Sperm Demand and Allocation in Decapod Crustaceans

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Abstract and Keywords
This chapter examines trends in male gametic strategies in relation to female sperm demand among gonochoristic decapod crustaceans. Female lifetime fecundity and number of eggs per spawn can vary much more among decapod species than in other taxa in which gametic strategies have been explored. Female anatomy and life history determine a gradient of complexity and potential duration for sperm storage, lasting from a few hours to several years. The spermathecae of some decapods have enormous capacity and filling may be antagonistic to ovary development. Sperm requirements associated with high female fecundity can be met by large sperm investments from individual males, promiscuity, and/or very effective use of sperm. As in many other taxa, male decapods may allocate sperm strategically as a function of female size (fecundity) and mated status, number of mating opportunities, and risk and intensity of sexual (sperm) competition.

Keywords: sperm storage, sperm competition, sperm requirements, female fecundity, gametic strategies, spermathecae
In most animal species, females produce a limited number of large nutrient-rich ova, whereas males produce numerous small sperm (Trivers 1972). Anisogamy is often associated with very different sex roles and maternal care, and it leads to the prediction that female reproductive success is maximized by choice of mates that confer material or genetic benefits, whereas male reproductive success is maximized by mating with as many females as possible (Trivers 1972, Clutton-Brock and Parker 1992). Competition for access to mates and sexual conflict arising from discordant female and male reproductive interests foster sexual selection that shapes many aspects of morphology, physiology, and behavior and that can lead to rapid speciation (Stockley 1997, Chapman et al. 2003, Shuster and Wade 2003).

Gametic strategies describe how much energy is invested into individual ova and sperm, how many ova and sperm are produced over a lifetime, and how those ova and sperm are allocated over time and among mates (Pitnick and Markow 1994). Female and male gametic strategies are composed of a suite of characters that coevolve within and between the sexes. Female gametic strategies include the number and size of eggs and the partitioning of egg production among reproductive episodes (Stearns 1992). Female sperm storage, when extant, is an integral part of the female’s broader mating strategy that can modify her mating frequency and favor the control/manipulation of male gametes (Neubaum and Wolfner 1999). Males were traditionally assumed to have an almost unlimited supply of sperm and a ubiquitous gametic strategy of dispensing sperm “recklessly” and in excess of female requirements (Trivers 1972). However, this traditional view of male behavior was changed by the recognition that sperm, and
the accessory fluids and/or spermatophores that accompany them, may be expensive to produce and can be depleted more quickly than they are renewed (Dewsbury 1982). Subsequent research that focused mainly on insects, birds, and fishes demonstrated tradeoffs between size and number of sperm and judicious sperm allocation patterns—which may even be suboptimal from the female perspective—in response to female traits, number of mating opportunities, and the risk of sexual competition at the organism or gamete level (Parker 1970, Smith 1984, Gage 1994, Stockley et al. 1997, Birkhead and Møller 1998, Wedell et al. 2002). Males of insect and vertebrate species with promiscuous females may also have evolved larger testes and/or sperm production rates when sperm competition follows a “raffle” mode (Svard and Wiklund 1989, Pierce et al. 1990, Gage 1994, Stockley et al. 1997), whereby the share of offspring fathered by one male depends wholly or partly on the number of sperm he contributes relative to other males (Parker 1993).

Female and male gametic strategies can vary considerably among species and higher taxonomic groupings, in reflection of phylogenetic, life history, and ecological/environmental constraints and adaptations. Comparisons of gametic strategies across different taxa can therefore challenge the universality of responses to sexual competition and conflict and provide a broader insight into the evolution of mating behaviors and systems (e.g., Pitnick and Markow 1994, Stockley et al. 1997). To date, models for the study of gametic strategies have included mainly insects and birds (I refer to these as “traditional models” below) and, to a lesser degree, reptiles, mammals, and fishes. Here, I explore gametic strategies within the crustacean order Decapoda (hereafter, decapods), which includes the familiar crayfishes, shrimps, lobsters, and crabs. This is a very diverse group, with more than 10,000 described species representing about one-quarter of known crustaceans. The range of maximum size at maturity for decapods is probably uniquely high among orders of the Animal Kingdom: the leg span can vary from scarcely a couple of millimeters to as much as 3.5–4 meters (Hartnoll 1983, Manning and Felder 1996). Decapods can be found in terrestrial coastal habitats, in freshwater habitats, and in the oceans from the Arctic to the Antarctic and from the intertidal to the deep sea. Some species live more than 10–15 years.
The basic aspects of decapod reproduction are the following. Decapod sperm are aflagellate and nonmotile, and they are packaged by groups of tens to millions into spermatophores; both sperm and spermatophores may differ considerably in shape and size among species (Krol et al. 1992). The spermatophores are transferred directly on or into the female, accompanied by or containing varying but sometimes copious amounts of seminal fluids (Subramoniam 1993). Eggs are brooded on the pleopods beneath the female’s abdomen, except in penaeid shrimp, where females broadcast them directly into the environment (Bauer 1986). Development is usually indirect with free-living planktotrophic or lecithotrophic larvae hatching from the eggs; however, a few species exhibit almost direct development and extended maternal care. Because of the diversity of decapod morphology, life history, habit, and habitat, this order undoubtedly features a very high yet insufficiently appreciated number of mating systems/strategies (Christy 1987, Correa and Thiel 2003; see also chapter 2) even at the family or genus level (Orensanz et al. 1995, Brockerhoff and McLay 2005a).

This chapter focuses on sperm supply and allocation (male gametic strategies) as they relate to female sperm demand in gonochoristic (i.e., separate-sex) decapods. I begin by reviewing how female life history and sperm storage complexity interact to determine the potential mating frequency and immediate and lifetime sperm requirements, and how these factors are reflected in female sperm storage capacity. Aspects of male fertility, sperm allocation, and sperm competition are then discussed in relation to female requirements and population intrinsic and extrinsic factors. My review emphasizes the very few species for which most of the fundamental aspects of sperm transfer, female sperm storage, and sperm competition have been quantified. However, they alone provide an interesting insight into the scope of possible gametic strategies that have evolved among the decapods.

Sperm Demand
Female Life History Pattern and Sperm Storage Mode

Life history patterns divide female decapods into two categories (Hartnoll 1983). Females in the first category have indeterminate growth and continue to molt after first maturity. In these species, the time between molts and the number of spawns produced per intermolt period generally increase as females become larger (older). Females in the second category have determinate growth. The puberty molt during which they acquire external traits of maturity is their last molt and is followed by the production of one or more spawns until the onset of senescence and death.

Sperm storage structures of decapod females rival those of traditional insect and vertebrate models in diversity, in complexity of form (and perhaps function), and in potential for long-term sperm storage (e.g., reviewed by Neubaum and Wolfner 1999). Female decapods exhibit a phylogenetic trend of sperm storage complexity (p.194)
Bauer 1986, Subramoniam 1993) that seemingly correlates with potential duration for sperm storage (Fig. 9.1). In many shrimps, some crayfishes, some lobsters, and all anomuran crabs, females lack internalized sperm storage organs. Males plaster or attach their spermatophore(s) onto the female's abdominal sternites, which may be provided with protuberances or recesses forming specialized receptor areas that facilitate species recognition, mate assessment, and positioning and adherence of spermatophores (George 2005). This is “ephemeral” storage because sperm is used at the next oviposition and the period of time between insemination and sperm use/disposal is short relative to the female's potential reproductive lifespan, usually hours to weeks and exceptionally up to several months (MacDiarmid and Butler 1999). In other shrimps, crayfishes, and lobsters, and in primitive brachyuran crabs, females have partially or completely internalized chitinous storage areas. These structures have little extensibility and are shed along with their contents at each molt. Sperm may be stored between molts but usually serves to fertilize only a small subset of the female's lifetime spawns over a period of time—usually a few weeks/months but exceptionally up to 2–3 years (Waddy and Aiken 1986)—that varies from short to moderately long relative to female reproductive lifespan.

Figure 9.1 Decapod female reproductive types (with genus examples) based on life history and sperm storage mode. Type I, II, and III females have indeterminate growth combined with ephemeral, short-term, or long-term sperm storage, respectively. Type IV females have determinate growth and long-term sperm storage. The pale gray circle represents a molt; the dark gray arrow tail and line represent insemination and subsequent sperm storage on or in the female; the vertical black line represents ovaries, and the diagonal black lines indicate ovipositions. Dashed segments indicate optional or within-type variable events. The time (distance) between insemination and oviposition varies among species within each type.
The most elaborate female sperm storage organs are found in the higher brachyuran crabs (Krol et al. 1992). Each of the paired spermathecae is composed of an extensible dorsal reservoir with a glandular epithelium, derived from and connecting to the oviduct, which opens into a ventral chitinous area leading to the exterior via a vagina (Fig. 9.2). Accessory or transitory sperm storage chambers may also exist (Jensen et al. 1996). Chitinous parts of the female reproductive tract are shed at molting, but sperm may be retained across molts within the dorsal reservoir in some but not all species (e.g., Swartz 1978, Orensanz et al. 1995). Sperm acquired during one mating period may remain viable and be used over the female’s full reproductive lifespan, which may last up to at least 4–6 years (Kon and Sinoda 1992, Gardner and Williams 2002, B. Sainte-Marie, unpublished data), and so this represents “long-term” storage. Gamete fusion or fertilization is thought to occur internally in the higher brachyurans (but see discussion in Lee and Yamazaki 1990), whereas it is external in all other decapods (Bauer 1986, Krol et al. 1992).

I recognize four basic female reproductive configurations based on life history and sperm storage mode. These are ranked in Figure 9.1 from left to right by order of potentially decreasing frequency of mating and of potentially increasing sperm requirements at individual mating episodes. Type I females, represented by the spiny lobster (*Jasus edwardsii*), grow indeterminately, have ephemeral sperm storage, and hence must mate each time before extruding eggs. Type II females, represented by American lobster (*Homarus*...
Americanus), grow indeterminately but can retain sperm between molts for multiple (two to three) spawnings, and thus mating episodes may be reduced to once after each molt. Type III females, represented by rock crab (Cancer p. 196) irrortatus), grow indeterminately and may retain sperm across molts, and therefore may be relieved from mating for substantial periods of time. Type IV females, represented by blue crab (Callinectes sapidus), have determinate growth and long-term sperm storage. Females can further be divided into those that mate only when soft shelled (i.e., postmolt), those that mate first when soft shelled but can (optionally) also mate later when hard shelled, and those that mate only when hard shelled (e.g., Hartnoll 1969).

Female Sperm Requirements

Females will need enough sperm to fertilize their immediate spawn, and depending on the interaction of life history, sperm storage mode, and ecology, they may need excess sperm for future use. Spawn weight or volume is usually positively correlated with female mean size across species of similar body configuration and with female individual size for any given species. In brachyurans and other decapods with rigid body walls, spawn size may be limited by internal body volume available for ovary development, and there may be a tradeoff between egg number and egg size (Hines 1982). The number of eggs in a spawn is highly variable among decapod species and spans five orders of magnitude, ranging from a few eggs in the minute pinnotherid crab Nannotheres moorei (Manning and Felder 1996) to a few million in some cancrid and portunid crabs (Shields 1991, Hines et al. 2003). Moreover, within the same species, fecundity can vary by up to two or three orders of magnitude between the smallest and the largest female (Shields 1991, Gardner 1997), and this feature should promote male choosiness. Such extensive variability in female fecundity is generally not found among the traditional insect or vertebrate models used for the study of gametic strategies.

Female immediate sperm requirements will depend on the number of eggs to be fertilized in the next spawn. Excess sperm requirements will depend on the product of eggs per spawn by the number of spawns that might or must be fertilized “autonomously” after one mating episode. This product may reach up to $54 \times 10^6$ eggs, partitioned among 18 spawns, in the blue crab (Hines et al. 2003).
Little is known of the efficiency of sperm use in decapods. Calculated decreases in number of stored sperm through one or more autonomous fertilizations resulted in rather similar expenses of about 25 and 70 sperm per ovum, respectively, for the blue crab (Hines et al. 2003) and the snow crab *Chionoecetes opilio* (B. Sainte-Marie and Lovrich 1994), which are both thought to mix gametes or to fertilize internally. Hines et al. (2003) indicated that these ratios are lower than in most animals, and considering that decapod sperm are nonmotile, this can suggest selection for improved efficiency in use of sperm. Although intuitively it would seem that decapods with external gamete fusion and fertilization should be less efficient at using sperm, Heisig (2002) found that the operational sperm-to-egg ratio ranged only from 21 to 37 in the spiny lobster *Panulirus argus*.

It is likely that females of many decapods can perceive how much sperm (or ejaculate) they have stored, as appears to be the case in some insects (e.g., Sakurai 1998, Wedell 2005). In the snow crab, females do not extrude eggs when the ratio of sperm to ova is less than 7:1 (B. Sainte-Marie and Lovrich 1994). Moreover, genetic analysis shows that recently but unilaterally inseminated female snow crabs may fertilize their eggs only with sperm from the freshly provisioned spermatheca when (p.197) the other spermatheca contains few or no sperm (M. Carpentier, B. Sainte-Marie, and J.-M. Sévigny, unpublished data). This is possible because a commissure between the two ovaries (Fig. 9.2) allows females to discharge (and fertilize) eggs via one side of the reproductive tract only (Diesel 1989). Females with external sperm storage may perceive the number and size of accumulated spermatophores by tactile means, whereas perception of sperm reserves in species with partially or completely internalized sperm storage might involve tensors, muscles associated with the dorsal reservoir of spermathecae, or even chemosensory means.
Advantages and Capacity of Female Sperm Storage

Sperm storage is advantageous to female decapods in the same ways that it may be to other animals (Neubaum and Wolfner 1999). Ephemeral or short-term storage is essential in decapods where female receptivity and mating are temporally dissociated from ovary maturity and fertilization. Females need long-term storage to realize their full reproductive potential when they are limited to one mating period but produce multiple broods in a lifetime, for example, the gall crab *Hapalocarcinus marsupialis* (Kotb and Hartnoll 2002) and the blue crab (Jivoff 2003). Long-term sperm storage may protect other females against variable and sometimes unfavorable mating contexts, for example, a female-biased sex ratio, a scarcity of males, and sperm-depleted or infertile males (Elner and Beninger 1995). The genus *Chionoecetes* provides a striking example of predictable ontogenetic changes in mating context. Primiparous (first-time spawning) females mate in loose mesoscale aggregations over a protracted period of time in the winter, while multiparous (repeat-spawning) females become receptive in high-density aggregations over a short period of time in the spring (Stevens et al. 1993, Elner and Beninger 1995, Duluc 2004). These two contrasting spatial and temporal patterns of receptivity may determine different variances of mating success (Shuster and Wade 2003; see also chapter 2) for the two female ontogenetic stages: primiparous females are always mated, whereas some multiparous females in need of sperm may go unmated (B. Sainte-Marie et al. 2002, Duluc 2004).

Sperm storage may reduce female mating frequency and thus decrease her exposure to physical stresses (e.g., desiccation and heat for intertidal species) or predators when advertising or searching for mates (Morgan et al. 1983, Koga et al. 1998; see also chapter 10), to male inflicted injuries or microbe introduction (Elner and Beninger 1995), and likely, by analogy with insects, to sexually transmitted diseases (Knell and Webberley 2004). Finally, sperm storage, whether ephemeral, short, or long term, may afford females the opportunity to accumulate sperm from several males (e.g., type I females, MacDiarmid and Butler 1999; type II females, Gosselin et al. 2005; type III females, Jensen et al. 1996; type IV females, Diesel 1991), resulting in genetically more diverse progeny and/or the possibility of “cryptic” (postcopulatory) mate choice (Eberhard and Cordero 1995). For the time being, evidence to
support cryptic mate choice in decapods is scarce and conjectural. In the snow crab, multiparous females preparing to fertilize a spawn using sperm stored over from a previous mating period may express glandular spermathecal activity, which seems implicated in the mobilization of sperm, vis-à-vis only one of many stored ejaculates (G. Sainte-Marie et al. 2000). Females of the rock shrimp *Rhynchocinetes typus* manipulate spermatophores attached to their sternites and selectively discard some prior to fertilizing (Thiel and Hinojosa 2003). Whether these two behaviors have any adaptive value—material or genetic—is still unclear, as are the criteria for and the mechanisms of sperm selection.

The extent to which short- and long-term sperm storage can potentially release females from the obligation to remate depends on storage capacity relative to female intermolt or lifetime sperm requirements and survivorship of stored sperm. The capacity of female sperm storage areas or organs has been investigated in very few decapods. For comparative purposes, I have calculated a female sperm reserve index (SRI) as the ratio of storage area loading (i.e., weight of attached spermatophores) or of storage organ (content or total) weight to female body weight. The range of mean SRI values is very large among the various female types, and there appears to be a gradient of increasing relative capacity from type I and II to type IV females (Table 9.1). The two extremes of SRI represented by American lobster and blue crab are separated by about one to two orders of magnitude, although the SRI value for lobster is somewhat deflated by inclusion of the exceptionally large chelae in body weight (chelae account for about 30% of total body weight of mature females). The number of sperm and the volume or weight of stored ejaculate are positively correlated in recently inseminated female decapods (Heisig 2002, B. Sainte-Marie et al. 2002, Hines et al. 2003), but over time that relationship may break down owing to volumetric attrition of seminal fluids (matrix) and sperm mortality or losses (B. Sainte-Marie 1993, González-Gurriarán et al. 1997, Hines et al. 2003, Wolcott et al. 2005).

The average values of SRI in Table 9.1 mask the fact that some type III and IV female decapods have highly extensible spermathecae whose limit capacity is determined by unoccupied internal body space (e.g., G. Sainte-Marie and Sainte-Marie 1998). The maximum recorded value of relative ejaculate capacity among female snow crabs is 7%, which is
similar to the average 8–10% relative weight of ovaries or recently extruded eggs (B. Sainte-Marie, unpublished data). The extreme extensibility of some spermathecae has two possible implications. First, sperm storage may be antagonistic to ovary development because the two processes compete for space in the female body cavity. This problem is skirted when female receptivity is temporally dissociated from ovary maturity and the initially large volume of stored ejaculate is progressively reduced as ovaries develop, as in the blue crab (Hines et al. 2003, Wolcott et al. 2005). Alternatively, in the snow crab, primiparous females can accumulate very large sperm reserves by mating several times after oviposition (in addition to mating, usually once, immediately before oviposition) when the spent ovaries do not hinder expansion of spermathecae, and then—as in the blue crab—the volume of the spermathecae decreases gradually as ovaries mature again (B. Sainte-Marie 1993, Urbani et al. 1998). Attrition of spermathecal content may be largely caused by loss of seminal fluids (matrix). The functions of seminal fluids in decapods are poorly understood: demonstrated roles in sperm competition are obstruction of female sperm receptor areas or their accesses and blocking or displacement of rival sperm; hypothetical roles are sperm nourishment, sperm stabilization, and bacterial/microbe control (Diesel 1991, Subramoniam 1993, Beninger and Larocque 1998, Wolcott et al. 2005). Additional roles that should be considered because they exist in the insects are provision of nutrients to the female and male control of female receptivity by saturation of sperm receptor areas or chemical control (Chapman and Davies 2004, Wedell 2005). Second, highly extensible spermathecae may allow the orderly storage of large numbers of ejaculates, thereby favoring last male sperm precedence or female (p.199)
Table 9.1. Female reproductive configuration (♀ type; refer to Fig. 9.1), eggs per spawn and sperm reserve capacity, and male sperm reserve and allocation in decapod crustaceans.

<table>
<thead>
<tr>
<th>Species</th>
<th>♀ Type</th>
<th>Eggs</th>
<th>SRI (%)(^a)</th>
<th>♀ N(_{\text{sperm}})</th>
<th>VSI (%)</th>
<th>EJI (%)</th>
<th>EJ N(_{\text{sperm}})</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock lobster</td>
<td>I</td>
<td>(10^5)</td>
<td>0.07</td>
<td>?</td>
<td>0.15</td>
<td>15</td>
<td>?</td>
<td>MacDiarmid 1989 Mauger 2001</td>
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<td><em>Jasus edwardsii</em></td>
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<tr>
<td>American lobster</td>
<td>II</td>
<td>(10^3)</td>
<td>0.03</td>
<td>?</td>
<td>0.17</td>
<td>16</td>
<td>?</td>
<td>Gosselin et al. 2003</td>
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<tr>
<td><em>Homarus americanus</em> (^b)</td>
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<tr>
<td>Rock crab</td>
<td>III</td>
<td>(10^5)</td>
<td>0.19(^c)</td>
<td>?</td>
<td>0.74</td>
<td>&lt; 7(^d)</td>
<td>?</td>
<td>B. Sainte-Marie, unpublished data</td>
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<td><em>Cancer irratus</em></td>
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<tr>
<td>Stone crab</td>
<td>III</td>
<td>(10^5)</td>
<td>?</td>
<td>(6 \times 10^6)</td>
<td>?</td>
<td>8</td>
<td>(5 \times 10^6)</td>
<td>Wilber 1989</td>
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<td><em>Menippe sp.</em></td>
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<tr>
<td>Giant crab</td>
<td>III</td>
<td>(10^6)</td>
<td>0.26(^c)</td>
<td>?</td>
<td>0.39</td>
<td>&lt; 27(^d)</td>
<td>?</td>
<td>Gardner and Williams 2002</td>
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<td><em>Pseudocarcinus gigas</em> (^b)</td>
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<td><em>Libinia emarginata</em></td>
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\(^a\) Sperm reserve index (SRI) = (♀ N\(_{\text{sperm}}\) + VSI) / EJI

\(^b\) Data from B. Sainte-Marie, unpublished

\(^c\) Estimated

\(^d\) Percentage of EJ

\(^e\) Number of eggs per spawn
<table>
<thead>
<tr>
<th>Species</th>
<th>♂ Type</th>
<th>Eggs</th>
<th>SRI (%)(^a)</th>
<th>♀ N(_{sperm})</th>
<th>VSI (%)</th>
<th>EJI (%)</th>
<th>EJ N(_{sperm})</th>
<th>Reference</th>
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<tr>
<td>Snow crab</td>
<td>IV</td>
<td>10(^4)</td>
<td>0.82</td>
<td>5 \times 10(^7)</td>
<td>2.03(^f)</td>
<td>2</td>
<td>5 \times 10(^6)</td>
<td>Sainte-Marie and Lovrich 1994 Sainte-Marie et al. 2002, unpublished data</td>
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<td><em>Chionoecetes opilio</em></td>
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<tr>
<td>Blue crab</td>
<td>IV</td>
<td>10(^6)</td>
<td>2.21</td>
<td>8 \times 10(^8)</td>
<td>3.27</td>
<td>47</td>
<td>8 \times 10(^8)</td>
<td>Hines et al. 2003, Jivoff 2003</td>
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<tr>
<td><em>Callinectes sapidus</em></td>
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Abbreviations: SRI, female sperm reserve index—wet weight (WW) of sperm reserve as a percentage of female body WW; ♀ N\(_{sperm}\), number of sperm in storage; VSI, vasosomatic index—WW of vas deferens as a percentage of male body WW; EJI, ejaculate size index—WW of ejaculate or number of sperm (for *Menippe* sp. only) as a percentage of vas deferens WW or sperm count; EJ N\(_{sperm}\), number of sperm transferred to the female by one male.

\(^a\) When not provided by the author, I calculated ♀ SRI and VSI from length-weight relationships published elsewhere (available from the author upon request);  
\(^b\) species with disproportionately large chelae;  
\(^c\) weight of spermatheca included;  
\(^d\) calculated assuming weight of spermathecal contents were transferred in one mating;  
\(^e\) value for old-shell (abraded) males;  
\(^f\) value for intermediate-shell males.
cryptic choice. In some majid crabs, there is no visual (by histology) evidence of sperm mixing even when females accumulate five to eight ejaculates in each spermatheca, and sperm precedence mechanisms may be effective even when females are intensely promiscuous (Diesel 1991, G. Sainte-Marie et al. 2000). By contrast, multiple ejaculates apparently mix extensively in the spermathecae of the ocypodid crab *Macrophthalmus hirtipes* (Jennings et al. 2000), and sperm precedence mechanisms in other animals may become ineffective when females mate with more than two males (e.g., Zeh and Zeh 1994).

**Sperm Supply**

**Male Sperm Reserves**

There is for the decapods a stunning sexual asymmetry in the information available on fertility. While it has been routine practice to measure female reproductive output, there is little information on most aspects of male fertility except for the size at onset of sperm production. The issue of sperm quality—functionally speaking—has barely been touched upon, although it is becoming of interest for species with potential for aquaculture. In penaeid shrimps, for example, larger and older males may have a greater proportion of live sperm and a smaller proportion of deformed sperm than smaller or younger males (Ceballos-Vázquez et al. 2003). There is a suggestion that male snow crabs may, perhaps uniquely, pass different types of sperm and spermatophores adapted either for short- or long-term storage (Elner and Beninger 1995, Moriyasu and Benhalima 1998, G. Sainte-Marie et al. 2000). In other animal taxa, the sperm of individual males may differ in fertilization success, and this may be related to environment, age, reproductive experience, phenotype, and/or genotype (e.g., Jones and Elgar 2004, Pizarri et al. 2004).

The better documented aspect of male fertility in decapods is the size of reproductive organs. In decapods, sperm develop and mature completely or partly in the testes, while spermatophores are formed and stored with seminal fluids in the so-called vas deferens and associated structures (Krol et al. 1992). Under normal circumstances, mature males seem to always have sperm in reserve. Depending on the species, the testes may be as large as the vas deferens (MacDiarmid 1989, Sato et al. 2005) or much smaller (Homola et al. 1991, B. Sainte-Marie et al. 1995), and this difference may relate to a shifting balance between sperm production rate and sperm reserve capacity that reflect different mating systems/strategies. There are striking differences among species in the
vasosomatic index (VSI), which is the ratio of vas deferens weight to male body weight. Overall, there seems to be a trend of increasing VSI from species with type I females to species with type IV females (Table 9.1). The VSI is slightly more than one order of magnitude greater in the blue crab, in which female sperm requirements at mating are very high, than in the lobsters *Jasus edwardsii* and *Homarus americanus* in which female immediate needs are comparatively small.

There is considerable variability in the size of sperm reserves among individual males within decapod species. One reason for this is that size at maturity can be as plastic in males as it is in females, and this can determine steep size-dependent gradients of male reproductive potential. Indeed, the vas deferens usually increases in size with growing male body size (e.g., MacDiarmid 1989, Homola et al. 1991, (p.201) Gosselin et al. 2003, Jivoff 2003), and where examined, the number of stored sperm is positively correlated to vas deferens or male size and can vary by up to two orders of magnitude from the smallest to the largest male (MacDiarmid 1989, Wilber 1989, Sato et al. 2005). Also, the VSI increases with time elapsed since last molt, so relatively old males have larger sperm stores than recently molted males of the same size (Homola et al. 1991, B. Sainte-Marie et al. 1995). Therefore, larger and “older” males can potentially inseminate individual females more generously or can equally inseminate more females than can smaller males (MacDiarmid and Butler 1999, Jivoff 2003, Sato et al. 2005).

However, it is increasingly evident for decapods that male ability to service females can be limited by sperm reserve and regeneration rate. The time necessary for males to fully recover their sperm reserve after sexual activity may be substantial: 9–21 days after only one mating in some subtropical or temperate crabs (Ryan 1967, Kendall and Wolcott 1999) and from more than 28 days to up to one year or more after one season of intensive mating in species from colder waters (Mauger 2001, Rondeau and Sainte-Marie 2001, Sato et al. 2005). In populations subject to intense male-only fisheries, surviving large males may become sperm depleted or never achieve sperm reserve levels recorded in prefishery times or in currently unfished populations (B. Sainte-Marie et al. 1995, Hines et al. 2003, Sato et al. 2005). The male’s ability to recuperate sperm reserves may be affected by various factors, notably, population abundance and availability of food
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resources (B. Sainte-Marie, personal observations). Sperm supply at the population level is therefore a composite function of male number, size and age structure, and physiological condition.
Sperm Allocation

Sperm allocation by male decapods has been poorly studied, and there is a problem of currency for interspecies comparisons. Most often, studies have reported only the duration of coitus (e.g., Hartnoll 1969), which says nothing of the quantity of sperm transferred, although the two variables may in some cases be correlated (e.g., B. Sainte-Marie et al. 1997). Only a small number of studies have documented the number of sperm and/or the volume or weight of ejaculate passed to females and their relationship to male sperm reserves. Nevertheless, it is clear from these few studies that sperm allocation varies widely among species and that males of a given species allocate differently depending on their characteristics and the socioeconomic context.

Differences in the potentially accessible share of female lifetime egg production and in the risk, intensity, and outcome of sperm competition probably explain some striking patterns of sperm allocation among decapods (Table 9.1). The largest absolute and relative values of sperm allocation belong to the blue crab, in which a sole brief period of female receptivity and male postcopulatory guarding make female promiscuity an uncommon event (< 10% of females) of low intensity (two mates at most). Males that succeed in mating a female are therefore likely to father a large part or all of the female’s prolific lifetime production of eggs (Hines et al. 2003, Jivoff 2003). The smallest relative value (about 2%) belongs to the snow crab *Chionoecetes opilio* in which females are frequently (70–100% of females, depending on socioeconomic context) and intensely promiscuous (two to four mates each on average) during their first breeding season and may mate again later as multiparous females (Urbani et al. 1998, p.202, B. Sainte-Marie, N. Roy, and J.-M. Sévigny, unpublished data). Sperm competition is almost certain to occur in snow crab, and the outcome may be independent of male contribution because of effective sperm precedence mechanisms and the possibility of cryptic female choice. Under some circumstances, the first father’s sperm may never serve again. The scarce other decapod species examined to date fall somewhere between these two extremes (Table 9.1). In the American lobster, female promiscuity is uncommon and of low intensity (0–20% of females depending on population, maximum of two to three mates per female), and when sperm competition occurs, the outcome is mixed paternity seemingly conforming to a raffle
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(Gosselin et al. 2005). However, an individual male lobster will never fertilize more than one, two, or perhaps three spawns out of one female's lifetime production, because his sperm will be shed when the female molts, and therefore he should not invest excessively into any single mating event.

Within decapod species, male characteristics may influence the quantity and rate of sperm transfer. In a noncompetitive context, the quantity of ejaculate passed to each female is positively correlated with male body size in the white shrimp *Litopenaeus vannamei* (Ceballos-Vázquez et al. 2003), the spiny lobster *Panulirus argus* (MacDiarmid and Butler 1999), and the blue crab (Jivoff 2003). In the American lobster, large males pass more ejaculate than do small males, but it represents a smaller share of their total sperm reserves (Gosselin et al. 2003). Female American lobsters prefer large males and may queue up in front of their dens and stagger their molts (i.e., control their receptivity) to mate with them (Cowan and Atema 1990), a preference that may be explained in part by the greater allocation of sperm (Gosselin et al. 2003). However, the amount of sperm transferred to individual females is independent of male body size in crabs of the genus *Chionoecetes* (Adams and Paul 1983, B. Sainte-Marie and Lovrich 1994) and the species *Hemigrapsus sexdentatus* (Brockerhoff and McLay 2005b). Additionally, in the snow crab, large adult males pass their sperm during one or two long copulations, whereas small adult males partition their allocation among several brief copulations. These two behaviors represent alternative mating strategies reflecting the fact that large males are not easily displaced from mating pairs while small males are (B. Sainte-Marie et al. 1997). Size-related sperm allocation patterns may be subordinated to VSI. In both the blue and snow crabs, males with a large VSI pass more ejaculate than do males with a small VSI (Kendall and Wolcott 1999, Rondeau and Sainte-Marie 2001, Jivoff 2003).

Sociosexual context encompasses population characteristics such as the quality and abundance of reproductive females and competing males, and the distribution of female receptivity in time and space. Female attributes that modify number of eggs per spawn or lifetime egg production—that is, the potential return on the male's investment—may change a male's motivation to mate and his sperm allocation. Female size clearly influences sperm allocation in some species, when it is a good index of fecundity. Males in three lobster species
increase the weight of ejaculate they allocate by a factor of 2–6 over a female carapace length range of about 40 mm (MacDiarmid and Butler 1999, Mauger 2001, Gosselin et al. 2003). In the rock shrimp, dominant males double the number of spermatophores they pass to individual females over a carapace length range of about 8 mm (Hinojosa and Thiel 2003). In the intertidal crab *Hemigrapsus sexdentatus*, males increase the amount of ejaculate about 10-fold over a female carapace width range of 23 millimeters (Brockerhoff and McIay 2005b). However, males do not scale sperm allocation to female size in the blue crab, where (exceptionally) it is not a particularly good index of fecundity (Hines 1982), or in the snow crab (B. Sainte-Marie and Lovrich 1994), where it is a good index but the risk of sperm competition is very high.

Female mated status may also affect decapod sperm allocation as in other taxa (Wedell et al. 2002). In the snow crab, successive male mates may inject increasingly larger ejaculates that more effectively displace and isolate previously inserted ejaculates away from the oviduct (Rondeau and Sainte-Marie 2001), thereby reducing the probability of immediate paternity for previous rivals and perhaps facilitating female cryptic choice later. Other easily detected attributes of type IV females that might signal a potentially low return on male investment and cause sperm allocation to be reduced are physical handicaps, for example, missing limbs that hinder foraging or predator avoidance, and an old shell indicating the female has little residual reproductive output because senescence is imminent (Carrière 1995).

The abundance of potential mates and the intensity of male competition may strongly influence male sperm allocation. Laboratory studies have shown that male decapods guard longer and pass more sperm at larger than at smaller male-to-female ratios, and this is considered to be a mate monopolization strategy and a response to increased risk of sexual/sperm competition (Wilber 1989, Jivoff 2003; see also chapter 8). In the snow crab, dominant males also scale guard time and sperm allocation inversely to number of mating opportunities (Rondeau and Sainte-Marie 2001). However, rather than reflecting a response to inevitable sperm competition, this pattern may reflect a balance between a male bet-hedging strategy for partitioning a limited sperm reserve among a variable number of mates (Pitnick and
Markow 1994) and a female sperm extortion strategy that operates by delaying oviposition (i.e., increasing male mating costs by forcing more extensive guarding) until some desired amount of sperm is obtained (B. Sainte-Marie and Lovrich 1994).

Sociosexual context may be subject to ecological or environmental forcing. In the snow crab, populations may experience large decadal swings in the sex ratio of mature individuals that are caused by the interaction of pronounced sexual size/age dimorphism with intrinsic or environmentally mediated multiyear patterns of autocorrelated recruitment (B. Sainte-Marie et al. 2002). As a consequence of this variability, primiparous females are in some years an extremely limited resource and are all intensely promiscuous (by choice or by force) and accumulate large sperm stores that represent more than their lifetime requirements; in other years, they outnumber all classes of mature males, may be sperm limited due to parsimonious allocation by dominant males, exhibit relatively low frequency and intensity of promiscuity, and accumulate small sperm reserves. The difference in mean quantity of ejaculate or number of sperm stored by primiparous females in different years may reach up to one order of magnitude (Fig. 9.3). In many decapods, the latitudinal and depth distributions of species are sufficiently ample to produce steep temperature (or other ecological and environmental) and demographic gradients that modify female size at maturity, intermolt duration, lifetime spawning frequency, and ova size and number per spawn and result in different “ecomorphs” (chapter 7). For example, females reproduce annually in warmer and biennially in colder parts of the range of the Dungeness crab, Cancer magister (Swiney et al. 2003), or produce many more broods and eggs per year and lifetime in the southern than in the northern part of the blue crab.
Therefore, female lifetime sperm requirements, intensity of male competition and costs of mating may differ among environments, and this is expected to be reflected in among-population differences in reproductive behavior (see chapter 7).

Future Directions

This review has illustrated the surprising paucity of information on male gametic strategies in decapods, which is particularly distressing because many species are subject to intense male-only fisheries. With very few exceptions, biological research and management practices for decapods continue to reflect the archaic assumption that males, once sexually mature, have virtually unlimited resources for inseminating females. It follows from this review that future investigations of decapods should put as much emphasis on deciphering gametic strategies for males as for females. More fundamentally, because of the very high female fecundity and seemingly attenuated anisogamy, the decapods apparently offer fertile ground for the exploration of relationships among (1) female lifetime fecundity, (2) female temporal partitioning of receptivity and fecundity, (3) female sperm storage, (4) male lifetime fecundity, (5) potential for and outcome of sperm competition, and (6) sperm allocation patterns in variable ecological and environmental contexts. These aspects of reproduction ultimately determine the variance and

Fig. 9.3 Mean (±95% confidence interval) number of sperm (log$_{10}$-transformed) stored by primiparous female snow crabs (*Chionoecetes opilio*) at different sex ratios in a wild population. The mean is based on a sample of 38–41 females having matured in the year indicated beside the data point. The least squares regression line is significant ($r^2$ =0.816, $P$ =0.014). Data from B. Sainte-Marie et al. (2002).
covariance of reproductive success in groups of individuals, which is the raw material for operation of sexual selection (Shuster and Wade 2003; see also chapter 2).

Decapod researchers should strive for consistency in the way they report information on male (and the case arising, female) sperm reserves and ejaculate size (as weight and number of sperm) and provide appropriate reference information (body weight or, better still, body claw-free weight) for scaling these traits to facilitate interspecies comparisons. There is also a need to quantify sperm competition in nature, in terms of both its frequency/intensity of occurrence and its outcome, because laboratory studies may be biased (Shuster and Wade 2003). The existence, the criteria, mechanisms, and adaptive value of cryptic mate choice require attention. In species with internal and external sperm storage, the possibility that components of seminal fluids offer nutritional benefits or serve to control female mating behavior or receptivity (Neubaum and Wolfner 1999, Wedell 2005) still remains to be explored. The potential conflict between female internal sperm storage and ovary development, and how this relates to temporal patterns of mating and oviposition, is an intriguing issue. The relationships of sperm size and quality and of spermatophore size and properties to the duration of storage, the efficiency of sperm use, and the potential for sperm competition require attention (Elner and Beninger 1995, G. Sainte-Marie et al. 2000). Finally, decapod species with small size at maturity and low female fecundity may provide an interesting contrast to the larger, usually highly fecund species that have been studied so far.
Summary
This review examined trends in male gametic strategies in relation to female sperm demand among gonochoristic decapod crustaceans. Female lifetime fecundity and number of eggs per spawn can be considerably variable within and among decapod species and usually much more so than in other taxa in which gametic strategies have been explored (insects, birds, mammals). Female anatomy and life history determine a gradient of complexity and potential duration for sperm storage, from ephemeral external attachment of spermatophores to fully internalized sperm storage, lasting from a few hours to several years. The spermathecae of some decapods have enormous capacity, and filling may be antagonistic to ovary development. Sperm requirements associated with high female fecundity can be met by large sperm investments from individual males, promiscuity, and very effective use of sperm. As in many other taxa, male decapods may allocate sperm strategically as a function of female size (fecundity) and mated status, number of mating opportunities, and risk and intensity of sexual (sperm) competition. Vas deferens size may be tuned more to reflect female sperm requirements than it is to the risks of sperm competition. The species extremes of sperm allocation strategies are illustrated by the blue crab and the snow crab. In the former, males allocate a very generous share (about 50%) of their large sperm reserves to virgin females, which are never receptive again, have enormous potential lifetime fecundity, and are little inclined to promiscuity. In the snow crab, sperm allocation by dominant males to virgin females is extremely parsimonious (about 2% of their reserve), reflecting a bet-hedging strategy adapted to periodic episodes of high female relative abundance, a very high frequency and intensity of female promiscuity after first oviposition, and an outcome of sperm competition (or hypothetically of sperm cryptic selection) that favors a single male even when females have mated several times. I conclude that crustacean decapods are a most interesting group for the study of animal gametic strategies, albeit largely unappreciated to date.
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