown	Northeast Atlantic to Mediterranean	Ng (1998); Muñio et al. (1999)

Table 1. (Continued).

Species name	Juvenile habitat	Adult habitat	Juvenile carapace	Adult carapace	Distribution	References
14 <i>Menippe adina</i> Williams & Felder, 1986	Interstices of oyster shells	Mixed hard and muddy bottoms, mud borrows, oyster reefs.	Wide variety of colours and markings	Uniformly dark, blue/black	Western North Atlantic, North Carolina to Belize	Geiger & Bert (2006)
15 <i>Menippe mercenaria</i> (Say, 1818)	Crevices among barnacles, sponges, tunicates, calcareous algae and bryozoans	Burrows and crevices among rocks in seagrass and sand/shell hash habitats	Wide variety of colours and markings	Brownish red with spots	Western North Atlantic from North Carolina to Belize	Geiger & Bert (2006)
16 <i>Metacarcinus anthonyi</i> (Rathbun, 1897)	–	Intertidal; among rocks in bays and estuaries	May have mottled carapace with white, brown or tan markings	Brownish-red to yellowish-orange	Northeast Pacific	Wicksten (2008)
17 <i>Portunus pelagicus</i> (Linnaeus, 1758)	Intertidal (mangrove creeks and mudflats)	Subtidal	Pale-coloured with pinkish hue	Males bright blue with white spots; females dull greenish-brown	Western Indian Ocean to Eastern Pacific	Jensen (1995); Svane & Hooper (2004)
18 <i>Pseudozoeus cavstrus</i> (Adams and White, 1849)	–	Cobble beaches	Polymorphic, often patterned	Polymorphic, occasionally patterned	Red Sea to Southwest Pacific	Simoes et al. (2001)
19 <i>Pugettia producta</i> , (Randall, 1840)	Intertidal and subtidal red algae habitats	Subtidal giant kelp habitats	Red	Amber	Alaska to Mexico	Hultgren & Stachowicz (2008)
20 <i>Uca capricornis</i> Crane, 1975	River/stream mouths (brackish water)	River/stream mouths (brackish water)	Often patterned with bright and striking colours	Darker and duller in colour than juveniles	Southwest Pacific	Crane (1975)
21 <i>Xantho poressa</i> (Olivier, 1792)	Colourful pebbles; intertidal and shallow subtidal	Rocky substrate; intertidal and shallow subtidal	Higher proportion polymorphic; white transverse stripes	Lower proportion polymorphic	Mediterranean and Northeast Atlantic	Reuschel & Schubart (2007)

patterns and colours (and habitat preference) is absent. Changes in patterning and/or colouration are not restricted to any particular taxon of crabs, suggesting that they could have arisen independently in many families—perhaps as a response to local environmental conditions where such shifts could confer a selective advantage.

Of the 16 species listed in Table 1 that are polymorphic and/or patterned as juveniles and monochromatic as adults, the juvenile habitat is only known for ten. Six of these species move from one environment to another as they mature and it is possible the accompanying shift in patterning and/or colouration is adaptive, i.e. there exists phenotype-environment matching that reduces predation risk (Todd et al., 2006). The remaining four species, *Cancer pagurus* Linnaeus, 1758, *Echinoecus pentagonus* (A. Milne-Edwards, 1879), *Halicarcinus innominatus* Richardson, 1949 and *Hemigrapsus oregonensis* (Dana, 1851) undergo changes from colourful juvenile morphs to duller adults, but do they not appear to migrate between environments with age. This non-migration was also inferred for the eight species in Palma et al. (2003), as the authors did not record separate habitats for juveniles and adults. If the juvenile colours are camouflaging, they could be lost at maturity simply because adults are less vulnerable and thus do not need this kind of protection from visual predators (Palma

& Steneck, 2001). Alternatively, the information regarding their habitats might be incomplete. We found that the most critical information, i.e. the microhabitat where the juvenile spends the majority of its time and is thus most potentially at risk (Endler, 1978), was frequently missing, making it difficult to decipher what reported changes in patterning/colouration mean.

The rationalisations above do not elucidate why *Atergatis floridus*, *A. integerrimus* and *Pugettia producta* are patterned or coloured (albeit differently) as both juveniles and adults or why *Chiromantes haematocheir* and (male) *Portunus pelagicus* have more brightly coloured adults than juveniles. There are various reasons that may explain these incongruous findings; the most likely is that adults move to another type of habitat where camouflage might be better provided by different patterns or colours. For example, *Pugettia producta* changes from red to amber with age (a result of sequestration of pigments from the algae it inhabits and eats) and yet maintains an excellent phenotype-environment match (Hultgren & Stachowicz, 2008). Alternatively, it is possible that ontogenetic shifts in colouration are not predation-related, but instead associated with intraspecific, or intrageneric, communication, e.g. for crabs to signal their social status or breeding condition. Finally, bright adult colouration could be aposematic; but

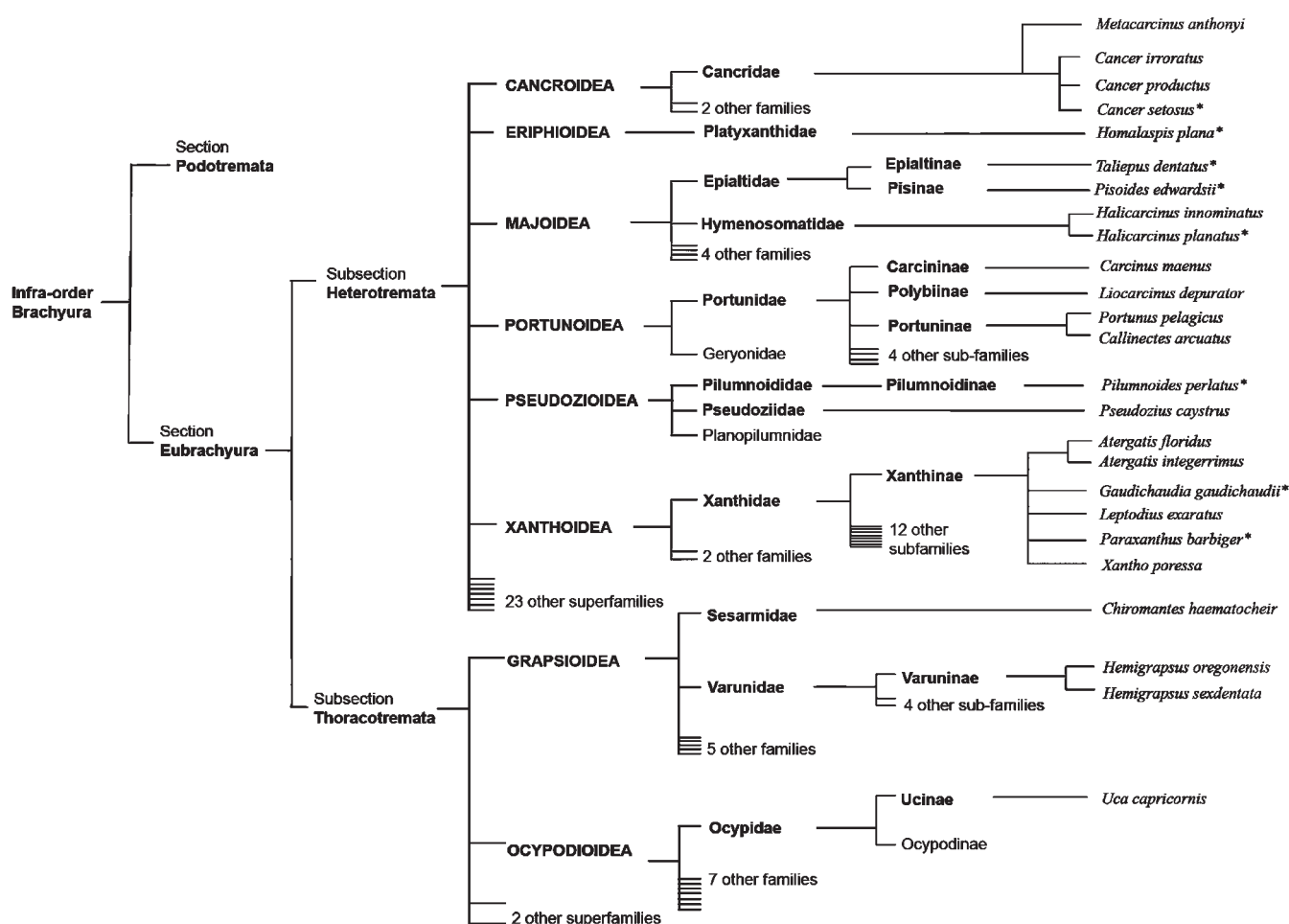


Fig. 1. Taxonomic tree showing spread among superfamilies, families and sub-families among the species found to exhibit different carapace patterns between adults and juveniles. Species from Palma et al. (2003) are marked with an asterisk (*). Taxonomy and nomenclature follows Ng et al. (2008).

aposematism is associated with distastefulness (Ruxton et al., 2004) which most crabs are not (although they might be mimicking a distasteful organism).

Berke & Woodin (2008) list ontogenetic shifts in setal morphology and decorating behaviour in many species of decorator crab. Decoration is an effective camouflage (Hultgren & Stachowicz, 2008) and its loss with age is analogous to the ontogenetic loss of carapace patterns and colours discussed in this paper. Berke & Woodin (2008) demonstrate an energetic cost to decorating, arguing that that this, combined with the size-refuge achieved by adults, would lead to a shift away from decorating. A similar mechanism may be involved in the ontogenetic shifts in carapace patterns and colouration discussed in this paper. Todd et al. (2006) noted that the process of losing markings in *C. maenas* could be accentuated if the pigments involved require an energetic cost to maintain. This potential cost has not yet been quantified, but it is unlikely to be as great as it is for decorator crabs.

Some crabs, such as *Uca capricornis* (Crane, 1975), can undergo rapid changes in colouration (Detto et al. 2008), but it is probable that the shifts discussed here occur between moults. More work is required on the species listed in Table 1 to confirm this. Crothers (1968) kept a single *C. maenas* through three moults and noted that it first gained some white pigment before losing it again. Hogarth (1983) found that approximately 30% of young *C. maenas* changed patterns between moults, but only a third of these did so dramatically. The precise timing of ontogenetic shifts in colours and patterns is also poorly known, as is the potential for multiple changes over time.

The results presented in Table 1 represent a wide range of searches and sources, but they are not exhaustive. For example, it was not feasible to search foreign language papers for mention of ontogenetic shifts in the same manner that we searched English language articles. Geographic biases in where reports originate are evident, for instance, by searching specifically for polymorphic and/or patterned juvenile crabs Palma et al. (2003) found eight species in central Chile alone. Very few papers describe both juvenile and adult patterns and colours in subtidal and intertidal species and we predict that more directed studies would uncover similar trends to Palma et al. (2003). Generally, a better understanding of microhabitat use, as well as behaviour and ecology in relation to defence, would help elucidate the function of ontogenetic shifts in carapace patterning and/or colouration in intertidal and subtidal brachyuran crabs.

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