



The conquest of freshwater and land by marine crabs: adaptations in life-history patterns and larval bioenergetics

K. Anger

Biologische Anstalt Helgoland, Meeresstation, D-27483 Helgoland, Germany

Abstract

Life-history patterns in marine, limnic, and terrestrial brachyurans are reviewed to discern special adaptations associated with transitions in life style. Among marine crabs, the Grapsidae have been especially successful invading freshwater and terrestrial environments, in particular a group of closely related neotropical Sesarminae species, which has evolved through a conspicuous radiation process. Compared with marine grapsid crabs, freshwater and terrestrial species show the following tendencies: (1) increasing habitat specialization, (2) reduced geographic range (endemism), (3) low fecundity, (4) brood protection, (5) large egg size, (6) unusually high carbon contents and C:N ratios in eggs and early larvae (indicating an enhanced lipid content), (7) abbreviated larval development, (8) high larval tolerance of physico-chemical stress, (9) nutritional independence (lecithotrophy), (10) no or only little larval growth, (11) possibly energy saving mechanisms in exuvial and respiratory losses of larvae. Most of these tendencies were found also in two semiterrestrial species with intermediate life histories, *Sesarma curacaoense* and *Armases miersii*. Factors selecting for these life-history traits are discussed. Among them, there may be two major driving forces in the evolution of freshwater and land crabs: (1) food-limitation in freshwater/terrestrial breeding habitats selects for large egg size, lecithotrophy, and abbreviated larval development; (2) once adaptations to the adult habitat have evolved in the larvae (for instance, in semiterrestrial species with an abbreviated, partially lecithotrophic larval development, as in *S. curacaoense* and *A. miersii*), intense pelagic predation in the shallow coastal fringe should select against an export strategy (offshore transport of larvae), and thus for larval retention in and continued adaptation to non-marine environments.

Keywords: Abbreviated development; Crab larvae; Lecithotrophy; Life cycle; Semiterrestrial

1. General life-history patterns in benthic marine invertebrates

The majority of benthic marine invertebrates have no direct development from the egg to an adult-like juvenile, but pass through a pelagic larval phase (Thorson, 1946, 1950; Mileikovsky, 1971). This is true also for marine decapod crustaceans in general, and brachyuran crabs in particular, which are the main focus of this paper. Most taxa produce a high number of small eggs, from which small planktotrophic larvae hatch, whereas a number of others produce few large yolky eggs, which allow food-independent development based on endowed energy reserves (lecithotrophy). The duration of the planktonic phase tends to be shorter in lecithotropic than in planktotrophic larvae (Vance, 1973); in some groups (e.g. colonial ascidians) it may last only a few minutes or hours. A pelagic phase is considered a prerequisite for a wide geographic range and genetic exchange between separate populations of benthic invertebrates. Lecithotrophy, on the other hand, offers the advantage of trophic independence from fluctuating food supplies in the pelagic environment (Vance, 1973; Chia, 1974).

This basic categorization of developmental modes is still widely accepted (see review by Roughgarden, 1989). However, the need to consider the significance of flexibility or variability in life-histories has also been recognized and increasingly emphasized (Hines, 1986a,b). Mixed developmental strategies may include the deposition of benthic egg capsules, from which planktonic larvae hatch later, or larvae may show nutritional flexibility between the extremes of planktotrophy and lecithotrophy. Some apparently non-feeding larvae were either shown to take up dissolved organic matter (e.g. in molluscs, echinoderms: Manahan, 1990), or they may eat particulate food, when it is available (facultative lecithotrophy; e.g. in some opisthobranchs: Kempf & Todd, 1989; echinoderms: Emlet, 1986; decapod crustaceans: Anger & Schuh, 1992). In the Decapoda (as well as in many other invertebrate taxa), there exist numerous examples of variable degrees of abbreviation of larval development, including intraspecific variability in the number of larval stages (Gore, 1985; Rabalais & Gore, 1985).

Life-history patterns show also latitudinal gradients. For instance, the percentage of benthic invertebrate species with pelagic larvae decreases from the equator to the poles (Thorson, 1946). Such variation in climatic gradients indicates that the mode of development is subject to selection and thus, it should reflect adaptations to specific types of environment, although there are also phylogenetic constraints (Strathmann, 1977).

One of the most drastic and hence, biologically most fascinating adaptive processes is the transition of marine species to freshwater or terrestrial environments. Among the major marine invertebrate taxa, decapod crustaceans have been particularly successful in this respect. Since, among the Decapoda, the brachyuran crabs show the greatest variability in life style, I will focus on this group. However, this is not an attempt to review life-cycle traits in brachyuran crabs in general, or those in freshwater and terrestrial crabs in particular; excellent syntheses of these subjects were given by Hines (1986b) and Hartnoll (1988), respectively. Rather, I will use one of the most successful crab families invading

freshwater and land, the Grapsidae, as an example. They are particularly interesting in the context of life-cycle adaptations, because they show an intermediate position between marine and freshwater/terrestrial life-styles. Hence, comparison of their life-history traits with those in fully marine, freshwater, and terrestrial crabs may be useful in the analysis of evolutionary changes that are associated with the conquest of freshwater and land. Before treating this group in more detail, I will first give a brief account of common traits in freshwater and land crabs.

2. Life-history patterns in freshwater and land crabs

Life-history patterns of terrestrial brachyurans were extensively reviewed in the already classical treatise “Biology of the Land Crabs” by Burggren & McMahon (1988; especially in Hartnoll’s chapter “Evolution, Systematics, and Geographical Distribution”), and those of limnic crabs by Bott (1969, 1972). Thus, only the most important traits of non-marine brachyurans shall be summarized here to contrast them with those in marine and transitional species. Since most species are restricted to either land or freshwater, but do not regularly occur in both types of environment, these two groups will be treated in separate sections.

2.1. Freshwater crabs

Larval development in freshwater is associated with great physiological problems, as it is difficult to maintain the internal balance of water and salts (Powers & Bliss, 1983). Thus, both a reduction of the larval phase or an “export” of the pelagic larvae to marine waters appear to be effective alternative strategies to avoid those problems. Most brachyurans living in freshwater belong to the Potamoidea, a superfamily with world-wide distribution, comprising 11 families (Bowman & Abele, 1982). Very much like the crayfishes (Astacidea), the potamid crabs have become entirely independent of the sea, showing direct development and parental brood care (Gurney, 1942; Bott, 1969). They lay only few large eggs (up to about 500; in contrast to mostly several thousand, up to about two million, in marine crabs), from which fully developed, adult-like juveniles hatch. These “cling to their mother for some days before leaving her to begin a life of their own” (Bliss, 1982). The potamid crabs had already appeared in the middle tertiary, soon after an initial explosive radiation in the Brachyura (Bott, 1972). This relatively long history, among the brachyurans, may explain why they have evolved far-reaching life-history adaptations to freshwater, including a complete reduction of the larval phase.

Except for some Ocypodidae and Mictyridae (Johnson, 1965; Barnes, 1967; Shokita, 1990), practically all records of non-potamid freshwater crabs refer to species of the Grapsidae, mostly Sesarminae. Among these, one centre of

Table 1
Western Atlantic grapsid crab species: geographical distribution; preferred type of habitat and salinity

Species	Distribution	Habitat	Salinity	CW (mm)	Egg size (mm)	Egg number	N _e /CW	Zoeal stages
<i>Planes minutus</i> [P. cyaneus] (J)	E and W Atlantic, Pacific, Indian Ocean	Oceanic, on floating objects	M	20 [17]	0.36 [30]	?	?	?
<i>Euchirograpsus americanus</i>	W Atlantic (North Carolina to Barbados), E Pacific	Deep-water species (31-508 m [48]), off shore	M	16 [28]	?	?	?	5-6 [50]
<i>Euchirograpsus millenensis</i>	Bahamas, Caribbean, Gulf of Mexico [48]	Deep-water species (192-430 m [48]), off shore	M	?	?	?	?	?
<i>Cyrtograpsus affinis</i>	Brazil to Argentina	subtidal	M	5 [9]	?	?	?	5(?) [42]
<i>Percnon gibbesi</i> (J)	E and W Atlantic, E Pacific [22]	Rocky shores, subtidal	M	34 [22]	0.36 [30]	?	?	6 [39] [42]
<i>Grapsus grapsus</i> (J)	E and W Atlantic, E Pacific	Rocky shores, intertidal, subtidal	M	77 [12]	0.35 [26, 31]	?	?	6 (?) [23]
<i>Hemigrapsus sanguineus</i>	E and W Pacific; introduced to NW Atlantic [34]	Rocky shores, intertidal, subtidal	M	29 [29]	0.38 [29]	?	?	?
<i>Gemagrapsus lividus</i> (J)	E and W Atlantic, E Pacific	Stony beaches, intertidal	M	14 [12]	0.35-0.40 [26]	?	?	?
<i>Pachygrapsus transversus</i> (J)	World-wide in tropical & subtropical seas	Stony beaches, intertidal	M	17 [49]	0.28 [26, 30]	?	?	?
<i>Pachygrapsus corrugatus</i>	Bahamas, Caribbean	Coastal rocks, intertidal	M	13 [12]	?	22,314 [37]	1440	?
<i>Cyclograpsus integer</i> (J)	E and W Atlantic, Indo-Pacific	Stony Beaches, intertidal	M	10 [26]	0.35 [26]	?	?	?
<i>Plagusia depressa</i> (J)	E and W Atlantic	Coastal rocks, intertidal	M	62 [49]	0.45 [26]	?	?	5-6 [24]
<i>Cyrtograpsus altimanus</i>	S Brazil to Argentina	Under stones, subtidal, low intertidal [9]	(B)-M	12 [4]	0.30 [4]	2300 [4]	192	>6(?) [51]
<i>Pachygrapsus gracilis</i> (J)	E and W Atlantic	Mangrove roots, river banks	B-M	17 [26]	0.25 [26]	14996 [37]	1250	>13 [10]
<i>Araus pisonii</i> (J)	Florida to S. Brazil; E Pacific	On mangrove trees, supratidal	B-M	23 [26]	0.30 [26]	34000 [14]	1478	3-4 [18]
<i>Goniopsis cruentata</i> (J)	Bermuda to S. Brazil; Gulf of Mexico	Mangroves, intertidal	B-M	50 [12]	0.35 [26, 30]	?	?	?
<i>Armaes cinereum</i>	Maryland to Florida; Gulf of Mexico	Salt marshes, mangroves, inter and supratidal	B-M	17 [46]	0.32 [46]	15000 [46]	882	4 [15]
<i>Armaes ricordi</i> (J)	Bermuda to Surinam; Gulf of Mexico	Mangroves, supratidal, dry forest	B-M	16 [26]	0.40 [26]	?	?	4 [19]
<i>Chasmagnathus granulata</i>	Brazil to Argentina	Salt marshes, supratidal and intertidal [9, 47]	B-(M)	36 [32]	0.40 [32]	78000 [32]	2167	4 [9]
<i>Melasesarma rubripes</i>	Central America to Uruguay	Mangrove swamps, estuarine salt marshes [11]	B-(M)	17 [11]	?	4350 [11]	259	4-5 [19, 35]
<i>Sesarma rectum</i>	West Indies to S. Brazil	River banks, estuaries, mangroves	B-(M)	30 [21]	?	?	?	3 [21]
<i>Sesarma reticulatum</i>	Massachusetts to Florida; Gulf of Mexico? [52]	Estuarine salt marshes, intertidal [45]	B-(M)	22 [46]	0.45 [46]	12000 [46]	554	3 [16]
<i>Sesarma</i> spec.	Gulf of Mexico [52]	Estuarine salt marshes, intertidal [52]	B-(M)	27 [52]	0.45 [52]	18000 [52]	667	3 [52]
<i>Sesarma curacaoense</i> (J)	S Florida to NE Brazil, West Indies	Mangrove swamps	B-(M)	15 [12]	0.60 [26]	1500 [44]	100	2 [5, 44]

<i>Cyrtogobius angulatus</i>	Brazil to Argentina; F: Pacific	Shallow beaches, subtidal, low intertidal [9, 47]	(F)-B-M	36 [32]	0.40 [32]	79,000 [32]	2194	5 [32]
<i>Arnases miersi</i> (J)	Bahamas, Florida West Indies	Rocky shores, mangroves [5, 43]	(F)-B-M	20 [12]	0.59 [44]	2,860 [44]	118	3 [5, 43]
<i>Sesamia crassipes</i>	Caribbean (Costa Rica), N. Brazil	Estuaries [13]	(F)-B-(M)	23 [2]	?	?	?	?
<i>Arnases benedicti</i>	Surinam to Venezuela	Rivers, under stones and wood	(F)-B-(M)	16 [2]	?	?	?	?
<i>Arnases angustipes</i>	Bahamas to S. Brazil (not Jamaica [2])	River banks, streams [6], mangroves	F-(B-M)	18 [2]	?	?	?	4 [6]
<i>Arnases roberti</i> (J)	West Indies; not mainland America	Rivers, streams, mangroves	F-(B-M)	27 [12]	0.45 [26]	?	?	4 [44]
<i>Arnases americanus</i>	Caribbean coast; only mainland Central America	River banks, streams	F-(B-M)	19 [2]	?	?	?	?
<i>Eriocher sinensis</i>	China; introduced to Europe [38] and USA [36]	Rivers, lakes, upper estuaries [36, 38]	F-(B-M)	65 [40]	0.39 [38]	920,000 [40]	14,154	5, 6 [5]
<i>Platychiropaps spectabilis</i>	Mexico; introduced to Florida [35]	Rivers [8, 12, 41]	F	?	?	?	?	?
<i>Glyptochiroaps jamaicensis</i> (J)	Endemic to Jamaica [8, 12, 41]	Rivers, streams, under stones [2, 12, 25, 41]	F (C)	40 [12]	1.80 [25]	?	?	?
<i>Sesamia bidentatum</i> (J)	Endemic to Jamaica [2, 12, 25, 41]	Rivers, streams [20, 49]	F	24 [25]	1.40 [44]	250 [44]	?	2 (?) [25]
<i>Sesamia wandor</i> (J)	Endemic to Jamaica [20]	Rivers, streams [2, 25, 41]	F	>20 [20]	?	?	?	2 [44]
<i>Sesamia verleyi</i> (J)	Endemic to Jamaica [2, 25, 41]	Subterranean caves [2, 25, 41]	F-T	21 [12]	>1 [25]	?	?	?
<i>Sesamia jarvisi</i> (J)	Endemic to Jamaica [1, 2, 25, 41]	Dry forests [1, 2, 25, 41], in snail shells [7]	(F) T	12 [1]	1.32 [1]	28 [7]	?	?
<i>Sesamia cookei</i> (J)	Endemic to Jamaica [1, 2, 27]	Dry forests leaf litter [1, 2, 27]	(F) T	19 [1]	1.25 [1]	21 [1]	?	?
<i>Metopaulias depressus</i> (J)	Endemic to Jamaica [2, 25, 41]	Dry forests, on bromeliads [2, 25, 41]	(F) T	19 [25]	1.50 [25]	100 [25]	5	2 [25]

M: marine; B: brackish; F: freshwater; T: terrestrial; in parentheses: species commonly but not predominantly associated with a given category, or only during larval development; maximum female carapace width (CW); egg size: egg number (N₁); N₂: CW ratio; number of zoeal stages (N_Z); J: species recorded from Jamaica. For taxonomic status of *Planes minutus* and *P. cyaneus*: see Chace (1951), Melo et al. (1989). ??: no data available; after N_Z: only partial description of larval development available, or approximate N_Z estimated from congeneric species with known development. General characterization of distribution, habitat, and salinity preference: after textbooks and other comprehensive publications: Abele, 1992; Boschi et al., 1967, 1992; Chace & Hobbs, 1969; Garth, 1978; Hartnoll, 1964, 1965; Holthuis, 1959; Keith, 1985; Melo et al., 1989; Powers, 1977; Rathbun, 1918; Williams, 1984. Key numbers [in brackets] for more specific and additional references: 1. Abele & Means (1977); 2. Abele (1992); 3. Anger (1991a); 4. Anger (unpubl.); 5. Anger & Schultz (1995); 6. Anger et al. (1990a); 7. Bäuerle & Diesel (1993); 8. Benedict (1892); 9. Boschi et al. (1992); 10. Bossi-Garcia & Rodrigues (1993); 11. Capitoli et al. (1977); 12. Chace & Hobbs (1969); 13. Coelho & Ramos (1972); 14. Conde & Diaz (1989); 15. Costlow & Bookhout (1960); 16. Costlow & Bookhout (1962); 17. Crothers & Crothers (1990); 18. Diaz & Bevilacqua (1987); 19. Diaz & Ewald (1968); 20. Diesel & Schuh (unpubl.); 21. Fransozo & Hebling (1986); 22. Garth (1946); 23. Gohar & Al-Kholy (1957); 24. Gore & Scott (1982); 25. Hartnoll (1964); 26. Hartnoll (1965); 27. Hartnoll (1971); 28. Kurata (1962); 29. Kurata (1968); 30. Lebour (1950); 31. Lebour (1950); 32. Luppi, Bas, Spivak, Anger (unpubl.); 33. Marchand (1946); 34. McDermott (1991); 35. Montu et al. (1990); 36. Nepszy & Leach (1973); 37. Ogawa & Rocha (1976); 38. Panning (1938); 39. Paula & Hartnoll (1989); 40. Peters (1933); 41. Rathbun (1918); 42. Seelzo & Lichstein (1979); 43. Schuh & Diesel (1995a); 44. Schuh & Diesel (unpubl.); 45. Seiple (1979); 46. Seiple & Salmon (1987); 47. Spivak et al. (1994); 48. Turkey (1975); 49. Turkey & Diesel (1984); 50. Williams (1984); 51. Wilson (1980); 52. Zimmerman & Felder (1991).

adaptive radiation has been found in the Indo-Pacific region, with 23 species of *Geosesarma* (previously assigned to the genus *Sesarma*; Sèrene & Soh, 1970). Most of these species, however, appear to be terrestrial rather than aquatic. Two grapsid species in this region, *S. jacobsoni* (Ihle, 1912) and *S. cerberus* (Holthuis, 1964), are cavernicolous, possibly living or developing in freshwater.

A second radiation centre of Sesarminae species is found on the island of Jamaica, including the only non-potamid crabs that are known to pass their entire life cycle in freshwater: *S. bidentatum*, *S. windsor*, and possibly, *S. verleyi*. While the first two species are found in mountain streams and rivers (Hartnoll, 1964; Türkay & Diesel, 1994), the third may be terrestrial. It lives in subterranean limestone caves with freshwater (Rathbun, 1918; Hartnoll, 1964). All these endemic crabs are closely related with terrestrial Sesarminae, *S. jarvisi*, *S. cookei*, and *Metopaulias depressus*; they are believed to have evolved from a common marine ancestor, most probably a near relative of an extant species, *S. curacaoense* (Hartnoll, 1964, 1971).

According to their large egg size (Table 1), all endemic freshwater and land Sesarminae from Jamaica have an abbreviated larval development. In all known cases (*S. windsor*, *S. jarvisi*, *M. depressus*), there are two zoeal stages and a megalopa. They develop in the same environment, where the adults live, entirely independent of the sea. The same pattern, with two zoeal stages and a megalopa developing in freshwater, was found also in the only *Geosesarma* species for which a larval description has become available, *Geosesarma perracae* (Soh, 1969). These Sesarminae species are the only known Brachyura which pass their entire life cycle in freshwater, and still maintain a free-swimming larval phase. While this type of life history is known also from some palaemonid and atyid shrimp species (e.g. Magalhães, 1989; Jalihal et al., 1993, 1994), all other limnic Decapoda have either completely reduced their larval phase (crayfishes, potamid crabs, some shrimps), or their larvae develop in the sea (export strategy; Strathmann, 1982).

Among the freshwater decapods that depend during larval development on marine or brackish water, the larvae of some species are released in freshwater, whereas in others they hatch only in estuarine or coastal marine waters, after downstream migrations of the females. In the first group, the larvae must be able to tolerate freshwater for one or a few days, until they may reach the lower estuary with outflowing currents. Examples of this strategy have been found in *Cyrtograpsus angulatus* (Anger et al., 1994), *Armases angustipes* (Anger et al., 1990), and in some east Asian *Sesarma* species (Hashimoto, 1965; Saigusa & Hidaka, 1978). Seaward migrations of females may be common in the Varuninae. In the Chinese mitten crab, *Eriocheir sinensis*, such migrations can extend over more than 1000 km (Panning, 1938). Similar patterns were observed also in the Japanese mitten crab, *E. japonicus* (Kobayashi & Matsuura, 1991), and in *Varuna litterata* (Ryan & Choy, 1990), a freshwater crab from the Indo-Pacific region. Thus, this strategy may occur also in *Glyptograpsus jamaicensis*, another endemic Jamaican freshwater grapsid (Rathbun, 1918), which belongs to the same subfamily.

2.2. Terrestrial crabs

In their treatise of the biology of land crabs, Burggren & McMahon (1988) list 11 species of land hermit crabs (Anomura; with 10 coenobitid and 1 diogenid species) and 71 brachyuran crabs (12 Gecarcinidae, 36 Grapsidae, 12 Ocypodidae, 11 Potamoidea), not including intertidal species which only occasionally may be found on dry land. However, this list contains only 5 of the 23 known *Geosesarma* species (all are considered more or less terrestrial; Hartnoll, 1988); thus, the total number of known terrestrial grapsid crabs should actually comprise 54, that of terrestrial Brachyura 89 species. The high proportion of Grapsidae shows, once more, how successful this family has been in the conquest of freshwater and land.

The differential degree of terrestrialization in these decapod groups is further stressed, when their developmental modes are considered. All hermit crabs, all gecarcinids, and all ocypodids are classified as having a “pelagic marine” (PM) mode of development, i.e. they produce many small eggs, and the females release pelagic larvae in coastal marine waters. Their development usually comprises 4–5 zoeal stages and a megalopa. Only the ocypodid crab *Uca subcylindrica* is known to have an abbreviated larval development (Rabalais & Cameron, 1983; it is erroneously classified as “PM” in this table). Among the 54 grapsid species, in contrast, only 24 are known or presumed to follow the “PM” strategy, whereas 30 (*Metopaulias depressus*, probably all 23 *Geosesarma*, and 6 *Sesarma* species) show an abbreviated larval development (Hartnoll, 1988), or in some cases, maybe direct development (Johnson, 1965).

As in freshwater, the greatest extent of life-cycle adaptation is found in terrestrial potamid crabs: all 11 species have a direct development, and hence have become completely independent of the sea. However, the terrestrial grapsids may show the same degree of independence, in spite of maintaining a larval phase. As far as this is known, their larvae develop in special breeding reservoirs with small volumes of freshwater. The best-known case is the bromeliad crab, *M. depressus*, whose larvae develop in rainwater that is collected in the leaf axils of bromeliads (Hartnoll, 1964). In *S. jarvisi*, Bäuerle & Diesel (1993) observed breeding within empty terrestrial snail shells, with very small amounts of water that is introduced by the females. In the Malayan land crab *Geosesarma perracae*, the larvae probably develop within partly water-filled burrows that are dug by the adults (Soh, 1969).

2.3. Brood protection in decapod crustaceans

Development in freshwater or terrestrial environments implies great physiological problems for larval stages, which lack, or have only rudimentary mechanisms of water and ion regulation (Powers & Bliss, 1983; Greenaway, 1988). Their survival is jeopardized by food-limitation (Anger, 1995b), sometimes also by predation (Diesel, 1992b). In adult terrestrial crabs, enhanced intraspecific aggression, territorialism, and competition for limited food resources or habitats

have been described (Powers & Bliss, 1983; Wolcott, 1988). Thus, transitions from marine to freshwater or terrestrial life styles imply at least some of the primary conditions that Wilson (1975) considered selective for the evolution of brood care: (1) early life-cycle stages are particularly endangered; (2) there is enhanced competition for limited resources. Hence, it is not surprising that brood protection has evolved independently in numerous taxa, and it seems likely that all decapod species, which pass their entire life cycle in freshwater or terrestrial habitats, may show brood protection behaviour.

When juveniles cling for some time to the mother or other adult conspecifics, without becoming a victim of (otherwise wide-spread) cannibalism, this may be considered the most primitive form of brood protection. It is a common trait in freshwater crayfish and potamid crabs (Gurney, 1942; Burggren & McMahon, 1988), where Bott (1969) considers it one of the principal preadaptations allowing for the invasion of freshwater. In cases of extreme habitat specialization, possibly also in high latitudes, this form of brood protection may be found also in marine decapods, for instance in sponge crabs (Dromiacea), which often show an abbreviated or direct development (Montgomery, 1922; Hale, 1925). Two similar cases have been documented also in the brachyuran family Xanthidae: *Pilumnus vestitus* (Hale, 1931) and *Pilumnus novaezealandiae* (Wear, 1967). These species have large eggs (≈ 1.5 mm) and an abbreviated larval development, hatching as benthic megalopae, which remain for several days crawling on the female. Direct development and brood protection were observed also in a spider crab (Majidae) species, *Naxioides (Naxia) serpuloides* (Rathbun, 1914). Among the marine decapod crustaceans, a reduction of the pelagic larval phase appears to be common in species from high latitudes (Makarov, 1968). Brood protection, however, has been documented only in one species, the subarctic shrimp *Sclerocrangon ferox* (Koelbel, 1886). As in crayfish, its early juveniles possess special hooks for clinging to the adults (Wollebaek, 1906).

Among the freshwater and land crabs, brood protection does not occur in species that exhibit an export strategy (Gecarcinidae, Ocypodidae, most Grapsidae), but only in species that retain their larvae in the adult habitat, usually showing an abbreviated or direct mode of development. All these traits decrease the dependence on the sea and thus, should be considered important prerequisites for a successful invasion of freshwater or land. Among the grapsids, parental brood care has been described in *Geosesarma noduliferum* (Pesta, 1930), *G. notophorum* (Ng & Tan, 1995), *M. depressus* (Diesel, 1989, 1992a,b), and *S. jarvisi* (Bäuerle & Diesel, 1993; Diesel & Horst, 1995); it has to be expected also in other freshwater and terrestrial Sesarminae.

3. Traits and tendencies in the life histories of western Atlantic Grapsidae

Relationships between life-history traits of brachyuran crabs (egg size, development duration, size in later life-cycle stages) were investigated in great detail by Hines (1982, 1986b). Thus, I will concentrate on those which might be relevant for

the adaptation to non-marine conditions. The Western Atlantic grapsid species are used as an example, because they show, within a limited geographical region, all transitions in life style, from oceanic to fully limnic or terrestrial. In Table 1, the species are ranked in a sequence of apparently decreasing dependence of the sea (indicated by habitat and salinity preference, according to literature data). The order within groups of species assigned to the same category (e.g. “marine”, M) does not necessarily imply further internal ranking. Naturally, this order is to some degree arbitrary, but no sufficient data on better defined (numerical) ranking criteria such as egg size or number of zoeal stages are available at present.

3.1. Relationships between adult ecology, development, and geographic range

Among the 40 species listed in Table 1, only four are confined to the subtidal (two of these are deep-water species), one is commonly found on drifting objects in the ocean. The overwhelming majority (36 species, or 90%) shows, as is generally known from the Grapsidae, terrestrial tendencies. Most of these live in the intertidal and supratidal zones, one third can live in freshwater (at least as adults), and three or four species are fully terrestrial.

Adult female size (maximum given, where available) does not show a relationship with either ecological or distributional traits of a species but, naturally, with the number of eggs. In order to reduce the effect of adult size (carapace width, CW) on egg number (N_E) the ratio $N_E: CW$ is given as a fecundity index in Table 1. Among the marine and brackish-water species, size-specific fecundity does not show a relationship with ecological or distributional data, but it is clearly lower in limnic and terrestrial species. Exceptionally low fecundity was found also in *S. curacaoense* and *A. miersii*, two semiterrestrial species, while maximum values occurred in an introduced freshwater species, which migrates to lower estuaries for larval release, the mitten crab *Eriocheir sinensis*.

Due to allometric constraints (limitations on space available for yolk accumulation in the body cavity; Hines, 1982), fecundity is determined not only by female body size, but also by average egg size. This general trade-off is reflected by a negative correlation between size and number of eggs (Hines, 1986b). Egg size is in brachyurans not generally correlated with adult size (Hines, 1986b), which is true also in the Western Atlantic Grapsidae (Table 1). In marine and brackish water species, egg size varies mostly between 0.25 and 0.45 mm, without showing a relationship with specific ecological traits; only *S. curacaoense* and *A. miersii* have much larger eggs (0.7 and 0.6 mm, respectively), which explains their low fecundity. True freshwater and terrestrial species show the largest egg size, consistently exceeding 1 mm.

The mode of larval development is described in Table 1 by the number of zoeal stages (N_z). Among the marine and brackish-water species, there is much interspecific, in some cases also intraspecific variability, without showing a clear relationship with ecological traits. Most of these species have 4–6 zoeal stages. Major deviations occur only in *Pachygrapsus gracilis*, with at least 13 zoeal stages, and again, in *S. curacaoense* and *A. miersii*, which have an abbreviated develop-

ment (2 and 3 zoeal stages, respectively). The true freshwater and land crabs show also an abbreviated larval development, with 2 zoeal stages in all species where data are available.

In spite of a general relationship (see above), the predictability of developmental mode from egg size is limited by phylogenetic constraints (Strathmann, 1977). When only the Western Atlantic grapsid crabs are considered, the data in Table 1 show a significant negative correlation between egg size and number of zoeal stages, N_Z ($r = -0.816$; $p < 0.001$; after logarithmic transformation of data; in cases of variability in N_Z : the most frequently occurring number).

In his extensive review of brachyuran life-history patterns, Hines (1986b) did not find a significant general correlation between length of larval period and geographic range. However, the actual duration of larval development in the field is often difficult to assess, as not enough data are available on temperature-dependence of larval development, temperature variation in regions or depths of larval occurrence, nutritional effects, etc. Furthermore, the geographic range of a species may be limited by climatic constraints (specific adaptation to certain ranges of temperature or salinity), and dispersal patterns of decapod crustaceans are often controlled by complicated rhythms of hatching and larval behaviour.

When the number of zoeal stages instead of development duration is taken as a measure of dispersal capacity, a rather clear relationship with the geographic range can be seen in Table 1. All true freshwater and land crabs (with only two zoeal stages) are endemic to Jamaica. Among the marine and brackish water species with only 2–4 zoeal stages, 11 have a limited distribution within the Western Atlantic region. *Aratus pisonii* is the only species in this category that occurs also in the Pacific; however, this tropical species was probably introduced there rather than dispersed naturally. Species with ≥ 5 zoeal stages show in general a wider geographic range. Disregarding the introduced freshwater species *E. sinensis*, there are in this category only two species with a limited distribution within the western Atlantic region, two occur on both sides of the Atlantic Ocean, and six species are found also in the Pacific.

The data summarized in Table 1 show significant gaps in our knowledge. Yet, the available data confirm some general peculiarities in true freshwater and terrestrial crabs, compared with marine species: (1) advanced habitat specialization, (2) limited geographic range, (3) large egg size, (4) low fecundity, (5) abbreviated larval development.

3.2. Larval tolerance of physical and chemical stress

The transition from marine to freshwater or terrestrial conditions implies the necessity to adapt to entirely different physico-chemical conditions. While physiological adaptations in the adult phase of crustaceans have been studied extensively (Powers & Bliss, 1983; Burggren & McMahon, 1988), those in early life-history stages are much less known. Diesel (1989, 1992a) and Diesel & Schuh (1993), showed in the nursery habitat of the terrestrial crab *M. depressus* (i.e. in rain water collected in leaf axils of bromeliad plants) extreme variations of pH,

oxygen, and calcium concentration. Although this harsh microclimate is mitigated by maternal brood care, it still requires an unusual degree of physiological tolerance in the larval stages (Diesel & Schuh, 1993). It is remarkable that the pH optimum of their larvae shows a shift to values <7 , so that they can survive in water with high tannic acid concentrations, but not in slightly basic (pH 8) water from mountain streams and rivers (Anger & Schuh, 1992), where this species most probably evolved (Hartnoll, 1964). Also seawater, from where the ancestors of freshwater and land crabs had originated, is in general slightly basic.

While the oxygen concentration in bromeliad leaf axils may decrease periodically at night, when there is no photosynthetic activity of microalgae (Diesel, 1992a), it should be always low in snailshells, where *S. jarvisi* breeds (Bäuerle & Diesel, 1993). These shells are partly filled with wet particles of leaf litter and other organic matter and usually contain only little water and air (pers. obs.). Hence, one may expect that larvae and juveniles developing therein should reveal an extreme tolerance of low oxygen concentrations. This may be crucial also in species, whose larvae breed in partly water-filled burrows of the adults, most probably in *Geosesarma perracae* (Soh, 1969) and *S. curacaoense*.

In semiterrestrial species that breed in small water bodies within marginal habitats adjacent to the sea (e.g. mangrove swamps in *S. curacaoense*), also larval salinity tolerance should be important. Fig. 1 shows that *S. curacaoense* larvae tolerate a range at least from full-strength seawater (32 ‰ S) to about half this salt concentration. Enhanced mortality and development duration at 15 ‰ S shows that *S. curacaoense* larvae are euryhaline, but probably not able to survive in low salinities (<15 ‰ S). Future studies should ascertain the actual conditions in the natural breeding habitat of this species.

The larvae of another semiterrestrial crab, *A. miersii* were observed developing in supratidal rock pools, where conditions may vary between freshwater and hypersaline (Schuh & Diesel, 1995a; Anger, 1995b). In laboratory experiments, the larvae showed tolerance of both hypo- and hypersaline conditions, allowing

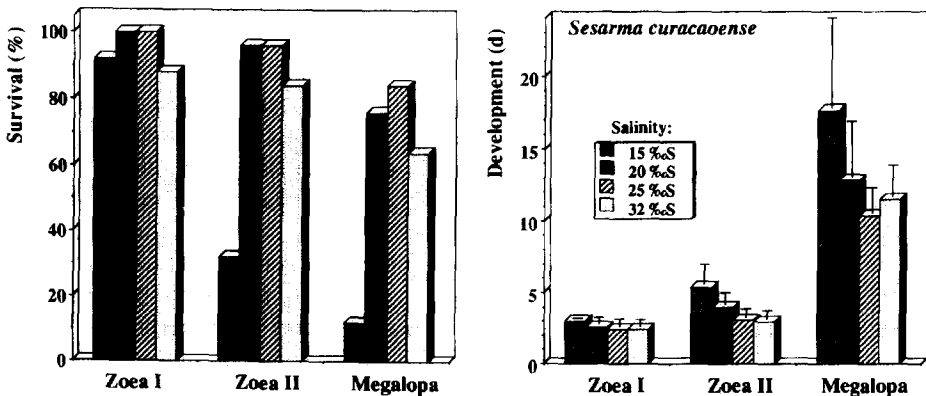


Fig. 1. Survival (%; initial $n = 25$) and duration of development (days; $\bar{x} \pm SD$) of *S. curacaoense* larvae reared in the laboratory at 24°C under different salinity conditions (Anger, unpubl.).

for complete development in salinities between 5 and 55 ‰ *S* (Schuh & Diesel, 1995b). When the larvae are exposed to different salinity conditions only from the megalopa stage, they can develop through metamorphosis even in freshwater (Schultze, unpubl.).

3.3. Larval tolerance of nutritional stress

It is widely accepted that free-swimming planktotrophic larvae represent the original mode of development in marine invertebrates, while abbreviation is secondary (Jägersten, 1972). A reduction of the pelagic larval phase requires early modifications in the developmental programme (Wray & Raff, 1991), apparently representing an irreversible evolutionary process (Strathmann, 1978, 1985). It appears to be an adaptation to low or unpredictable planktonic food production in freshwater and terrestrial environments, which select for the evolution of large, yolky eggs, and an abbreviated or direct, at least partially lecithotrophic larval development. First experimental evidence of food limitation in a semiterrestrial breeding habitat (supratidal rock pools) has been shown only recently (Anger, 1995b).

3.3.1. Maternal energy investment: biomass of eggs and freshly hatched larvae

The primary prerequisite for nutritional independence is an enhanced maternal energy investment per offspring, which can be measured in biomass of eggs and early larvae. In freshwater and terrestrial species (*S. windsor*, *M. depressus*), the eggs are about 2 to 3 times larger in size (Table 1), containing about 10 to 20 times more carbon than in semiterrestrial species (Fig. 2). While the percentage C values appear only slightly higher in *S. windsor* and *M. depressus*, the C:N ratio is clearly enhanced in the eggs of these species (Fig. 2). This indicates that the lipid store of their yolk is proportionally more enhanced than the protein fraction, providing an energy-rich biochemical substrate for food-independent zoeal development in these freshwater and terrestrial species.

Biomass in freshly hatched zoea larvae of some Western Atlantic grapsid crabs is compared in Fig. 3. Again, there are striking differences among species with different ecological and life-history patterns. The smallest larvae, with lowest C and C:N values, are found in species that follow an export strategy, i.e. development in coastal marine waters: *E. sinensis*, *Cyrtograpsus angulatus*, *Chasmagnathus granulata*. The initial C:N values in the semiterrestrial species *A. roberti* are near the upper limits known from crab larvae with a marine pelagic development, and thus might point to an initial phase of facultative lecithotrophy. This would be an advantage for early larvae, if they are released in freshwater and then migrate downstream to lower estuaries. Freshly hatched larvae of semiterrestrial species which presumably are retained and develop in the adult habitat (*S. curacaoense*, *A. miersii*), show intermediate C:N values; those of the terrestrial crab *M. depressus* have clearly the highest figures.

In both the eggs and early larvae, there is also significant intraspecific variability. As Hines (1986a,b) pointed out, heritability of such traits should be

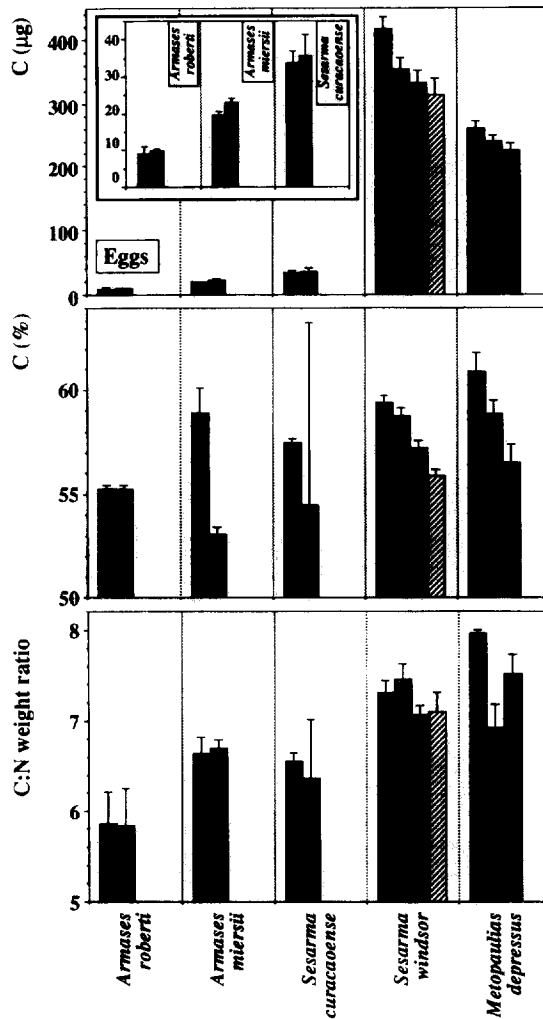


Fig. 2. Biomass (carbon, C; in $\mu\text{g}/\text{individual}$, % of dry weight, and in relation to nitrogen, N; $\bar{x} \pm \text{SD}$, $n \geq 5$) in the eggs of neotropical grapsid crab species. Different shadings: data (Anger, unpubl.) from different broods (grouped in sequence of increasing stage of embryonic development).

studied more intensively. Larger genetic variability in maternal energy allocation per egg might partially explain phylogenetic constraints, i.e. why some taxa (e.g. the Sesarminae) have undergone a greater adaptive radiation than others.

3.3.2. Larval starvation resistance and lecithotrophy

Planktotrophic marine decapod larvae show in general little tolerance of starvation, and thus are not able to develop in the absence of food to subsequent stages (Anger, 1987). Lecithotrophic larvae, in contrast, reach metamorphosis with endowed energy reserves (e.g. *Geosesarma perracae*; Soh, 1969). As an

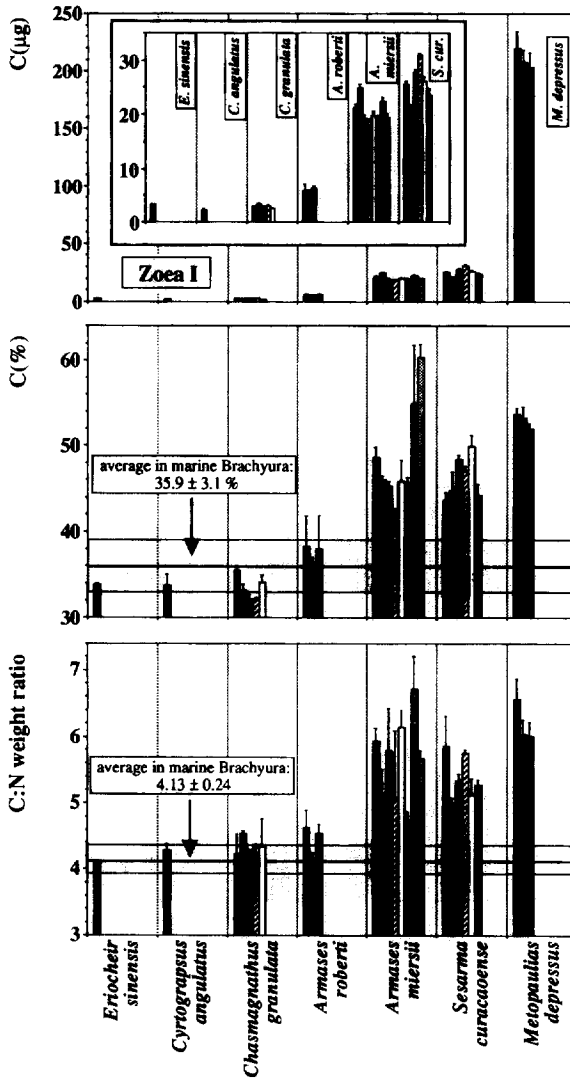


Fig. 3. Biomass (as in Fig. 2) in freshly hatched zoea larvae of western Atlantic grapsid crab species. Different shadings: data from different hatches. Average ($\bar{x} \pm SD$, $n \geq 5$) in freshly hatched marine brachyuran larvae: from Hirota & Fukuda (1985), Anger & Harms (1990) and Anger (unpubl. data); representing 74 hatches from 17 species.

intermediate step in the evolution of nutritional independence, facultative lecithotrophy occurs in the larvae of *S. reticulatum* (Staton & Sulkin, 1991), *M. depressus* (Anger & Schuh, 1992), *A. miersii* (Anger, 1995a), and *S. curacaoense* (Anger, 1995c; Anger & Schultze, 1995). The degree of endotrophic potential varies among these grapsid crab species, reaching without food the first juvenile

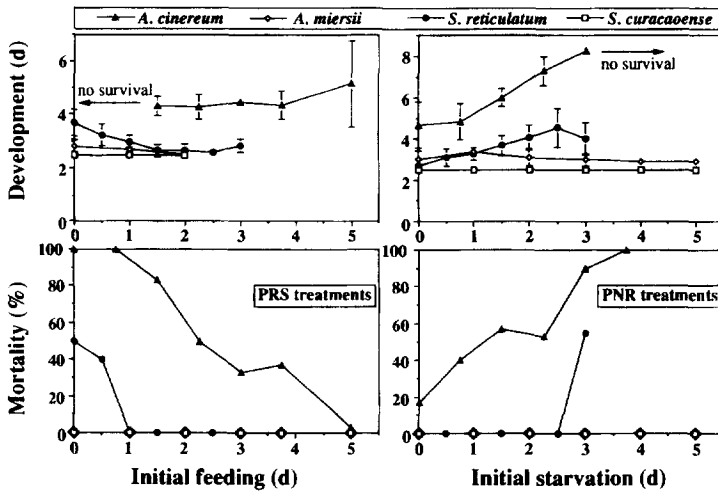


Fig. 4. Mortality and duration of development (at 25°C) in the Zoea I of four grapsid crab species exposed to different point-of-reserve-saturation (PRS) and point-of-no-return (PNR) treatments of feeding and starvation. Data from Staton & Sulkin (1991) and Anger (1995a, c).

(*M. depressus*), the megalopa (*S. curacaoense*), the Zoea III (*A. miersii*), or only the Zoea II (*S. reticulatum*).

Fig. 4 compares larval development and mortality in point-of-no-return (PNR) and point-of-reserve-saturation (PRS) experiments carried out with the three last-mentioned species and one that has planktotrophic larvae, *A. cinereum*. Both the PNR and PRS are indices of larval starvation tolerance: the PNR is the average time of initial food deprivation that will cause irreversible damage (no recovery after later re-feeding), whereas the PRS gives the minimum time of initial feeding that is necessary to allow for later food-independent development to the next stage (Anger, 1987). As shown in Fig. 4, the average duration of the Zoea I stage (in continuously fed control groups) increases in the same sequence as the overall effects of starvation (i.e. increasing mortality, prolonged development), while egg size decreases in this order (cf. Table 1): *S. curacaoense*–*A. miersii*–*S. reticulatum*–*A. cinereum*. Fatal effects of prolonged starvation were observed only in *A. cinereum* and (less) in *S. reticulatum*, whereas no mortality occurred in experiments with the other two species. Thus, no PRS or PNR can be given for the Zoea I of *S. curacaoense* and *A. miersii*; they show facultative lecithotrophy.

In summary, some semiterrestrial grapsid crabs show a partial independence of food. Their lecithotrophy is not as highly developed as in a terrestrial crab, *M. depressus*, but much higher than in marine species with planktotrophic development (including the closely related *A. cinereum*). Increasing lecithotrophy is consistent with increasing egg size, C content in eggs and early larvae (as far as data are available), and decreasing duration of development in fed larvae,

consistently indicating a sequence of increasing terrestrial life-history adaptation in: *A. cinereum* < *S. reticulatum* < *A. miersii* < *S. curacaoense* < *M. depressus*.

3.3.3. Energy saving in larval metabolism and exuviation

Larval development implies significant losses of assimilated or stored energy, namely by exuviation, respiration, and excretion. While the excretion of nitrogenous waste products (primarily ammonia) appears to play only a minor role, the other losses may be quite high within the larval energy budget (Anger, 1991b). Thus, one may expect that exuvial and respiratory energy losses might be minimized in species which partially or fully depend on limited internal reserves, e.g. in freshwater and terrestrial species.

In *M. depressus*, relatively low larval respiration rates were measured, and exuvial losses amounted to only 2–3% of late premoult C in the zoeal stages, and <10% in the megalopa (Anger & Schuh, 1992). In a marine species (*Hyas araneus*), in contrast, 8–9% and 16%, respectively, are shed with the larval exuviae (Anger et al., 1989). Recent data of larval exuvia production in *S. curacaoense* and *A. miersii* (Anger & Schultze, 1995) are similar as those in *M. depressus* and thus, point to possible energy saving mechanisms also in the larval development of these semiterrestrial species. However, our present knowledge of this aspect is extremely scarce, and thus considerably more data are needed, before final conclusions on its significance become possible.

3.3.4. Larval cannibalism: a nutritional buffer?

In terrestrial and semiterrestrial species with facultative lecithotrophy, the endotrophic potential decreases during the course of larval development, so that late stages depend increasingly on external food sources (Anger & Schuh, 1992; Anger, 1995a,c). In *A. miersii* larvae, for instance, which develop in food-limited supratidal rock pools, this may cause an increasing nutritional stress in late stages. This is consistent with an increasing trend in the cannibalistic activity of subsequent stages, reaching a maximum in the megalopa (Anger, 1995b). Hence, multiple release of Zoea I in rock pools provides younger larvae as a potential food source for older conspecifics, and larval cannibalism may be a nutritional buffer (comparable with nurse eggs) in this food-limited breeding habitat. If *S. curacaoense* larvae develop, as suspected, in the burrows of the adult crabs, predation of older by younger larvae, in particular of zoeae by megalopae, might play a similar role in its recruitment and population dynamics.

3.4. Patterns of larval growth

Larval growth patterns in marine decapod crustaceans have been studied intensively in terms of moulting frequency and increase of size (Rice, 1968; Gore, 1985; Hines, 1986b), more recently also as an accumulation of organic matter (Anger, 1991b). While measurements of size can describe only the growth between consecutive instars, biomass data show also patterns of growth within individual larval moult cycles. In addition, they reflect more precisely variation in nutritional

or other factors that may influence the accumulation of body mass, but not necessarily larval size. Hence, I shall focus here exclusively on growth data in terms of biomass, commonly measured as carbon content.

Fig. 5 compares, in a diagrammatic representation, growth patterns in the larvae of three crab species, which all have only two zoeal stages (abbreviated development): the terrestrial grapsid crab *M. depressus*, the closely related semiterrestrial species *S. curacaoense*, and a marine spider crab with planktotrophic pelagic development, *Hyas araneus*. *M. depressus* has very large eggs, with $>200 \mu\text{g C}$ at the time of hatching (see above). Since its two zoeal stages show obligatory lecithotrophy, they lose during development about 20% of their initial C. The megalopa may further develop without feeding through metamorphosis, but it will eat and grow when food is available (facultative lecithotrophy; Anger & Schuh, 1992).

S. curacaoense has, among the Grapsidae, also unusually large eggs and high initial C content in the Zoea I (see above; Figs. 2 and 3), allowing for facultatively

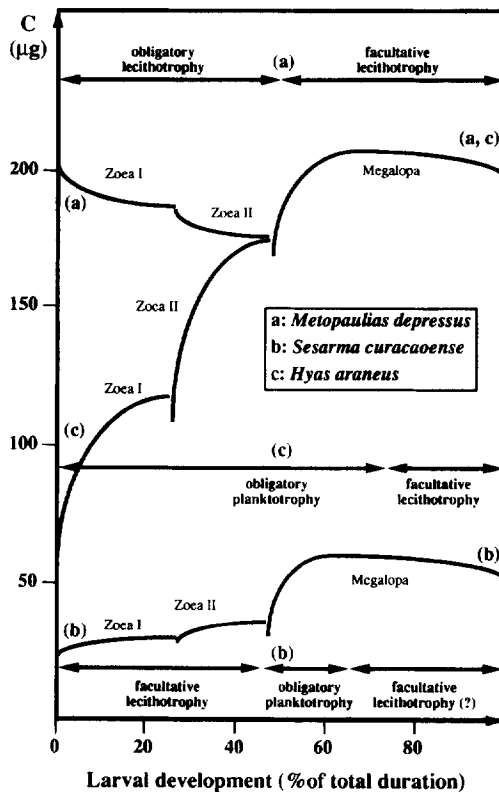


Fig. 5. Diagrammatic presentation of different larval growth patterns (given in μg carbon, C, per individual) in brachyuran species having two zoeal stages and a megalopa: *M. depressus* (terrestrial), *S. curacaoense* (semiterrestrial), *Hyas araneus* (marine). After data from Anger et al. (1989), Anger & Schuh (1992), and Anger & Schultze (1995).

lecithotrophic zoeal development. Even when food is available, the zoeae grow only little, probably due to partially food-independent degradation of yolk materials. Anger & Schultze (1995) measured a net gain of only 12% from hatching to the end of the Zoea II stage. The megalopa has to feed in the beginning, but probably only for a limited period; the final phase of its moult cycle seems again to be facultatively lecithotrophic (unpubl. data).

In *Hyas araneus*, as in most marine decapods, all larval stages need planktonic food to develop successfully. Only the final phase in each moult cycle is potentially independent of food (PRS, see above); for simplification, this is not indicated in Fig. 5, except for the megalopa. This final food-independence, however, depends on optimum growth in the initial phase of each moult cycle, implying that the zoeae are able to accumulate large amounts of exogenous organic matter. Under optimum conditions, their biomass can multiply by a factor of almost 6 during development from hatching to the end of the second zoeal stage (Anger et al., 1989).

Larval growth is described in Fig. 5 in absolute terms ($\mu\text{g C}$ per individual), not as a percentage increase, in order to show that the initial biomass per se (i.e. size and carbon content of the eggs and early Zoea I) may not be a good predictor of the developmental mode or larval growth patterns, when species from different families are compared. As indicated by zoeal growth factors in various decapod taxa (Table 2), cumulative growth from hatching to the megalopa stage is positively correlated with the number of zoeal stages. This confirms earlier findings by Hines (1986b), who concluded from size data that "larval growth was primarily a function of the number of zoeal instars" in the Brachyura. However, the tightness of this relationship clearly increases, when only data from closer related groups are considered: the coefficient of determination (r^2) is 0.291 for all Decapoda listed in Table 2 (20 species), 0.450 for all Brachyura (12 species), and 0.889 for the Grapsidae (5 species); all these correlations are statistically significant ($p < 0.02$). This points to phylogenetic constraints by lineage (family) as observed and discussed by Rice (1980) and Hines (1986b).

4. Selection of life-history patterns: conclusive remarks

Consistent with bimodal patterns in the empirical data (Thorson, 1946, 1950), Vance (1973), Christiansen & Fenchel (1979), and Roughgarden (1989) suggest from theoretical considerations that there should be only two evolutionary stable types of life history in marine invertebrates: (1) production of a large number of small eggs with planktotrophic development; (2) production of a small number of large eggs with lecithotrophic or direct development. On the other hand, Hines (1986a,b) argues convincingly (and the present review adds further examples) that also intermediate life histories occur frequently. However, this is no proof of their evolutionary stability. When the size-frequency distribution of eggs in grapsid crabs (Table 1) is considered, these data support the assumption of a dichotomous distribution in distinct categories rather than a continuum of gradually increasing

Table 2
Zoeal growth factor

Species	Systematic position	N_z	F_G	Reference
<i>Pandalus montagui</i>	Caridea, Pandalidae	≥ 8	28.8	Schultze (1993)
<i>Crangon allmanni</i>	Caridea, Crangonidae	≥ 8	8.7	Criales (1985)
<i>Crangon crangon</i>	Caridea, Crangonidae	≥ 5	4.7	Criales (1985)
<i>Nephrops norvegicus</i>	Astacura, Nephropidae	3	5.4	Anger & Püschel (1986)
<i>Homarus gammarus</i>	Astacura, Nephropidae	3	2.8	Messerknecht & Anger (unpubl.)
<i>Pagurus bernhardus</i>	Anomura, Paguridae	4	5.2	Anger et al. (1990b)
<i>Galathea squamifera</i>	Anomura, Galatheididae	4	4.7	Anger (unpubl.)
<i>Lithodes maja</i>	Anomura, Lithodidae	3 (3 o.L.)	0.7	Anger (unpubl.)
<i>Eriocheir sinensis</i>	Brachyura, Grapsidae	5–6	44.6	Mataliotaki & Anger (unpubl.)
<i>Liocarcinus holsatus</i>	Brachyura, Portunidae	5	22.0	Harms (1990)
<i>Chasmagnathus granulata</i>	Brachyura, Grapsidae	4	21.0	Ismael & Anger (unpubl.)
<i>Carcinus maenas</i>	Brachyura, Portunidae	4	10.2	Dawirs et al. (1986)
<i>Necora puber</i>	Brachyura, Portunidae	5	9.8	Anger (unpubl.)
<i>Cancer pagurus</i>	Brachyura, Cancridae	5	9.2	Anger (unpubl.)
<i>Hyas coarctatus</i>	Brachyura, Majidae	2	7.6	Jacobi & Anger (1985)
<i>Hyas araneus</i>	Brachyura, Majidae	2	5.6	Anger et al. (1989)
<i>Inachus dorsettensis</i>	Brachyura, Majidae	2	2.0	Anger (1988)
<i>Armases miersii</i>	Brachyura, Grapsidae	3 (2 f.L.)	1.8	Anger & Schultze (1995)
<i>Sesarma curacaoense</i>	Brachyura, Grapsidae	2 (2 f.L.)	1.1	Anger & Schultze (1995)
<i>Metopaulius depressus</i>	Brachyura, Grapsidae	2 (2 o.L.)	0.8	Anger & Schuh (1992)

F_G (calculation: maximum carbon content of last-stage zoea divided by minimum in freshly hatched Zoea I), and number of zoeal stages, N_z , in decapod crustacean species from different systematic groups; f.L., o.L.: number of facultatively or obligatorily lecithotrophic zoeal stages, respectively. References: sources of larval growth data.

egg size from marine to freshwater/terrestrial forms. Thus, intermediate life histories (*S. curacaoense*, *A. miersii*) may represent an unstable transitional stage in the evolution of freshwater and land crabs. If the abbreviation of larval development is irreversible (Strathmann, 1978, 1985), then such species may be in a continuing, unidirectional process of terrestrial adaptation. As an evolutionary stable alternative, other species (e.g. *Pachygrapsus* spp.) may follow an export strategy, avoiding non-marine conditions during their larval development (Strathmann, 1982). Both types co-exist in the same habitat. What factors may then select for one evolutionary course or the other?

Comparison of life-history traits in grapsid crabs (Tables 1 and 2) indicate that the mode of development, egg size, and larval growth are correlated with each other, but not with the adult life style. Rather, the environmental conditions, under which the larvae develop, are crucial. Thus, species that pass their entire juvenile and adult life exclusively in freshwater, but their larval development in the sea (export strategy; e.g. *E. sinensis*), have similar developmental traits as marine species: small eggs, many zoeal stages, high zoeal growth rates. Semiterrestrial species, in contrast, which do not necessarily enter freshwater, but remain

during their larval development in the adult habitat (retention strategy; e.g. *S. curacaoense*, *A. miersii*), show conspicuous life-history adaptations: large eggs, abbreviated zoeal development, low zoeal growth, i.e. similar tendencies (only weaker) as freshwater and terrestrial species (e.g. *M. depressus*).

Dispersal could be important (Thorson, 1950), but is now considered a side-product of long pelagic development rather than a selective force in life-history evolution (Strathmann, 1978, 1985). Physiological stress in non-marine and transitional habitats (e.g. by low salinity in estuaries) should indiscriminately select for either a reduction of the larval phase or an export of the larvae, i.e. against larval retention in such environments. However, comparative studies of larval salinity tolerance suggest that also this factor has only minor significance in selection (Morgan, 1987). This conclusion is supported by successful physiological adaptation in the larvae of limnic and terrestrial grapsids from Jamaica and Southeast Asia, and moreover by the existence of numerous shrimp species that also could retain their larval phase in freshwater.

Compared with physiological stress, biotic interactions may be evolutionarily more important. Extremely high pelagic predation in estuarine waters has been shown to select for special morphological and behavioural adaptations in decapod species that do not export their larvae to offshore waters (Morgan, 1990, 1992). As in estuaries, the shallow nearshore waters adjacent to the habitats, where *A. miersii* and, only slightly further inland, *S. curacaoense* live, reveal enormous densities of atherinid and other small planktivorous fishes (Fig. 6). The large, relatively slow, dark-pigmented larvae produced by these species in small numbers, may not have any significant chance of surviving in such an environment, whereas small, fast, transparent larvae produced in high numbers (e.g. *Pachygrapsus* spp.) might have a better chance to escape offshore.

Thus, I suggest that predation pressure may be a significant selection factor in the coastal mangrove fringe in Jamaica, where adaptive radiation of endemic Sesarminae most probably began: once adaptations to a non-marine adult environment have occurred in the eggs and larvae of a semiterrestrial species (production of larger eggs, decreasing fecundity, abbreviated development, trends toward lecithotrophy), coastal marine predators may preclude a return to a marine, planktotrophic type of larval development (export strategy). Since land-locked nursery habitats (e.g. supratidal rock pools, adult burrows) are physically and chemically harsh and lack a reliable plankton production, this combination of selective pressures should leave no other choice but to continue the adaptation to terrestrial or freshwater conditions: towards further increasing larval tolerance of physical and nutritional stress, increasing maternal energy investment per offspring, larger egg size, lower fecundity, reduction of larval development, and brood protection.

Since amphibious coastal environments such as mangrove swamps are considered primary immigration zones (Bott, 1972), more transitional life-history patterns may be expected in semiterrestrial Sesarminae living there, e.g. in *S. rectum*, *S. crassipes*, *A. benedicti*, and other little-known species (Table 1), probably also in *Geosesarma* spp.. Future comparative studies of their ecology, reproduction, and development should increase our understanding of one of the

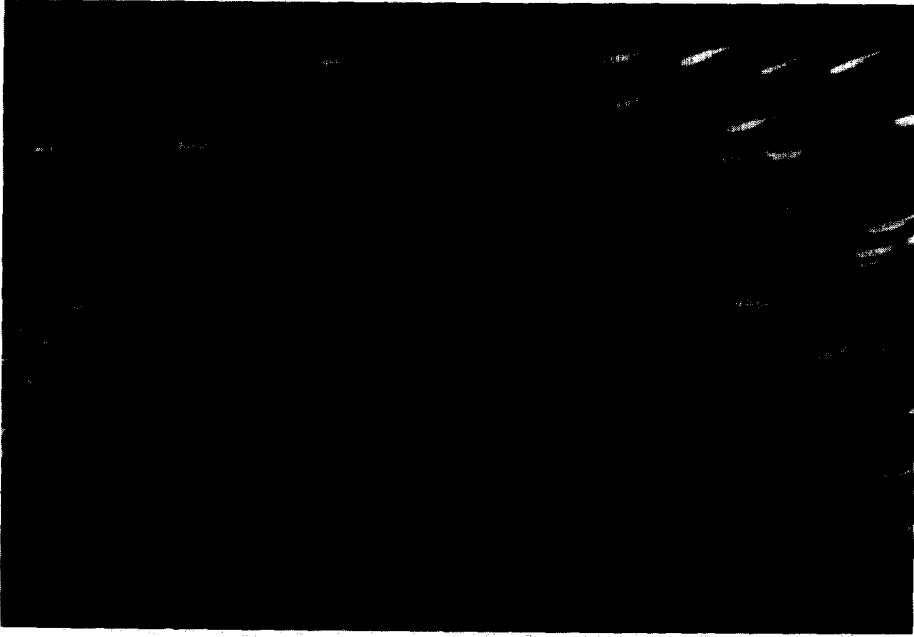


Fig. 6. Shoals of small planktivorous fishes in shallow water adjacent to a mangrove habitat of *A. miersii* and *S. curacaoense*; Discovery Bay, Jamaica. Foto: K. Anger.

major evolutionary transitions in biology: that of marine species to freshwater and land.

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