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Extended parental care in crustaceans – an update

Cuidado parental extendido en crustáceos – conocimiento actual

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ABSTRACT

Many crustacean species show extended parental care (XPC) for fully developed juvenile offspring. Herein, the present state of knowledge of the major patterns and consequences of XPC is reviewed, and furthermore important future research topics are identified. Crustaceans with XPC are found in marine, freshwater and terrestrial environments, but care for late juvenile stages appears to be more common in terrestrial environments. In all species, females participate or even take the main share of XPC activities. Crustaceans that carry their offspring during XPC commonly release early juvenile stages, while species inhabiting particular microhabitats may host offspring until these have reached subadult or adult stages. Apart from providing a suitable and safe microhabitat to small offspring, parents share food with, groom or actively defend their juveniles. Some of the most important benefits of XPC include improved juvenile growth and survival. XPC may also lead to conflicts among developing offspring or between parents and offspring, especially during later phases of XPC when resources (food and space) become increasingly limiting. Similarly, during long-lasting cohabitation, epibionts (e.g., parasites) may be transferred from parents to offspring, as is indicated by observational evidence. For several species, local recruitment, where juveniles recruit in the immediate vicinity of their parents, has been observed. Under these conditions, local populations may rapidly increase, potentially leading to intra-specific competition for space, thereby possibly causing a decrease in reproductive activity or a reduction in length of XPC. Another consequence of XPC and local recruitment could be limited dispersal potential, but some marine crustaceans with XPC and local recruitment nevertheless have a wide geographic distribution. It is hypothesized that the existence of suitable dispersal vectors such as floating macroalgae or wood can lead to a substantial increase in dispersal distances of crustaceans with XPC via rafting, surpassing that of crustaceans with pelagic larvae. Since crustaceans with XPC may be particularly susceptible to changing environmental conditions, especially in the terrestrial environment where populations are often small and locally restricted, conservation of biodiversity should focus on these (and other invertebrate) species with XPC.

Key words: Crustacea, Peracarida, reproduction, parental care, habitat, evolution.

RESUMEN

Muchas especies de crustáceos presentan cuidado parental extendido (XPC), donde individuos juveniles completamente desarrollados son cuidados por los padres. En la presente contribución se revisa el conocimiento actual del XPC, sus consecuencias y además se identifican tópicos importantes para ser investigados en el futuro. Los crustáceos que presentan XPC pueden ser encontrados en ambientes marinos, límnicos y terrestres, pero el XPC es más conspicuo y aparentemente más común en el ambiente terrestre. En todas las especies analizadas, las hembras desarrollan las principales tareas relacionadas con el XPC. Crustáceos que portan sus juveniles en alguna estructura del cuerpo (i.e. marsupio) durante el XPC liberan a estos tempranamente, mientras que las especies que habitan refugios pueden albergar a sus crías incluso cuando éstas alcanzan estadios tardíos de desarrollo, o bien, la adultez. Además de proveer un microhabitat adecuado y seguro para las crías, las madres comparten el alimento con, limpian y/o defienden activamente a sus juveniles. Entre los beneficios más importantes del XPC figura el incremento de las tasas de crecimiento y sobrevivencia de los juveniles. El XPC puede producir conflictos entre las crías o entre los padres y sus crías, especialmente durante la etapa tardía del XPC, cuando algunos recursos (alimento y espacio) pueden llegar a ser aún más limitantes. De manera similar, debido a la proximidad y frecuente interacción entre padres y crías, epibiontes (e.g., parásitos) pueden ser transferidos desde los padres hacia los juveniles con mayor frecuencia, como algunos estudios lo indican. Un reclutamiento localizado (i.e. juveniles colonizan la vecindad inmediata de los padres) ha sido descrito para varias especies de crustáceos que presentan XPC. En estas circunstancias, algunas poblaciones de crustáceos pueden aumentar rápidamente en número, pudiendo ocurrir un incremento de la competencia intra–especifica por espacio, y consecuentemente, una disminución de la actividad reproductiva y la duración del XPC. Una disminución respecto del potencial de dispersión, producto del reclutamiento localizado, puede ser considerada otra de las consecuencias del XPC. No obstante, varios crustáceos con XPC y reclutamiento localizado presentan una amplia distribución geográfica. Se hipotétiza que la existencia de vectores, tales como macroalgas flotantes o madera, representan un mecanismo mediante el cual la dispersión de crustáceos marinos con XPC aumenta sustancialmente (vía “rafting”), incluso pudiendo superar el potencial de dispersión de especies con estadios pelágicos tempranos (i.e., etapas larvales). Dado que los crustáceos con XPC pueden ser muy susceptibles respecto de cambios abruptos en las condiciones ambientales, especialmente en el ambiente terrestre donde las poblaciones son usualmente pequeñas y localmente restringidas, estudios que tengan por objeto la conservación de la biodiversidad deberían poner mayor énfasis en estas (y otras) especies de invertebrados que presentan XPC.

Palabras clave: Crustacea, Peracarida, reproducción, cuidado parental, hábitat, evolución.

INTRODUCTION

Parental care behavior has important consequences both for parents and for offspring (Clutton-Brock 1991). In general, any activity of parents towards their offspring that represents a cost for the parent qualifies as parental care (Clutton-Brock 1991). The return for these expenditures by parents is increased offspring growth and survival (e.g., Kobayashi et al. 2002), which improves the inclusive fitness of parents. Parental care is often highly developed in species that produce limited numbers of offspring and that inhabit extreme environments. Parental care may involve a wide array of different behaviors ranging from simple tolerance of juveniles on the parental body or in dwellings, to grooming or feeding of developing offspring and to aggressive defense of juveniles against attack or predation (e.g., Hazlett 1983).

In the majority of crustaceans, fertilization of eggs occurs on or in the body of the female, and the initial phase of embryonic development takes place on or in the female body (e.g., Dick et al. 1998, Baeza & Fernández 2002). Usually, offspring are released from the female's body at some early or intermediate stage of larval development, i.e., before reaching the juvenile stage – these offspring are planktonic and continue development away from the parent (Hazlett 1983). However, in some species, females care for their offspring on their body (in marsupial and abdominal brood pouches) until these have reached advanced larval or fully developed juvenile stages. Thus, at the moment of release, these offspring have similar morphological and physiological capabilities as their parents, and can lead a life-style similar to their parents. This creates a wealth of opportunities and problems distinctly different from crustaceans that release offspring as pelagic larval stages. If parents continue to care for offspring up to or beyond the first juvenile stage, this behavior is termed extended parental care (hereafter: XPC). While a previous review primarily described the patterns of extended parental care in crustaceans (Thiel 1999a), herein, I will focus on the evolutionary implications of raising offspring to and beyond the juvenile stage. The objective of this review is to present an overview of the present knowledge of XPC in crustaceans and to identify questions that need to be approached in the future in order to gain a better understanding of the consequences of XPC.

MATERIAL AND METHODS

The present review is based on an extensive data set comprising published reports on extended parental care behavior from a variety of different crustacean species. This data set represents an improved and extended version of a previously published database (Thiel 1999a). New reports have been added to the database and additional XPC parameters have been identified. In contrast to the qualitative evaluation of the database presented in the earlier review (Thiel 1999a), for present purposes, I conducted a quantitative evaluation of the data set. Below, I report number of species for which XPC characteristics and behaviors have been identified and provide proportional comparisons where appropriate. Copies of the complete data set are available upon request.

RESULTS AND DISCUSSION

Crustaceans with XPC have been reported from all major environments (Table 1). Certain forms of XPC and related behaviors are more common in benthic marine and in soil-dwelling terrestrial species, but this may be due to research bias towards species from these environments. The majority of crustaceans with XPC were peracarids, and among these, more than half of the species were amphipods (Table 2). Among the decapods, brachyuran crabs featured most species with XPC, followed by the Astacidea.

Forms of extended parental care

In the majority of crustacean species with extended parental care, offspring are carried on the maternal body (often in special structures, e.g., the marsupium of peracarids) before reaching the juvenile stage. In the species with extended parental care (n = 130), juveniles may remain in the female's brood pouch (nine species reported), on the female's body (19 species) or in the parental dwelling (61 species). In 41 species, juveniles have been reported with parents, but their physical relationship to their parents, i.e., whether parents host them on their body or in their dwelling, had not been clearly identified.

Juvenile offspring remaining in the maternal marsupium are primarily known from grazing amphipods (e.g., Kobayashi et al. 2002). In these species, the brood pouches appear to be expandable in order to accommodate growing juveniles, which may complete at least one juvenile molt while inhabiting the maternal brood pouch (Heller 1968, Borowsky 1980, Welton et al. 1983). Juveniles may even leave the brood pouch briefly, e.g., to grasp a food particle, and then return to it (Croker 1968, Sheader & Chia 1970). In other species, juveniles move from the brood structure to other body parts of their mother. For example caprellid amphipod and arcturid isopod juveniles, mostly suspension feeders, leave the marsupium and cling to the female pereopods or antennae where they may remain for several weeks, reaching advanced juvenile stages (Lim & Alexander 1986, Svavarsson & Davidsdottir 1995, Aoki 1999). In some crayfish with XPC, juveniles may temporarily leave their mother, but then return to her for shelter (Hazlett 1983).

The majority of crustaceans known to engage in XPC, host their juveniles in dwellings (e.g., Murata & Wada 2002). Parents may simply tolerate their offspring in their dwellings or they may construct (or manage) particular offspring cradles, e.g., females of the arboreal crab *Metopaulias depressus* care for their developing offspring in water-filled leaf axils (Diesel & Schubart 2000).

TABLE 1

Traits and characteristics of extended parental care (XPC) behavior in crustaceans with XPC; information based on data from 130 crustacean species (for further details see text)

Características del cuidado parental extendido (XPC) en crustáceos. Información basada en 130 especies de crustáceos con XPC (ver texto para mayores detalles)

	Aquatic			Terrestrial	
	Marine benthos	Marine pelagial	Limnic benthos	Soil	Arboreal
Forms of XPC					
Care for juveniles in brood-pouch	+		+	+	
Care for juveniles on/in body	+				+
Care for juveniles in dwelling	++	+	+	++	+
Maternal care	+	+	+	+	+
Biparental care	+			+	
Care-behaviors					
Feeding of juveniles	+	+	+	+	++
Grooming of juveniles	+	+			+
Defense of juveniles	+		+	+	+
Resource inheritance	(+)			(+)	
Overlapping offspring generations	+				+
Family recognition	+			+	
Consequences of XPC					
Improved juvenile survival	+		+	+	+
Improved juvenile growth	+				
Intra-clutch conflicts	+		+	+	
Inter-clutch conflicts	+				(+)
Parent-offspring conflicts	(+)				
Parasites/Symbionts	+			+	
Local recruitment	+			+	
Decreased reproduction & XPC-duration	(+)				
Restricted gene flow	+			+	+
Main selective forces for XPC					
Physical	+		+	++	++
Biological	+	+	+	(+)	(+)
Phys. & Biol.	+	+	+	+	+

++ commonly reported, + presence reported, (+) presence inferred from observations

In all known crustacean species with XPC, mothers participate in XPC-activities. Exclusive maternal care has been reported from 117 out of the 130 species, while biparental care is known from 13 species. Exclusive paternal care, as known from other marine arthropods (e.g., Tallamy 2000) to date has not been reported for crustaceans. In some stomatopods, males care for the developing brood during late stages of larval development while females incubate a subsequent brood (R. Caldwell, personal communication).

Duration of extended parental care

In crustaceans, care for juveniles may last from a few hours to several months (Thiel 1999a). Consequently, the offspring developmental stages reached during XPC may vary substantially in the different crustacean species. In the majority of species, parents only care for offspring during early juvenile stages, but in some species parents host offspring until these have reached subadult or even adult stages. Parents that carry juveniles (either in brood pouches or on other body parts) liberate their offspring during early juvenile development (Fig. 1A), while species that care for offspring in dwellings may cohabit with them until they have reached subadult or adult stages (Fig. 1B). Costs of carrying may be high and may not permit XPC beyond early juvenile stages, while costs of hosting offspring in dwellings may be comparatively low, permitting longer duration of XPC.

In the aquatic environment, juveniles of only about 10 % of species reach the subadult or adult stage while being cared for by a parent. This is more common in the terrestrial environment (Fig. 1C and 1D). Nevertheless, subadult and adult offspring stages have also been observed together with their parents in marine species (Duffy & MacDonald 1999, Thiel 2000a). In the marine environment, this long-lasting XPC has been documented in crustaceans that inhabit invertebrate hosts, such as sponges or ascidians (Duffy et al. 2000, Thiel 2000a). Usually a large proportion of potential hosts is occupied, suggesting that strong competition for hosts may impede host acquisition or monopolization by small individuals thereby favoring long-lasting XPC. Construction

TABLE 2

Number and percentage of species with extended parental care in different crustacean taxa

Numero y porcentaje de especies con cuidado parental extendido en los diferentes taxa de crustáceos

Taxon	Number of species	Percentage
Amphipoda	36	27.7
Isopoda	26	20.0
Tanaidacea	7	5.4
Mysidacea	1	0.8
Total Peracarida	70	53.8
Anomura	3	2.3
Brachyura	35	26.9
Caridea	6	4.6
Stenopodidea	1	0.8
Astacidea	15	11.5
Total Decapoda	60	46.2
Total Crustacea	130	100.0

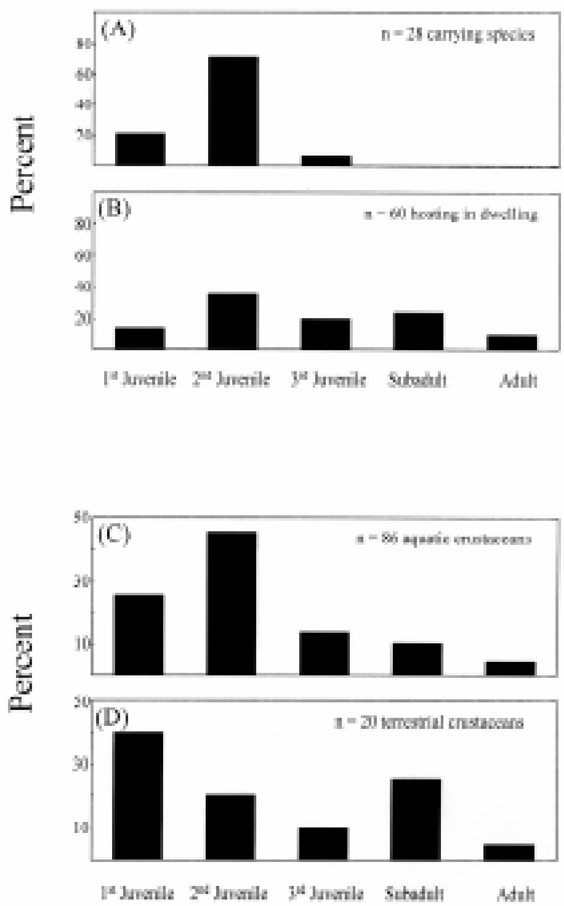

Fig. 1: Percentage of crustacean species in which offspring reach particular developmental stages during extended parental care, comparing crustacean species that (A) carry offspring, (B) host offspring in dwellings and species from (C) aquatic and (D) terrestrial environments.

Porcentaje de los crustáceos que desarrollan cuidado parental extendido (XPC) donde los juveniles alcanzan diferentes estados de desarrollo. Se comparan especies de crustáceos que portan sus juveniles en el cuerpo (A), que albergan juveniles en sus refugios (B), y que ocurren en ambientes acuáticos (C) y terrestres (D).

of stable burrows or acquisition of suitable dwellings in the terrestrial environment may also require substantial amounts of time and energy, and small juveniles may not be able to obtain suitable dwellings, which may be the reason for long-lasting XPC (with juveniles reaching subadult and adult stage) in the terrestrial environment. Most terrestrial crustaceans species with XPC inhabit burrows in soil or wood.

Overlapping offspring generations have been reported from six crustacean species with XPC – in all cases parents care for offspring in or on a dwelling. The absence of overlapping offspring generations has been reported for 14 crustacean species. In some (7) of these latter species, females host their offspring on their bodies, and they may produce subsequent broods after separating from juveniles.

Parental care behaviors

As outlined above, parents primarily provide a microhabitat for growing offspring. Some parental crustaceans have also been observed engaging in specific parental care behaviors. Feeding of juveniles has been observed in a variety of species from different habitats, while grooming and active defense has not been reported from all habitats from which crustaceans with XPC are known (Table 1). In general, cohabitation of crustacean parents with their offspring appears to be facilitated by reduced levels of parental aggression towards juvenile stages during XPC (e.g., Hazlett 1983, Growns & Richardson 1988). Food sharing with offspring may thus simply be a result of parental tolerance towards offspring while consuming own food resources – this form of intrafamilial commensalism is often observed in crustacean species that host growing juveniles in their brood pouches (e.g., Shillaker & Moore 1987, Coleman 1989, Kobayashi et al. 2002). Grooming is presently only known from four epibenthic crustacean species. Similarly, active defense, where parents attack intruders, has only been observed in some epibenthic species (Stephan 1980, Aoki & Kikuchi 1991). The fact that grooming and active defense of juveniles is only known from epibenthic crustaceans to date, may be due to the fact that these species are relatively easy to observe in the field or in laboratory aquaria. Indirect defense of juveniles against intra- and interspecific aggressors and predators (e.g., by providing a safe dwelling) is reported from several endobenthic species (Thiel 1999b), but whether these species also engage in grooming and active defense remains uncertain.

For three crustacean species, it has been inferred that offspring may inherit dwellings from their parents (Duffy 1996, Thiel 1999c, del Valle 2002), but whether this truly occurs has not been confirmed. Inheritance of dwellings may occur in crustaceans in which most available dwellings are occupied or in which dwellings are costly to construct, i.e., those living in symbiotic relationships with other invertebrates or those inhabiting burrows in hard substrata (see also above).

Consequences of extended parental care

XPC may have consequences for the individual, the family group, or the population. Individual growth and survival as well as epibiont infestation may be strongly affected by XPC. Members of parent-offspring groups may interact directly and compete for resources, causing intra-group conflicts. These conflicts and other consequences of XPC can influence offspring survival and thereby the parent's inclusive fitness. The intensity and direction of these consequences may also affect the population dynamics of crustaceans with XPC, indicating that such reproductive behavior may have far-reaching implications.

Consequences of extended parental care: improved juvenile growth and survival

For six crustacean species it has been reported that XPC can improve offspring growth and survival, which has been confirmed by experimental studies (Aoki 1997, Thiel 1999b, Kobayashi et al. 2002). Juveniles of the caprellid amphipod *Caprella monoceros* survive better and grow faster when together with their mother (Aoki 1997). In the maternal dwelling, juvenile amphipods *Leptocheirus pinguis* and *Dyopedos monacanthus* are not affected by the presence of predators, but survival of similar-sized orphan juveniles in/on their own dwellings is significantly reduced by predators (Thiel 1999b). In the grazing amphipod *Parallorchestes ochotensis* juveniles remain in the expanded brood pouch of their mother. In presence of predators, juveniles in the maternal brood pouch have significantly higher survival rates than juveniles separated from their mothers (Kobayashi et al. 2002). In most of these species, XPC is facultative as indicated by the fact that juveniles are able to survive without their parents when maintained in a predator-free environment (Thiel 1998a, Kobayashi et al. 2002).

Consequences of extended parental care: epibiont transfer

In dense family groups, epibionts (such as ectoparasites) may be easily transferred among group members (e.g., Schmid-Hempel 1998). Some peracarid species that engage in XPC harbor ecto- or endo-symbionts that might aid in the digestion of cellulose or other substances (e.g., El-Shanshoury et al. 1994). Whether these ectosymbionts are transferred during XPC from parents to offspring is not known at present. Ectoparasites may also be transferred among family members. Juveniles may obtain ectoparasites via vertical (and horizontal) transfer as is suggested by several observations: Svavarsson & Davidsdottir (1995) observed lower infestation rates with epibiotic foraminiferans in female than in male *Arcturus baffini*, and they suggested that females may lose forams to their offspring during XPC. Similarly, for the burrow-living amphipod *Casco bigelowi* Thiel (1998b) found higher epibiont infestation of juveniles from mothers with high epibiont loads than of juveniles from clean mothers. Ectoparasite transfer among group members may also be responsible for higher parasite loads of snapping shrimp from large colonies compared with conspecifics from small colonies (Duffy 1992). Presently, the role of these epibionts is not well known, and no experimental studies have been done to test whether vertical transfer occurs during XPC.

Consequences of extended parental care: intra-familial conflicts

Presently, intra-familial conflicts are not well known from crustaceans with XPC, but the fact that these conflicts are commonly reported from other taxa (Clutton-Brock 1991) suggests that long-lasting cohabitation of juveniles with their parents may also cause a variety of intra-familial conflicts in crustaceans. Juveniles from the same brood may compete among themselves for space and food. In the burrow-dwelling amphipod *Leptocheirus pinguis* competition for space in the maternal burrow is probably common, as was indicated by a few juveniles leaving the burrow after each molting event (Thiel 1999d) and observed aggressive interactions among juveniles in the maternal burrow (personal observation). Competition for space may also lead to the gradual disappearance of juveniles from parental bodies or dwellings during XPC (e.g., del Valle 2002), whereas simultaneous molting of juveniles might reduce the risk of intra-clutch cannibalism among similar-sized offspring (e.g., Karplus et al. 1995). While there are strong indications for the presence of conflicts among offspring from the same clutch, it is not known whether similar conflicts also arise among offspring from subsequent clutches.

Conflicts may also arise between parents and their offspring. Offspring may consume food resources of parents or occupy space on the parental body or in the parental dwelling, thereby reducing the possibilities of parents to produce future broods. These conflicts may increase with increasing duration of XPC, and consequently when

TABLE 3:

Number of crustaceans for which particular traits, behaviours and consequences of extended parental care (XPC) has been observed, inferred or for which future research is warranted; information based on data from 130 crustacean species (for further details see text)

Número de crustáceos para los que alguna conducta particular, o consecuencias del cuidado parental extendido (XPC) se han descrito, inferido, o bien, donde se requiere de nuevos estudios. Información basada en 130 especies de crustáceos con XPC (ver texto para mayores detalles)

	Observed	Inferred	Research need
Forms of XPC			
Type of XPC	89	-	(+)
Parent engaging in XPC	130	-	(+)
Duration of XPC	(106)	-	++
Care-behaviors			
Feeding of juveniles	14	5	+
Grooming of juveniles	4	-	++
Defense of juveniles	11	-	++
Resource inheritance	-	3	+++
Overlapping offspring gens.	6	-	+
Family recognition	2	2	++
Consequences of XPC			
Improved growth & survival	6	-	++
Intra-familial conflicts	-	-	+++
Symbiont transfer	-	4	+++
Local recruitment	15	4	+
Density-dependent effects	-	2	+++
Restricted gene flow	2	-	+++

(+) relatively well known, + observations available, ++ little known, research required, +++ primarily based on inference and theoretical considerations, strong research need costs exceed the benefits of XPC for parents, it can be expected that they reduce XPC activities or even turn aggressive towards advanced offspring stages (e.g., Clutton-Brock 1991). In some semi-terrestrial crayfish, females feed on their own offspring towards the end of XPC (e.g., Figler et al. 1997). In other crustacean species, parents did not produce a second clutch while carrying their offspring, but immediately did so after offspring were experimentally removed (e.g., Aoki & Kikuchi 1991, but see Thiel 1997). Whether juvenile crustaceans take an active role in suppressing subsequent reproductive events of their parents is speculative.

Consequences of extended parental care: local recruitment

Since parents care for fully developed juveniles, it is not surprising to find that offspring recruitment in the immediate vicinity of their parents has been reported for a variety of crustacean species with XPC. Local recruitment has been reported or inferred for a total of 19 species (Table 3), and in the majority of these species (n = 18) parents harbor their offspring in a dwelling such as a burrow or invertebrate host. Upon leaving their parents, juveniles begin their own burrows originating from the parent's burrow (e.g., Thiel in press) or they remain in the host inhabited by their parents (Duffy & MacDonald 1999). This local recruitment may lead to the rapid establishment of dense assemblages of highly related individuals. Local recruitment and rapid build-up of dense populations may have important consequences for the biology of crustaceans with XPC, and it should therefore receive more attention in future studies.

Consequences of extended parental care: density-dependent effects

Intraspecific competition for food and space in dense crustacean assemblages may provoke en-

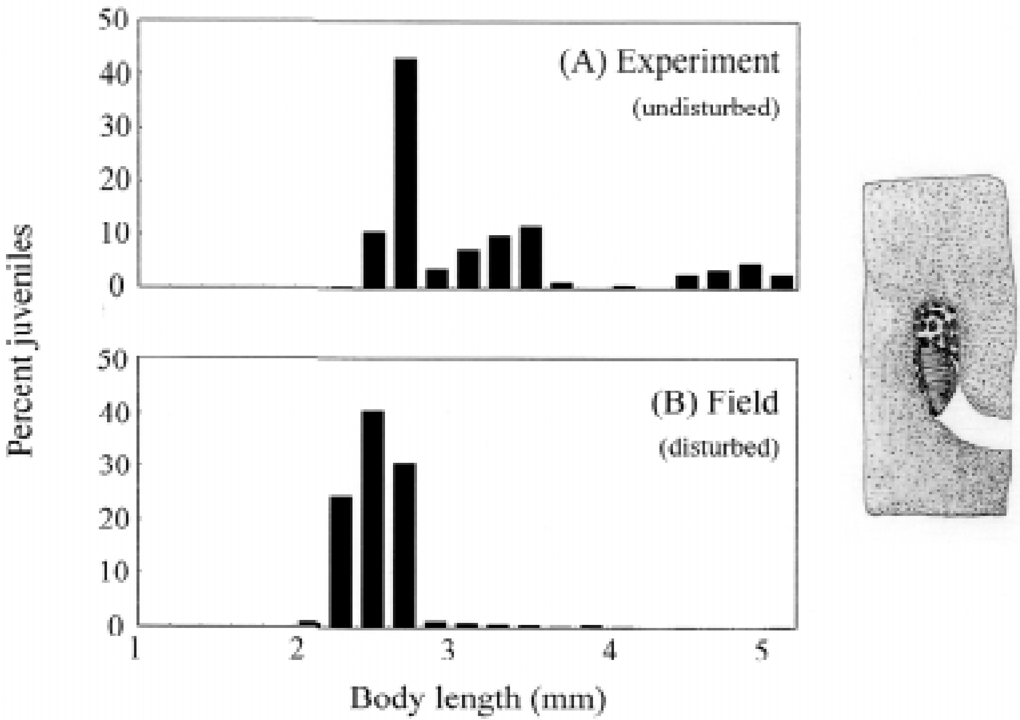

Fig. 2: Offspring sizes of juvenile *Sphaeroma terebrans* reached in the maternal burrow in (A) an experimental (undisturbed) environment where offspring-rearing females were maintained in individual containers, and (B) in the natural (disturbed) environment where offspring-rearing females were exposed to frequent inter- and intraspecific disturbance; data from Thiel 1999e and Thiel 2000c.

Tamaño alcanzado por los juveniles de *Sphaeroma terebrans* en el refugio parental cuando las madres son mantenidas en el laboratorio (A – ambiente sin perturbación), y cuando las madres son recolectadas desde el terreno (B – ambiente con perturbación). En el terreno, las hembras se encuentran frecuentemente expuestas a perturbaciones intra- e inter-específicas. Datos de Thiel 1999e y Thiel 2000c.

hanced emigration or reduced reproductive activity. Density-dependent effects on reproduction, as for example observed in bark beetles (Robins & Reid 1997), could also be expected for crustaceans in dense assemblages. In species that inhabit burrows, local recruitment may lead to dense populations with intense competition for resources. High population densities have been reported for some sediment- and wood-dwelling peracarids that engage in XPC (e.g., the amphipod *Corophium volutator* – Wilson & Parker 1996, the isopods *Sphaeroma terebrans* – Thiel 1999e, and *Limnoria chilensis* – Thiel in press). At high population densities, females with juveniles in their burrows may be exposed to frequent disturbance from neighboring conspecifics. Observations on juvenile *S. terebrans* from maternal burrows collected in the field (with intra- and interspecific disturbance) and in the laboratory (undisturbed) provide a first indication that population density may affect the duration of XPC in some crustaceans (Fig. 2A and 2B). In the field, females with offspring in their burrows may be exposed to high levels of intra- and interspecific (from juveniles of a congeneric isopod species) disturbance causing juveniles to leave at early developmental stages (Thiel 2000b). In contrast, in the undisturbed laboratory environment, females may raise their offspring to more advanced stages (Fig. 2A). Future experimental studies should examine whether density-dependent effects on emigration or reproductive activity occur in crustaceans with XPC.

Consequences of extended parental care: restricted gene flow

Local recruitment (i.e., limited dispersal) may also reduce gene flow in crustaceans with XPC. High genetic variability among neighboring populations has been reported from a sediment-dwelling amphipod (*Corophium volutator* - Wilson et al. 1997) and from a snapping shrimp (Duffy 1996). In both species, offspring may recruit in the immediate vicinity of their parents (e.g., Thamdrup 1935). While *C. volutator* can disperse via pelagic drift with tidal currents (Lawrie & Raffaelli 1998), pelagic dispersal is not known for snapping shrimp. In species that either drift themselves or on floating material, brief periods of isolation may continuously be disrupted by dispersal events. Species with effective dispersal mechanisms may have wide geographic distributions despite the fact that local recruitment is common. For example, juvenile isopods *Limnoria chilensis* often remain in kelp holdfasts inhabited by their parents, but nevertheless, these isopods have a wide geographic distribution along the SE-Pacific ranging from Peru to Patagonia (Paternoster & Elias 1980), which probably is facilitated by frequent dispersal via floating macroalgae (M. Thiel personal observations).

Evolution of extended parental care

Extended parental care has evolved in a variety of different environments. There are many reports of crustaceans with XPC from terrestrial and freshwater environments, even though the large majority of crustacean species are marine. This imbalance suggests that the evolution of XPC may have been favored in harsh environmental conditions that crustaceans face in terrestrial or in freshwater environments (Hazlett 1983). In the marine realm, crustaceans may also face harsh conditions (e.g., desiccation risk or osmotic stress in intertidal or estuarine habitats), which may have favored the evolution of XPC in marine crustaceans. The high predation risk in shallow coastal environments may also have contributed to the evolution of XPC, since juvenile survival may be substantially enhanced during XPC (see above).

Some crustacean groups may have phylogenetic preadaptations for XPC. For example, XPC is particularly common among peracarid species (70 of 130 crustacean species with XPC are peracarids), in which fully developed juveniles emerge from the maternal brood pouch. In these taxa, parents always are confronted with juveniles and the possibilities for XPC may be higher than in taxa where offspring usually is released before reaching the juvenile stage. Phylogenetic preadaptation may also have contributed to the high proportion of terrestrial decapods with XPC. Many of the presently known terrestrial decapods share common ancestors that featured direct development (e.g., Schubart et al. 1998, Scholtz 2002). Thus, many terrestrial Decapoda may show similar phylogenetic preadaptations for XPC as the Peracarida (i.e., direct development).

In general, XPC will evolve when benefits for parents and offspring outweigh the costs of this behavior (Clutton-Brock 1991). In crustaceans, these conditions may be given where successful juvenile development without parental assistance is unpredictable or impossible. Physical (desiccation risk, disturbance potential) and biological factors (competition for resources, predation pressure) may be the main environmental factors favoring the evolution of XPC in crustaceans. Future studies should examine how these factors affect survival and growth of crustacean offspring that enjoy XPC.

CONCLUDING REMARKS

Compared with our knowledge of XPC in vertebrates (e.g., Clutton-Brock 1991) or insects (e.g., Choe & Crespi 1997), research on XPC in crustaceans is still in its infancy. Nevertheless during the past decade some important progress has been made and some general patterns have been identified. It became evident that the findings of parent-offspring associations in crustaceans do not represent accidents but expressions of a particular reproductive behavior. XPC occurs in diverse crustaceans from a wide variety of habitats, and this behavior is not restricted to particular environments or areas of the world, although it may be more common in terrestrial than in marine crustaceans (e.g., among land crabs in Jamaica – Schubart et al. 1998, land crabs in Africa – Cumberlidge 1999, semi-terrestrial crayfish in Tasmania – e.g., Horwitz & Richardson 1986, Hamr & Richardson 1994). While many questions about XPC in crustaceans remain to be answered in the future, and all are equally deserving, there are two aspects emerging from this review that appear particularly intriguing.

Factors favoring and suppressing occurrence and intensity of XPC (feed-back cycles)

The availability of resources can have a strong influence on XPC (Clutton-Brock 1991). Strong competition for resources may favor the occurrence of XPC, since small juveniles may not be able to compete successfully for resources, and it may thus pay for parents to care for offspring until these have achieved competitive capabilities. On the other hand, limited resources may reduce the intensity of XPC since expenditure in present offspring may seriously compromise parental possibilities to produce future offspring. Considerations on resource limitations usually

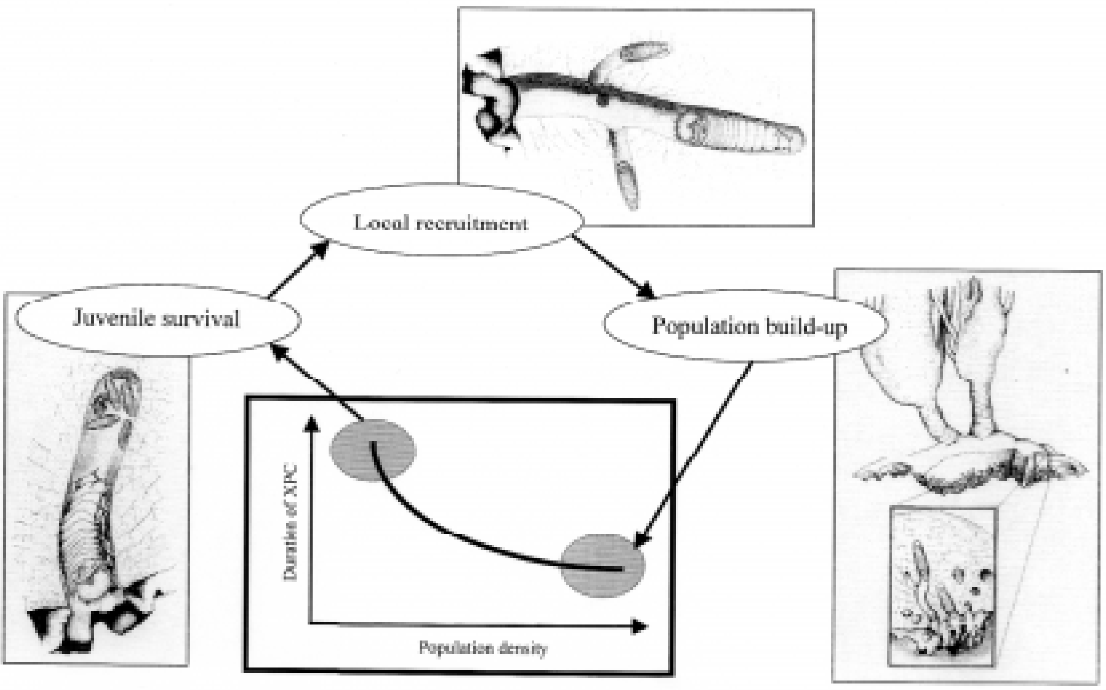

Fig. 3: Schematic diagram of a hypothetical feed-back cycle for burrow-dwelling crustaceans with extended parental care and local recruitment. At low population densities the duration of XPC and juvenile survival increases, leading to strong local recruitment and rapid population build-up. At high population densities the duration of XPC and consequently juvenile survival decreases, leading to weak local recruitment. Important stages in this feed-back cycle are exemplified with drawings of the burrow-living isopod *Limnoria chilensis* (after Thiel in press).

Diagrama esquemático de un ciclo de retro-alimentación hipotético en crustáceos que habitan refugios y desarrollan XPC, donde el reclutamiento es localizado. Cuando la densidad poblacional es baja, la duración del XPC y la sobrevivencia de los juveniles aumenta, ocurriendo un fuerte reclutamiento local y un rápido aumento poblaciónal. Cuando la densidad poblacional es alta, la duración del XPC disminuye, y consecuentemente, la sobrevivencia de los juveniles decrece y el reclutamiento local disminuye. Etapas importantes de este ciclo se encuentran ejemplificadas por el isópodo *Limnoria chilensis* (ver dibujos) que construye galerías en macroalgas (según Thiel in press).

center around food resources but in this review it became apparent that the presence of stable dwellings has great importance for many crustacean species with XPC. At high population densities, stable dwellings may become increasingly unstable and difficult to defend against interlopers. For example, in the sediment-dwelling amphipod *Corophium volutator*, burrows may become partially destroyed by the burrowing activity of neighbors, thereby impeding long-lasting XPC: maternal females may be inhibited to provide XPC to their offspring at high population densities due to increasing intraspecific disturbance. A simple feedback cycle can be envisioned to occur in these species (Fig. 3). At low population densities, parents may provide long-lasting XPC and consequently offspring survival is high. These offspring recruit in the immediate vicinity of their parents, leading to rapid population buildup. At high population densities, intraspecific disturbance may provoke continuous disturbance of parents with juveniles in their burrows and these may abandon burrows at early juvenile stages, reducing offspring survival. Such feedback cycles may be common in a wide variety of crustaceans with XPC, which inhabit burrows in wood, algae or in soft sediments (Fig. 3). Local recruitment has been observed or inferred for several burrow-dwelling crustaceans with XPC that also frequently occur in dense assemblages (Table 4). Whether these feedback cycles exist in natural communities, and which role they play in stabilizing population dynamics of crustaceans with XPC needs to be explored in future studies.

Long-lasting XPC and the dispersal potential (the XPC paradox)

The lack of pelagic larvae is usually viewed as an impediment to long-distance dispersal in marine invertebrates. Nevertheless there are many marine invertebrates with direct development (i.e., lacking pelagic larvae) that have a wide geographic distribution (e.g., O-Foighil & Jozefowicz 1999, Castilla & Guiñez 2000). Various authors have identified rafting as a highly efficient dispersal mechanism in organisms with direct development (e.g., Ingólfsson 1995). In the following, I will argue that XPC in combination with local recruitment can result in far-ranging dispersal surpassing that of most species with pelagic larvae.

The typical duration of larval life in crustacean species with pelagic larvae ranges around 30 to 100 days (Anger 2002), after which these larvae

TABLE 4

Crustacean species with extended parental care (XPC) for which local recruitment, high population densities and plasticity in the duration of XPC has been observed or inferred

Especies de crustáceos que desarrollan cuidado parental extendido (XPC) para las cuales se ha descrito o inferido un reclutamiento local, una alta densidad poblacional y plasticidad en la duración del XPC

Crustacean species with XPC	Local recruitment	High population density	Plasticity in XPC duration	Reference
Corophium volutator	+	+	P	1
Leptocheirus pinguis	+	+	P	2
Casco bigelowi	(+)	-	?	2
Dyopedos monacanthus	(+)	+	?	3
Sphaeroma terebrans	+	+	SI	4
Limnoria algarum	+	?	P	5
Limnoria lignorum	+	+	P	6
Limnoria chilensis	+	+	P	7
Lynseia annae	+	(+)	?	8
Heterotanais oerstedi	+	+	?	9
Tanais cavolinii	+	+	P	10
Callianassa kraussi	+	+	?	11

+ presence reported, (+) presence inferred from observations, - absence reported, ? unknown or uncertain, P presence probable, SI strong indication for presence

(1) Thamdrup (1935), Wilson & Parker (1996), (2) Thiel et al. (1997), (3) Thiel (1998c), (4) Thiel (1999d), (5) Menzies (1957), (6) Henderson (1924), (7) Thiel (in press), (8) Brearley & Walker (1995), (9) Bückle-Ramirez (1965), (10) Johnson & Attramadal (1982), (11) Forbes (1973)

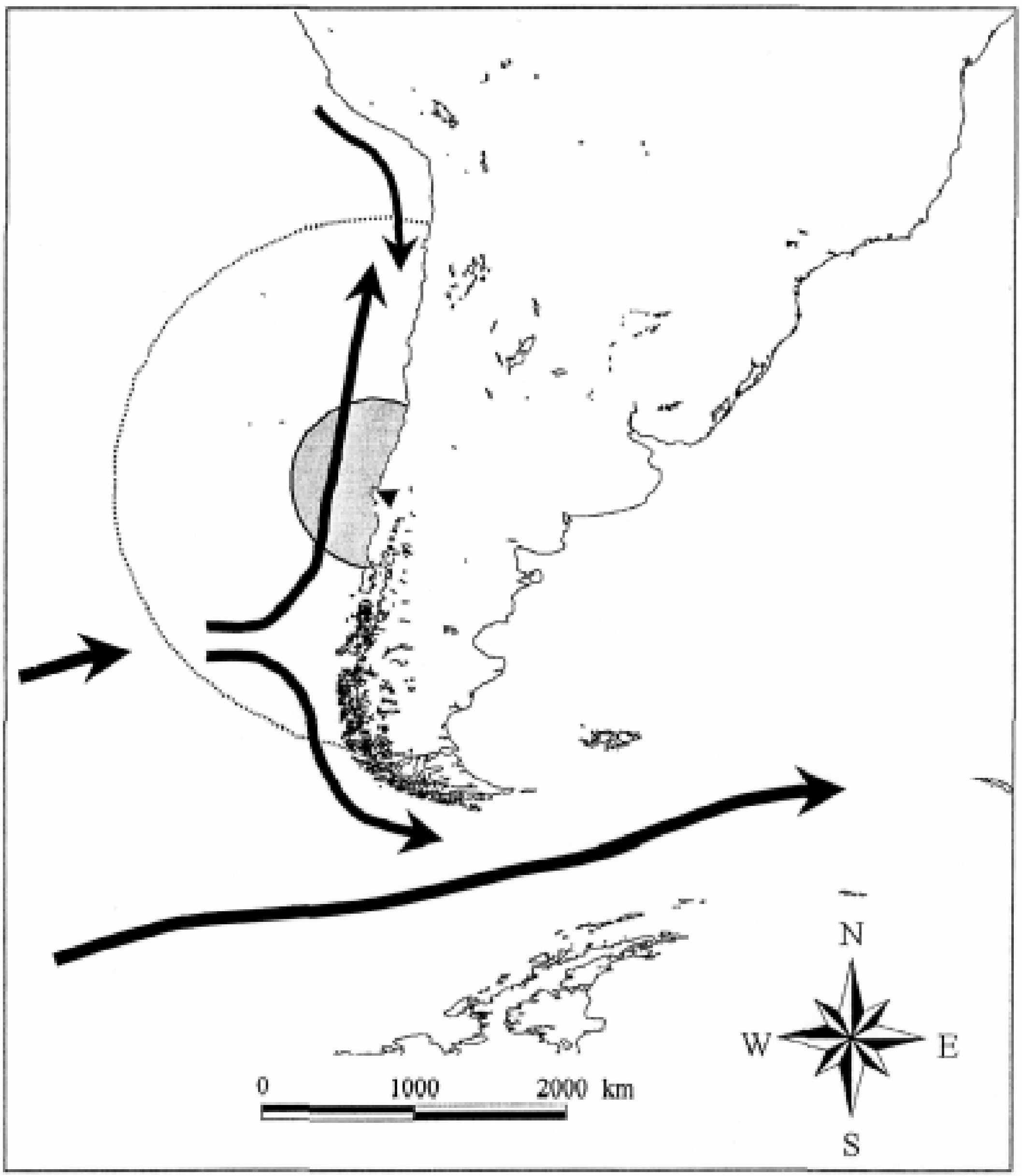

Fig. 4: Map showing dispersal potential of pelagic larvae or crustaceans rafting in coastal waters of the SE-Pacific, entirely dependent on oceanographic currents (major currents in SE-Pacific shown). Triangle indicates release site of propagules, and circles represent the maximum distances that drifting organisms can reach after 30 (shaded area) and 100 days (dotted line) if they drift continuously in the same direction at 20 cm s^{-1}, current velocities that are typically encountered within the coastal branch of the Humboldt Current (Strub et al. 1998); wind may affect direction and velocity of algal or wood rafts (Harrold & Lisin 1989); shaded area marks potential settlement area for pelagic larvae with a larval life of 30 days.

Mapa que muestra el potencial de dispersión de larvas pelágicas o de crustáceos que utilizan “rafting” en estructuras flotantes como mecanismo de dispersión. En ambos casos, la dispersión depende completamente de las corrientes oceanográficas (corrientes mas importantes mostrados). La triangulo indica el sitio de liberación de los propágulos, y los círculos representan la distancia máxima de dispersión que estos organismos pueden alcanzar después de 30 (área resaltada) y 100 días (linea punteada). Se asume una deriva continua y en la misma dirección, a una velocidad de 20 cm s^{-1}, comúnmente descrita para el brazo costero de la Corriente de Humboldt (Strub et al. 1998). El viento puede afectar la dirección y velocidad de deriva de maderas o algas flotantes (Harrold & Lisin 1989); el área resaltada indica las zonas en las que potencialmente puede ocurrir el asentamiento de larvas con una vida pelágica de 30 días.

need to find adequate settlement substratum (Gebauer et al. 2003). Thus, duration of larval life (among other factors) sets limits on the dispersal time and distance that these species can achieve. Many crustacean species with direct development and XPC are found on substrata that have a high floatation potential (Ingólfsson 1995, Hobday 2000a). Passengers that travel on suitable rafting material may reproduce and recruit within their rafts. Some rafting materials may remain adrift for time periods > 30 days (Hobday 2000b) and even >> 100 days (Helmuth et al. 1994), and take with them small populations of surviving inhabitants. As a consequence of local recruitment within rafts, crustaceans with XPC have the potential to establish persisting demes within rafts. All available evidence suggests that these travelers may occasionally colonize new and distant shores (see Castilla & Guiñez 2000). These theoretical considerations suggest that some crustaceans with XPC and local recruitment that live on suitable dispersal vectors may have a large dispersal potential, surpassing that of many crustacean species with planktonic larval stages (Fig. 4). Whether XPC and local recruitment on dispersal vectors such as macroalgae, wood and plastic debris indeed facilitates long-distance dispersal in these species, and whether these passengers are capable of successfully colonizing new habitats when cast ashore, needs to be examined in future studies.

These two scenarios demonstrate that XPC in crustaceans (and other marine invertebrates) may potentially have far-reaching ecological and biogeographical consequences. While our knowledge of XPC patterns has increased during the past decade, these and other important implications of this reproductive behavior have yet to be fully explored. In particular the effect of XPC on genetic population structure and on dispersal potential should receive research attention since this information is important with regard to the conservation of biodiversity. Crustaceans with XPC may be particularly susceptible to changing environmental conditions, especially in the terrestrial environment, since their populations may be small and locally restricted.

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