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SEMELPARITY AND ITEROPARITY

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Abstract

Diversity in reproduction schedules is a central component of life history variability, with life span and age at maturity as key traits. Closely linked is the number of reproductive attempts and if organisms reproduce only once followed by death (semelparity) or spread reproduction over multiple and separated episodes during the reproductive lifespan (iteroparity). Amphipoda and Isopoda are two crustacean groups with many semelparous species, but semelparity is also part of other groups such as Decapoda, Copepoda, and Lepostraca. We briefly review theories posited for the evolution of semelparity and iteroparity, covering models on demography in both deterministic and fluctuating environments, and examine models on optimal resource allocation. We provide predictions of these theories, a guide on how to test them in crustaceans, and illustrate how theory can help us understand the diversity within this major taxon. We also point out a few shortcomings of these theories. One is that immediate recruitment is usually assumed in studies of semelparity, which is a poor assumption for the many crustaceans that form egg banks with prolonged recruitment. Another is the lack of models where iteroparity versus semelparity emerge as a consequence of life history trade-offs, rather than the more common approach that assumes demographic parameters. Furthermore, we argue that treating semelparity and iteroparity as a dichotomy is sometimes problematic and that viewing these strategies as a continuum can be useful. We discuss life history correlates and the particularly relevant links between the semelparity-iteroparity axis and capital breeding and seasonality, parental care, and terminal molts. We also discuss some of the indirect methods used to conclude if a crustacean is semelparous or not, such as a rapid drop in adult abundance after reproduction or signs of growth or storage after reproduction. A central message in the chapter is the high value of life history theory as a guide when formulating explanations and projecting evolutionary changes in reproductive lifespan of crustaceans.

Life Histories. Edited by Gary A. Wellborn and Martin Thiel.

INTRODUCTION

Life history theory aims to explain the diversity of life schedules or life cycles as well as the evolution of life history traits and combinations of traits (Stearns 1989, Roff 2002). At the core of this theory is the analysis of how limited resources are best allocated to fundamental processes such as growth, reproduction, and storage of energy and nutrient reserves in order to maximize fitness (Williams 1966, Stearns 1992). Understanding life history trade-offs is therefore a central dimension of life history theory. It is intuitive that a limited amount of resources cannot simultaneously allow both maximum growth and reproduction or maximum survival and reproduction. The challenge, therefore, is to predict how resources should be divided between competing needs. Different solutions to life history trade-offs are optimal under different conditions and in different environments. For instance, reproductive effort models predict that organisms experiencing high adult mortality should favor reproduction over survival, whereas those in safer environments should favor growth and longevity (Williams 1966, Reznick et al. 1990). Crustaceans, with their diverse life histories (Fig. 4.1), offer great opportunities for investigations of these predictions. For example, short-lived cladocerans in freshwater ponds shift sooner from asexual to sexual reproduction

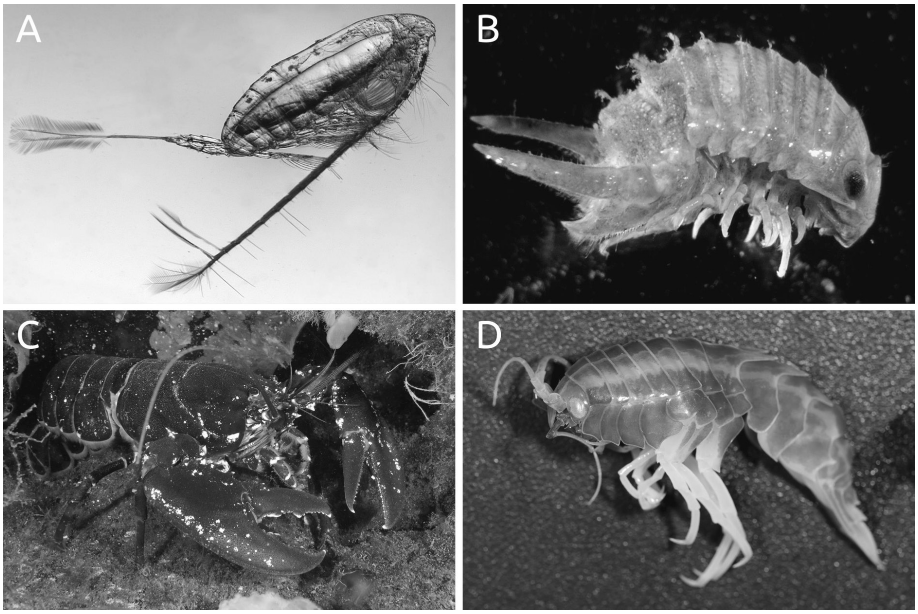

Fig. 4.1.
Photographs of crustacean representatives with life history strategies ranging from strict semelparity to long-lived species with iteroparity. See Fig. 4.3 for a schematic representation of the parity continuum. (A) Semelparous copepods of the genus *Neocalanus* spp., here represented by *Neocalanus plumchrus*. These copepods do not develop feeding appendices in their mature stage and rely on energy reserves for reproduction, with death following reproduction (see also Fig. 4.4). Note the well-filled oil sac, a large energy reserve. Photograph by Ross Hopcroft ©. (B) In the isopod *Paracerceis sculpta*, the females are strictly semelparous and die after one reproductive event, whereas males mate with multiple females and live longer. Depicted here is an "alpha" male known to attract and guard females from other males. Photograph by Alice Lodola ©. (C) Many lobsters and crabs, here represented by *Homarus gammarus*, are iteroparous. In these taxa iteroparity is often combined with indeterminate growth and long lifespans. Fecundity then typically increases with age and body size. Photograph by Erling Svensen/UWPhoto ©. (D) Many amphipods are semelparous, but some also represent the very iteroparous side of the continuum. *Eurythenes gryllus* is such an example of a long-lived, indeterminately growing, and iteroparous amphipod. Photograph by Armin Rose ©. See color version of this figure in the centerfold.

in riskier compared to safer environments (Ślusarczyk et al. 2012). In contrast, longer-lived shrimp species, such as *Palaemon adspersus*, may skip reproduction in response to adverse conditions (Berglund and Rosenqvist 1986), and in hermit crabs of the genus *Pagurus,* females continue to grow larger after first reproduction, and thereby invest in future reproductive success at the expense of current offspring production (Wada et al. 2008).

The diversity of life history strategies includes variability in how reproduction is scheduled through life. Some organisms have a short reproductive life span and reproduce only once followed by death (semelparity), whereas others spread reproduction over multiple, iterative attempts during life (iteroparity; Stearns 1992). Classic examples of the big-bang type (sensu Gadgil and Bossert 1970) of reproduction (i.e., semelparity) include salmonids migrating long distances from oceanic feeding grounds to rivers and lakes where they reproduce and afterward die (Crespi and Teo 2002, Quinn 2011), and *Lobelia* spp. or *Agave* spp. that live for many years before engaging in a single but massive reproductive episode (Young and Augspurger 1991). Examples of semelparity in Crustacea can be found in several groups, including marine (Shuster 1991) and terrestrial isopods (Warburg and Cohen 1991, Linsenmair 2007), amphipods (Sainte-Marie 1991), decapods (Kobayashi and Matsuura 1995), and marine copepods (Miller et al. 1984).

In this chapter, we (1) provide an introduction to the theories explaining the evolution of semelparity and iteroparity; (2) discuss how predictions from these theories can be tested and how Crustacea and the trait distribution within this group can serve as test cases; (3) argue for a need to view semelparity versus iteroparity more as a continuum and gradient than a dichotomy; (4) discuss some life history correlates, evolutionary relationships, and ecological consequences of semelparity in Crustacea, sometimes also with comparisons with other taxa; and (5) discuss the challenges and difficulties involved in determining semelparity and iteroparity from field data, the most common source of data for descriptions of life history diversity in Crustacea. Few in-depth analyses exist of the extent and adaptive value of semelparity and iteroparity within crustaceans. We start some of that work and add to more taxon-specific work provided earlier, such as the substantial review and analyses on amphipods (Sainte-Marie 1991), work on isopods (Harrison 1984), and perspectives provided for calanoid copepods (Hairston and Bohonak 1998, Varpe 2012).

Documenting and understanding the reproduction schedule is a central aim of empiricists. Quotes from studies of copepods can illustrate and inspire. As an example of death after reproduction, Miller et al. (1984) describe the spent stage of reproducing female copepods of the species *Neocalanus plumchrus* by writing that "[the] last clutch of eggs remain in the oviducts, the body tissue is entirely gone, and there is no visible ovary," and he further describes the females as "basically just exoskeletons." Kosobokova (1999), on the other hand, observes essential properties of iteroparity when describing the female reproductive biology of the copepod *Calanus glacialis*: "Many of them survive for several months after reproduction and are able to overwinter again."

THEORIES AND PREDICTIONS OF SEMELPARITY AND ITEROPARITY

Lamont Cole is often acknowledged for coining the terms semelparity and iteroparity (Cole 1954) in the first model to form a general, but overly simplistic, explanation of the adaptive value of semelparity versus iteroparity. Cole (1954) contrasted the population growth of annual and perennial organisms. An analysis of intrinsic population growth rates led him to conclude that any population of an annual organism able to produce just one additional individual offspring by sacrificing itself will grow in number at the same rate as a population of perennials. Because size of parents is usually much larger than the size of offspring, it seemed likely that by sacrificing itself any organism should be able to produce several more offspring than only one individual, and therefore an annual life history should be widely favored. The model by Cole was formulated with no explicit consideration of mortality (Gadgil and Bossert 1970), but the same result is achieved when mortality is included (Bryant 1971). The conclusion that the world should be filled with annuals dying after reproduction (later termed *Cole's paradox*) triggered a long-lasting debate in evolutionary biology on why iteroparity and a perennial lifestyle is so common. This debate led to a resolution of Cole's paradox but more importantly also brought forth three main and somewhat independent scientific threads that investigate the evolutionary drivers of survival and reproductive strategies, including evolution of parity. Subsequently, we provide a brief review of this theoretical development, highlighting the key characteristics and predictions derived under each approach, and then we link these to the diversity observed in Crustacea. Emerging from this review we also show that the routinely adopted dichotomous classification of life histories into semelparous or iteroparous, a consequence of decades dedicated to discussions of Coles' paradox, is crude and a potentially misleading simplification.

The Demographic Approach: Bet-Hedging in Fluctuating Environments

One of the first attempts to solve Cole's paradox focused on year-to-year variability. Using a computer model, Murphy (1968) showed that year-to-year stochastic variation in the number of offspring that recruit to the population promotes long-lived iteroparous forms. In contrast to annuals, reproduction in perennials can serve as a bet-hedging strategy (Slatkin 1974), because reproduction over several years increases the chances for favorable conditions for reproduction and recruitment. Schaffer (1974a) later showed that stochastic variation in adult survival, in contrast to uncertainty in fecundity, is expected to act in the opposite direction and promote semelparity. Several polemic articles followed, aiming at generalizations of earlier conclusions (e.g., Orzack and Tuljapurkar 1989). Important advancements were achieved by relaxing previous assumptions, such as inclusion of density-dependent juvenile recruitment (Bulmer 1985). The overall conclusion from these studies is that iteroparous reproduction is usually a response to a stochastically fluctuating environment, but general rules have proven difficult to formulate (Orzack and Tuljapurkar 1989, Benton and Grant 1999) and the topic is much discussed.

Among more recent and detailed studies, often with complex predictions, are those that introduced spatial structure (Ranta et al. 2000), combinations of gradual and stochastic change in environmental conditions (Zeineddine and Jansen 2009), and density-dependent vital rates in juveniles and adults (Benton and Grant 1999). How density dependence shapes costs and benefits of semelparity, and whether the density dependence operates via birth or death rates (Benton and Grant 1999), are central questions in the demographic approach. Sessile crustaceans such as barnacles could serve as a model group. Settlement probability in barnacles is usually negatively related to density, but growth rate and mortality of settled individuals are sometimes independent of density (e.g., Raimondi 1990). This circumstance allows separation of the density-dependent effects into components driven by recruitment and vital rates in adults and juveniles. More work on how density dependence operates across crustacean functional groups and taxa would be useful for our understanding of semelparity and iteroparity.

While theory provides complex predictions, rough generalizations are possible (e.g., Benton and Grant 1999). Before we stress some generalizations, it is important to note that the reviewed theory assumes immediate recruitment of offspring (e.g., no resting eggs). One generalization is that stochastic variation in fecundity selects for iteroparity, whereas uncertainty in adult survival promotes short life cycles with semelparous life history as one of the outcomes (Schaffer 1974a, Orzack and Tuljapurkar 1989). Barnacles illustrate these principles. In this group, selection towards iteroparity can be driven by the consequences of sedentary adults. Successful recruitment of larvae is highly dependent on whether a suitable habitat can be reached when ready to settle. As shown in *Semibalanus balanoides*, the year-to-year variability in transportation of planktonic larvae has much

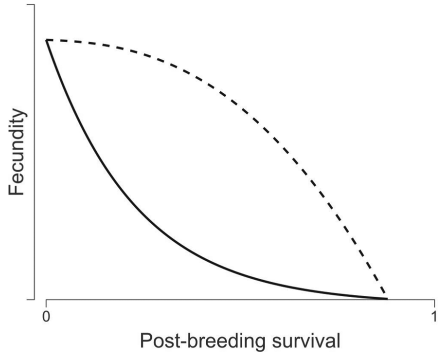

Fig. 4.2.
Schematic presentation of a central trade-off driving the evolution of reproductive life span. Faster-than-linear (convex, solid line) decline in fecundity with survival promotes semelparity. Under slower-than-linear (concave, dashed line) decrease in postbreeding survival, iteroparity or semelparity can evolve but iteroparity is more likely to be selected for (for details see Schaffer 1974b, Takada 1995).

impact on settlement probability and recruitment (Gaines and Bertness 1992); this stochastic variation in recruitment should select for iteroparity. Another generalization is related to the stability of reproductive success in iteroparous organisms. Whereas an iteroparous perennial lifestyle is a bet-hedging strategy that buffers the negative impact of poor years, it also comes with a price. The rule of thumb, supported by several intraspecific empirical estimates (e.g., see Fig. 4.20 in Roff 2002), is that offspring quality or number, or both, in a single reproductive event are greater in semelparous than in iteroparous organisms of similar size. This result suggests that extending reproduction to several years by iteroparous perennials comes with reduced maximum reproductive effort in years with favorable conditions. Hence, under stochastic variability, both strict semelparity and iteroparity with a particularly long reproductive life span are selected against (Benton and Grant 1999).

Here is a summary of the emerging predictions for semelparity versus iteroparity in fluctuating environments: (1) the greater the stochastic fluctuations in adult survival the stronger the selection toward semelparity; (2) the greater the stochastic fluctuations in fecundity the more iteroparous the lifestyle (however, semelparous organisms may buffer stochastic variation in recruitment by production of offspring that enter the population in different years, e.g., resting eggs, see the section "Dormant Eggs and Seed Bank Implications" below); (3) in a highly unpredictable environment, where strict semelparous and long-lived iteroparous organisms are selected against, intermediate strategies are promoted, including short-lived perennials or annuals with prolonged diapause or dormant eggs that hatch in different years.

The Demographic Approach: Deterministic Environments

Iteroparity as a bet-hedging strategy is only a partial solution to Cole's paradox. Given that the paradox emerged from a naively simple model, it might seem surprising that it took two decades to propose a solution based on a demographic process in a deterministic environment. Such a solution was offered when Charnov and Schaffer (1973) introduced differential juvenile and adult mortality to Cole's model. They concluded that evolution toward semelparity should indeed be expected when juveniles and adults suffer the same mortality risk. However, as juvenile survival, and so chances for recruitment, is usually much lower than adult survival, iteroparity should not be surprising. The higher the adult survival relative to juvenile survival, the more natural selection is expected to promote iteroparity. Semelparity is also expected to evolve when fecundity negatively affects adult postbreeding survival and an increase in offspring production results in a disproportionally higher decrease in the postbreeding survival (Fig. 4.2; Schaffer 1974b, Takada 1995). For instance, in semelparous species from the isopod family Sphaeromatidae, females perform a reproductive molt that highly affects their morphology and risk of mortality (Harrison 1984, Shuster 1991). The marsupium restricts female mobility and likely increases predation risk. Selection toward semelparity would be expected if production of a few more offspring (increased reproductive effort) disproportionally increases the mortality component related to the increased marsupium size and restricted mobility.

Other additions to the influential work by Charnov and Schaffer (1973) include flexible age at maturity (Young 1981) and density-dependent fecundity or juvenile survival (Charlesworth 1994). Overall, these additions confirmed the original conclusions that high adult survival and low juvenile survival should characterize iteroparous species. Semelparous organisms on the other hand are expected to have low postbreeding survival and relatively high chances of offspring recruitment. This is in contrast to conclusions derived under stochastically variable environments (see the previous section), which are sensitive to the form of density dependence in vital rates (e.g. Benton and Grant 1999).

The three emerging predictions in deterministic environments are: (1) increasing adult mortality should result in more semelparity, and increased juvenile mortality should select for iteroparity and a perennial lifestyle; (2) assuming positive scaling of fecundity with reproductive effort, semelparity is favored if adult survival decreases faster than linearly with an increase in fecundity (Fig. 4.2); and (3) iteroparity is a more likely outcome if postbreeding survival decreases slower than linearly with an increase in fecundity (Fig. 4.2).

The Optimal Resource Allocation Perspective

The demographic approach described above focuses on the differences between adult and juvenile prospects, but it ignores the underlying life history trade-offs that mediate these differences. For instance, the risk of death is unavoidably related to the duration of the juvenile period. A shortened juvenile phase, a potential driver of semelparity, would increase survival to maturity (Young 1981) but would also generate life history costs. One such cost is reduced body size, as the juvenile period is typically dedicated to growth. Because body size determines fecundity (Hines 1982, Corey and Reid 1991), smaller size would lead to fewer offspring, and a shortened juvenile period would not necessarily mean selection for semelparity. Similarly, the trade-off between costs of juvenile growth and future fecundity deserves closer attention. Theory predicts that adult size, and therefore future fecundity, is affected because growing juveniles compromise between safety and foraging (Werner and Anholt 1993, Abrams et al. 1996). In the salt-marsh grass shrimp (*Palaemonetes pugio*) for instance, juveniles migrate to shallow parts of the intertidal zone. These aquatic microhabitats, reached during high tide, are relatively safe because predatory fish occupy deeper parts (Kneib 1987). Safe habitats for juveniles affect the evolution of body size and, in line with this, the abundance of fish predators correlates negatively with the size attained by grass shrimps (Bass et al. 2001). Again, the effect of increased juvenile survival, expected to promote semelparity, is balanced by decreased fecundity. Growth strategies for juveniles may not only affect fecundity but also adult survival because in many crustaceans the juvenile and adult mortality schedules are dependent on size. *Hyalella azteca*, a freshwater amphipod, widely distributed and with an iteroparous but annual life cycle, is one example. Low growth rate in these amphipods, caused for example by food deprivation, extends the juvenile period, reduces body size at maturity, and as above, reduces fecundity (Moore and Farrar 1996). But it also affects mortality rate, and in fishless ponds, in contrast to ponds with fish predators, juvenile mortality exceeds adult mortality rate (Wellborn 1994). Hence, fishless lakes are inhabited by larger species of *Hyalella* than lakes with fish (Wellborn and Broughton 2008). Similarly, predation was suggested to explain spatial variability in reproductive investment in the amphipod *Gammarus minus* (Glazier 1999). In general, all the above examples show that the costs of growth, growth rate, and relations between survival of juveniles and adults in many cases are interdependent and cannot be understood in isolation. Understanding the combination of these processes is very valuable when predicting whether selection would favor semelparity or iteroparity. Life history trade-offs provide a mechanistic link between adult and juvenile survival, reproductive effort, and consequences of life history traits such as body size, size and age at maturity, or rate of aging. In a modeling perspective, iteroparity versus semelparity should therefore emerge as a consequence of life history trade-offs rather than assumed demographic parameters.

Growth-Reproduction Trade-off

Several life history trade-offs influence lifetime reproductive effort and schedules of juvenile versus adult survival. These trade-offs include current reproduction versus adult survival, mortality related to external parasites versus mortality and energetic costs of molting, reproductive effort versus rate of ageing, and foraging rate versus mortality rate. Allocation of resources to growth at the expense of reproduction deserves special attention here as larger size means higher fecundity (Hines 1982, Corey and Reid 1991). This trade-off should also include allocation to storage because energy reserves and other stores could often be viewed as an investment in future reproduction, although typically at a shorter time scale than growth (Varpe 2017, Ejsmond et al. 2015). In tanner crabs (*Chionoecetes bairdi*), primiparous females (i.e., breeding for the first time) are less fecund than females of the same size that have reproduced before. This was attributed to the fact that primiparous females grow and allocate resources to maturing oocytes (Somerton and Meyers 1983). The growth-reproduction trade-off is a significant factor in the evolution of parity in crustaceans also because numerous members such as decapods or many amphipods have indeterminate growth (i.e., they continue to grow after maturation). Indeterminate growth affects future fecundity and is age-specific as older, and thus larger, animals produce more offspring (see, for example, studies of the littoral prawn *Palaemon adspersus*; Berglund and Rosenqvist 1986). This effect of indeterminate growth changes the expectations of the demographic approach because higher fecundity due to increased size is an additional factor selecting for iteroparity. On the contrary, some crustacean species have determinate growth with a terminal molt, which we expect to select for a shorter reproductive phase and therefore potentially semelparity, a topic discussed further below.

In theoretical life history work that explores allocation trade-offs, most studies assume semelparity (Cohen 1971, Perrin and Sibly 1993) or that allocation to reproduction does not affect postbreeding survival (Kozłowski and Wiegert 1987, Kozłowski and Teriokhin 1999). However, life history models for plants have examined the link between evolution of parity and allocation of resources to growth and reproduction (Iwasa and Cohen 1989, Klinkhamer et al. 1997). In plants, it is relatively easy to determine the trade-off between current reproduction and future survival; a species is semelparous if no storage is left after reproduction and regrowth of vegetative parts after a harsh (e.g., winter) period is impossible (Iwasa and Cohen 1989, Klinkhamer et al. 1997). These models predict that semelparous annuals are favored when the growth season is short, when chances of surviving to the next breeding season decreases, or when large parts of storage are lost (Iwasa and Cohen 1989). Semelparity also brings fitness gains when reproduction attracts herbivores that cause higher mortality risk for adults (Klinkhamer et al. 1997). These predictions could be of value also to animal studies, including work on crustaceans. Many empirical studies on survival costs induced by reproduction in crustaceans show that multiple mechanisms are typically involved (see Browne 1982, Winfield and Townsend 1983, Sarma et al. 2002).

Overhead Costs

In many organisms, significant portions of survival and energetic costs related to reproduction are relatively constant and do not scale with fecundity. These costs are sometimes called "overhead" costs of reproduction. Overhead costs in Crustacea include energetic expenses related to a prebreeding molt (if a certain molt is obligatory for breeding), costs of migration to the breeding grounds, and physiological changes necessary for the onset of egg or sperm production. One example could be the synthesis of pigments for claw coloration in male fiddler crabs (*Austruca mjoebergi*). Colored claws attract females (Detto 2007) but may also attract predators. Links between semelparity and high overhead costs of reproduction have recently been postulated by Bonnet (2011), who was inspired by work on ectothermic vertebrates and viviparous snakes such as Aspic vipers (*Vipera aspis*). In this species reproduction comes with substantial energetic costs and for the relatively rare cases of iteroparity, females need two years to restore body condition and breed again (Bonnet 2011). Breeding females suffer high predation risk related to pregnancy (because they need to bask in the sun and are slower in escaping predators) but also a high postbreeding mortality rate; females are exhausted and in poor condition after releasing offspring. In a verbal model, Bonnet (2011) concluded that semelparity evolved because reproducing females pay high overhead costs (independent of the number of offspring produced). However, it is important to note that demographic costs of reproduction (high postbreeding mortality) and energetic costs of reproduction may influence adult and juvenile vital rates differently, therefore affecting the degree of selection for semelparity. Semelparity as a consequence of high overhead costs is therefore only partly supported by theory. High postbreeding mortality related to the poor condition of females is expected to select for shortened life and even semelparity.

The overhead cost of high postbreeding mortality applies to many crustaceans with determinate growth and a terminal molt, such as the snow crab *Chionoecetes opilio* (Sainte-Marie et al. 1995). Determinate growth with a terminal molt is possibly a constraint in some taxa, but it may also be an adaptation that increases current reproduction at the expense of life expectancy. A terminal molt restricts the ability to repair damage or remove external parasites via molting. Consequently, postbreeding mortality would rise and semelparity would be selected for. The role of energetic overhead, in selection for semelparity does however not seem to have theoretical support. In an early study, Schaffer (1974b) showed that fecundity should increase in an accelerating fashion (e.g., exponentially), with increasing reproductive allocation (including overhead costs) for semelparity to be optimal. To our knowledge, there are no examples of crustaceans in which offspring recruitment increases faster than linearly with reproductive allocation. This could perhaps be the case in species in which juveniles in a batch create a structure protecting themselves from predators, as in some insects, such that the more offspring in the batch, the higher the chance that the predator will not be able to break through the hypothetical shelter. However, Schaffer (1974b) showed that energetic overhead costs play a minor role in the evolution of semelparity because these do not scale with fecundity.

In sum, from the perspective of optimal resource allocation to reproduction or survival, theory predicts that (1) high mortality related to breeding accompanied by high costs of reproduction leads to semelparity, but the nature of reproductive costs is crucial; (2) life history trade-offs that increase juvenile survival at the expense of adult postbreeding survival create a selection gradient toward semelparity; and (3) the higher the overhead costs of reproduction in terms of high postbreeding mortality related to breeding, the more semelparity is favored (a terminal molt is a sign of selection for shortened life or even semelparity).

REVISITING DEFINITIONS AND CONCEPTS: DICHOTOMY OR CONTINUUM, ANNUAL AND PERENNIAL

The terms *semelparity* and *iteroparity* are not always easily applied. Traditionally, they are viewed as a dichotomy—as two contrasting solutions. Semelparity in the strict sense is death following *one* reproductive episode (Fig. 4.3A). A common challenge, however, is to evaluate what *one* reproductive episode is. Less strictly semelparous are those species that produce consecutive clutches

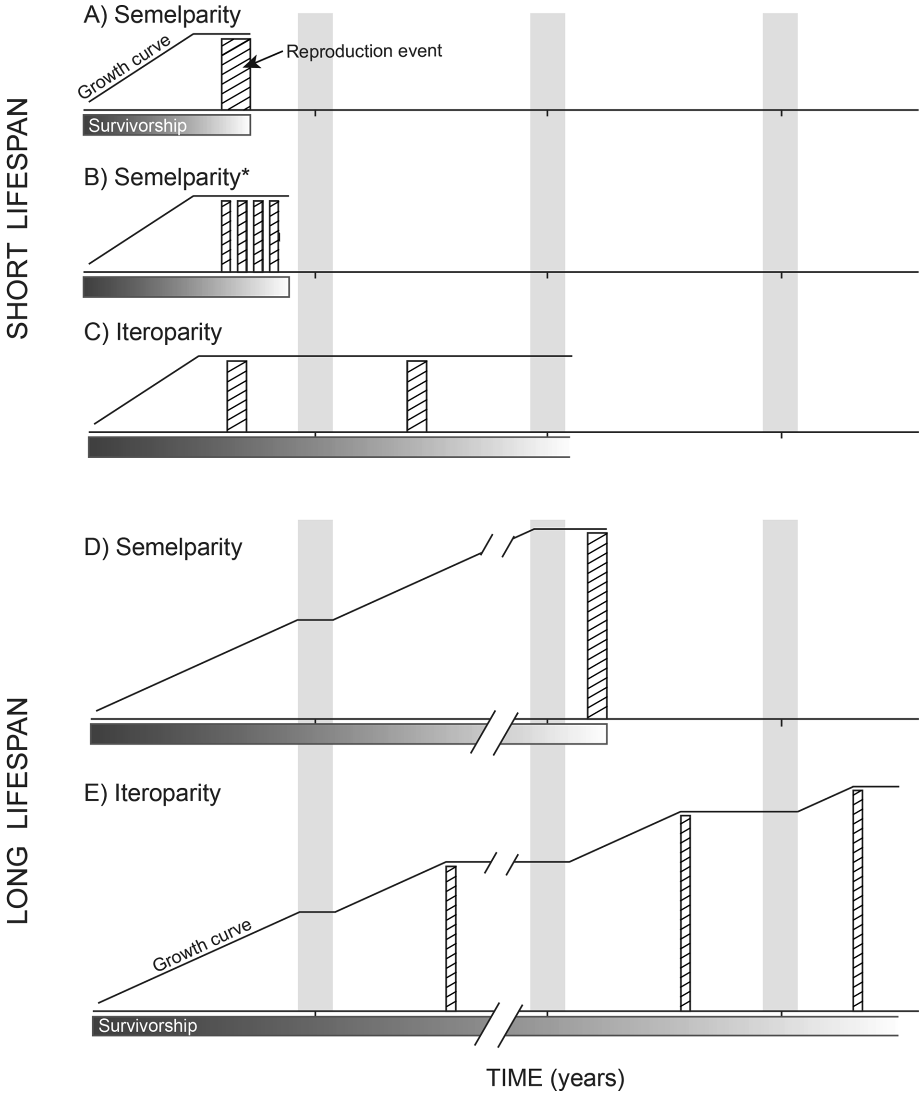

Fig. 4.3.

A schematic representation of life history variability and some of the forms that semelparity and iteroparity can take in an environment that to some degree is seasonal. The panels display a gradient in parity from (A) an annual and strictly semelparous strategy with immediate death following a big-bang reproductive event to (E) a long-lived iteroparous organism with indeterminate growth. (B) This represents the less clear situation where all reproduction falls within the same breeding season but is distributed in more or less separate clutches, which are here referred to as semelparity. Others have preferred terms such as "iteroparous annuals" for this lifestyle. (C) This represents iteroparity combined with a short life span. (D) This shows semelparity in species with a long life span but obviously short reproductive life span. The black line is a simplified and schematic growth profile. Hatched bars represent reproduction events. A nonfeeding season is conceptually marked with gray vertical bars (the duration of the nonfeeding period can differ in real cases). Survivorship is illustrated within the black- to gray-filled horizontal bar, kept closed to the right where death is certain and open where that is not the case. Time is assumed to represent years, although other timescales could be assumed.

of young over some time within the same breeding season, but still die afterward (Fig. 4.3B). Timescales, in particular reproducing during one year compared to multiple years, have sometimes been used as criteria for semelparity versus iteroparity, typically for work on mammals, birds, and plants (see Fritz et al. 1982 for discussion). In shorter-lived organisms this method works less well, and greater attention to how reproductive effort is distributed during the adult life span is needed, as is argued for insects (Fritz et al. 1982). This insect-based view would parallel cases seen in many crustaceans. Some have used "iteroparous annual" to describe the case of multiple sequential clutches within only one year or breeding season (e.g., Hairston and Bohonak 1998), whereas others have preferred to call this semelparity (e.g., Varpe 2012). In sum, timescales as described here are problematic and not a satisfying criterion for classification of semelparity and iteroparity. More fundamental properties are needed.

Begon et al. (1996) stressed that one should evaluate whether survival is prioritized or not between each reproductive event, and if it is indeed prioritized, one should consider it iteroparity. Recent and very interesting experimental work on plants suggests that there is variability within a semelparous strategy and that reproductive effort varies along a semelparous-iteroparous axis (Hughes and Simons 2014). Through experimental work modifying expected adult survival by manipulating expected season length, it was shown that this variability is generated by phenotypic plasticity (Hughes and Simons 2014).

Important insights on defining semelparity and iteroparity also come from theoretical models of optimal energy allocation in seasonal environments. In models that include capital breeding, it is optimal (i.e., brings the highest fitness gain) to allocate all stored energy within one day, which is physiologically impossible. Organisms are constrained with respect to the rate of transfer of resources from mother to eggs or offspring. If the rate of storage utilization is constrained, then the rate of reproduction per day decreases and the time necessary to utilize all reserves is much extended (Varpe et al. 2007, Varpe et al. 2009, Ejsmond et al. 2015). This allocation constraint gives resource acquisition and transfer from mother to offspring an important place in evaluating semelparity and iteroparity (see Houston et al. 2007). We would argue that if a female is not feeding between the clutches and dies afterward due to reproduction, it could belong in the semelparity category (or at least be closer to semelparity), compared to income breeders that feed again to build each new clutch (see also Capital Breeding and Seasonality section, below).

A continuum view is also evident in influential theoretical studies. For instance, in their work on the evolution of semelparity and iteroparity, Orzack and Tuljapurkar (1989) stated, "we regard this dichotomy as too simple and potentially misleading. Instead, we assume the temporal clumping and positioning of reproduction during life to be a continuous character." Extensive mapping of the reproduction and life history of gammaridean amphipods (Sainte-Marie 1991) also illustrated such a gradient. The copepod family Calanidae could be another case where semelparity (e.g., *Neocalanus* spp.; Miller et al. 1984) as well as perennial iteroparity (e.g., *Calanus hyperboreus*; Halvorsen 2015) are represented.

For strict semelparity, one may ask if death directly following reproduction is unavoidable. Semelparity is clearest when such a "programmed death" follows reproduction (Fig. 4.3A) and is caused by irreversible and dramatic changes in physiology as for instance in *Neocalanus* copepods (Miller 1984). Extreme cases include mothers that sacrifice themselves as a resource for their offspring, as in some semelparous *Schizidium* isopods in which offspring feed on the mother's body (Warburg and Cohen 1991). However, this type of semelparity can in some cases be "reversed" as in the desert spider (*Stegodyphus lineatus*) in which mothers separated from their offspring can produce a second clutch (Schneider and Lubin 1997). The desert spider example shows how a relatively simple behavioral decision about the timing of brood desertion is responsible for a species to be considered semelparous or iteroparous.

Death after reproduction is, however, more often an indirect effect due to heavy investment in reproduction and therefore less investment in maintenance, immune function, or predator avoidance. Death is in such cases less distinct. Reproductive investment would, for instance, drain resources that could be used to survive an inevitable and harsh period (e.g., the winter of seasonal environments). Thus, overwintering survival often trades off with reproduction. In this perspective, reproduction, instead of building up reserves, can be viewed as suicidal reproduction as offspring production decreases the chances to survive to the next reproductive event. But there are no clear-cut thresholds here, and therefore it seems more useful to consider semelparity and perennial iteroparity as endpoints of a continuum.

Furthermore, the extent that iteroparous organisms spread reproduction over independent breeding episodes can vary substantially (Fig. 4.3). Whereas semelparity covers a relatively narrow set of life histories, iteroparous strategies are diverse. Iteroparous crustaceans include short-lived species expected to breed for only two or three seasons (Fig. 4.3C), such as small isopods or large snow crabs, but also extremely long-lived species, such as the coconut crab (*Birgus latro*; Vogt 2012) that breed regularly for decades (Fig. 4.3D).

Reproductive Value

If we consider the evolution of parity with respect to demographic processes, fitness is closely linked to expected life duration and reproduction. If external mortality of adults is high, we would not observe long-lived iteroparous perennials. Life expectancy is a primary axis along which life histories are distributed (see Fig. 4.3 for this structure), but not a sufficient axis for a full understanding of the evolution of parity. We need to also consider reproductive value (Fisher 1930, Stearns 1992), a classic measure in evolutionary biology.

Reproductive value is the expected number of offspring an organism of a given age will produce throughout its remaining life. With respect to semelparity and iteroparity, it is also useful to refer to residual reproductive value (i.e., the reproductive value excluding the current reproductive event). In strictly semelparous species, the residual reproductive value at maturation is therefore extremely low. The duration of the juvenile phase can, however, vary considerably. Thus, we observe semelparity in short-lived as well as in long-lived species (Fig. 4.3A vs. Fig. 4.3D). If residual reproductive value decreases rapidly after reproduction (e.g., due to high postbreeding mortality), there would be strong selection to intensify early life reproductive allocation. Several mechanisms (reviewed above) can be responsible for a rapid decrease in residual reproductive value, and in turn evolution of semelparity. When using reproductive value as a fitness measure, we need to assume that the population is not in a long-term expansion or decline. In such cases, the reproductive success must be discounted according to trends in population numbers (Stearns 1992). Overall, considerations based on reproductive value are very useful starting points when attempting to position a given life history on the semelparity-iteroparity axis.

LIFE HISTORY TRADE-OFFS AND CORRELATES ON THE SEMELPARITY-ITEROPARITY AXIS

Can traits such as an exoskeleton or frequent molts preadapt crustaceans for either semelparity or iteroparity? Because of allocation trade-offs, life history theory predicts that certain combinations are more likely to occur than others (Stearns 1989, Roff 2002). We should ask if certain combinations of traits exist for crustaceans with semelparity and iteroparity as one of the focal traits. Here, we propose some candidate traits for such life history correlates, explain the logic behind them, and provide case studies of some crustacean groups as evidence. Questions related to these correlates could stimulate future studies.

Capital Breeding and Seasonality

Stores used for offspring production play a significant role in the life histories of crustaceans (Tessier and Goulden 1982, Varpe et al. 2009, Zeng et al. 2014). However, crustaceans are represented along the whole continuum from capital breeding to income breeding (Varpe et al. 2009, Griffen et al. 2012, Sainmont et al. 2014, Zeng et al. 2014). Capital breeders reproduce based on resources acquired in the past and stored until reproduction, whereas income breeders fuel reproduction with current acquisition. Semelparity often occurs in combination with capital breeding (Miller et al. 1984, Liu et al. 2011) as stored resources help maximize reproductive output when breeding takes place over a short time window (Tammaru and Haukioja 1996, Varpe et al. 2009). Pure capital breeders with lacking or impaired feeding appendages in adult stages, such as the copepod *Neocalanus* sp. (Miller et al. 1984; see Fig. 4.1A and Fig. 4.4) or females of the isopod *Paracerceis sculpta* (Shuster 1991; see Fig. 4.1B), are extreme examples of this case. There are several potential evolutionary drivers of capital breeding, with two deserving a closer look in relation to parity: the physical separation of feeding and breeding grounds (see Migration section, below), and seasonal variation in conditions that affect offspring prospects.

Seasonal variation in the environmental conditions that allow production of offspring is a fundamental constraint that affects breeding tactic and allocation strategy (McNamara and Houston 2008). Timing of reproduction affects reproductive value of released offspring, and this creates a life history dilemma for parents: when to grow, store, and reproduce over the season or year (Varpe 2017)? Capital

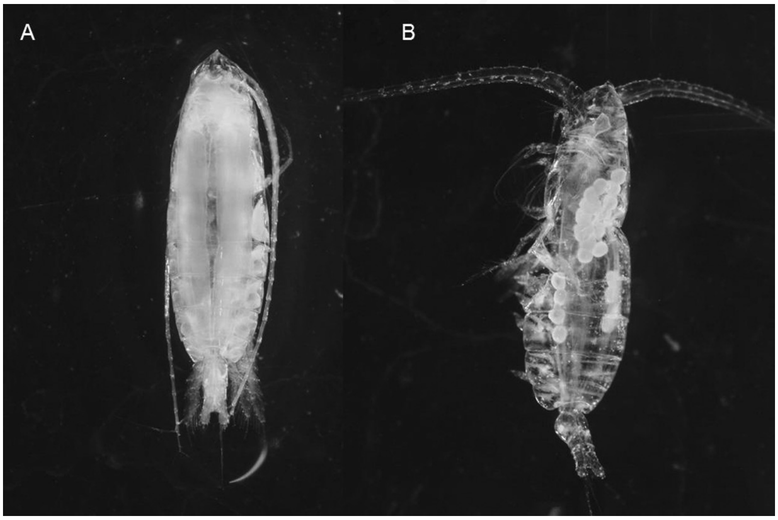

Fig. 4.4.
Two female individuals of the calanoid copepod *Neocalanus cristatus* in different reproductive stages. Individual (A) represents an early stage, full of energy reserves and with some of the early eggs seen. Individual (B) is almost fully spent, with only a few eggs left to be released, and little more than the exoskeleton remains (Miller et al. 1984). In this species, the mature female stage does not develop feeding appendages and is unable to feed. Egg production is therefore fully based on capital breeding through stores gathered near the surface the previous summer and brought to depth where the female later develops, releases eggs, and then dies. For a semelparous organism, it is adaptive to use all available resources for the single reproductive event, as illustrated by the spent stage in this copepod. In general, knowing that a given species cannot regain strength after reproduction (e.g., because of the inability to feed) represents strong evidence of semelparity. Photographs by Toru Kobari ©. See color version of this figure in the centerfold.

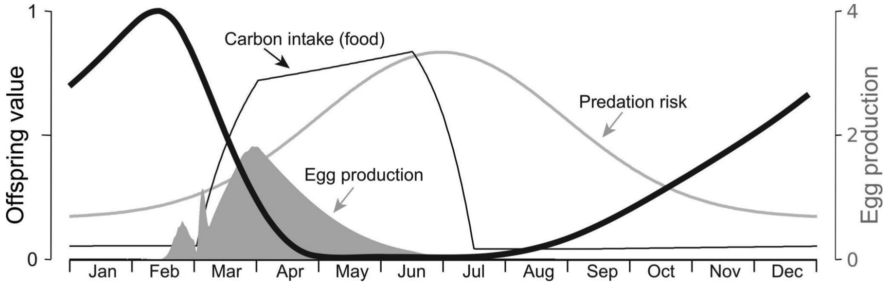

Fig. 4.5.
Semelparity and iteroparity have different consequences, for instance in seasonal environments where the windows of high offspring value are narrow, as illustrated by model predictions from a copepod life history model (Varpe et al. 2007, 2009). Seasonality in growth potential (thin black line) and predation risk (gray line) was assumed. The highly seasonal offspring value (thick black line) emerged, as possible in optimal annual routine models with fitness maximization by dynamic programming (McNamara and Houston, 2008). Note that peak offspring value is prior to the feeding season, selecting for some capital breeding. The population-level seasonality in egg production (filled gray area), as produced by individuals following the optimal state–dependent strategy, is mostly at times with intermediate and even low offspring value. These offspring are produced through income breeding. Because semelparity (only one breeding season per female) was assumed, egg production continued even if the late offspring had a very low probability to survive and contribute to future generations. If iteroparity had been allowed, it is more likely that the part of the feeding season with low offspring value would instead have been used for growth or storage, as preparation for future reproduction, as predicted by Ejsmond et al. (2015). For details on the copepod model and its outputs, see Varpe et al. (2007, 2009). Model predictions were originally for southern hemisphere seasonality, but are here shown for a northern hemisphere time axis.

breeding can be a response to seasonal environments because it allows high reproduction rate when prospects for offspring success are high (Varpe et al. 2009, Ejsmond et al. 2015), such as at times (or locations) when there is no food in the environment for income breeding. Calanoid copepods, which are abundant grazers in marine ecosystems, serve as an example. Capital breeding, based on energy reserves in well-defined lipid sacs (e.g. Vogedes et al. 2010), allows copepods to reproduce ahead of the phytoplankton bloom. This early reproduction allows offspring to exploit the phytoplankton growth in the same season (Niehoff et al. 2002, Daase et al. 2013). In a model by Varpe and colleagues (2007, 2009), with semelparity (or iteroparous annuals, sensu Hairston and Bohonak 1998) and deterministic environments assumed, some cases favored strategies that produced offspring in advance of the phytoplankton bloom, driven by a high fitness contribution by early-born young (Fig. 4.5). The model predicts that breeding (via capital breeding) should start when offspring prospects are maximal and continue (via income breeding) until death, even if the late produced offspring have a very low chance to survive and contribute to future generations (Varpe et al. 2007, 2009; Fig. 4.5). Instead, if iteroparity is assumed, we observe that mothers prioritize future survival late in the season by preparing for the next year (work in progress by the authors). In case of the copepods, this means rebuilding reserves preceding a long hibernation, instead of income breeding. We consequently believe that studies able to document breeding at times that are suboptimal from the offspring perspective would form valuable contributions to understanding evolution of semelparity in seasonal environments.

Migration

Spatially separated feeding and breeding grounds, and hence the associated breeding migrations, might select for semelparity and usually requires resources to be carried as stores (e.g., fat reserves) from the feeding to the breeding grounds (i.e., capital breeding). A famous crustacean example is the semelparous Japanese mitten crab (*Eriocheir japonica*) and Chinese mitten crab (*E. sinensis*), two closely related species (Tang et al. 2003). *Eriocheir japonica* and *E. sinensis* migrate from freshwater to the ocean to breed, and their egg production has a considerable capital breeding component (Wen et al. 2001, Dittel and Epifanio 2009). The catadromous lifestyle of the mitten crabs (Kobayashi and Matsuura 1995) resembles that of catadromous fish such as the European eel (*Anguilla anguilla*). Reproduction (which includes multiple broods) and migration in the mitten crab is exhaustive, and females die after one spawning season (Kobayashi and Matsuura 1995, Dittel and Epifanio 2009). We would refer to that as semelparity (Fig. 4.3B), but not in its strictest sense as multiple broods are possible. The first brood is usually the largest (Dittel and Epifanio 2009), and for the later broods there are indications of concurrent feeding (and therefore income breeding) because the hepatopancreas is not filled before egg production (Liu et al. 2011). Production of multiple broods may pay off better than a return migration and thus be optimal. These mitten crab examples show again that classification of a species into semelparous or iteroparous can be difficult and context dependent.

If a return migration to the feeding habitat is risky, then fitness may be maximized by semelparity (spawn and die) rather than preparations for another breeding in the future. In ornate rock lobsters (*Panulirus ornatus*), a large and commercially fished spiny lobster, juveniles travel about 500 km to spawn (MacFarlane and Moore 1986; Fig. 4.6), and a great majority of them die afterward. Mating and oviposition take place during the travel, a migration that typically starts in August. The breeding season is mostly from November to February. Up to three broods are produced, and there are several indications of high natural postspawning mortality (Moore and MacFarlane 1984, MacFarlane and Moore 1986). In sum, there is some support for evolution of crustaceans that combine long breeding migrations with semelparity (see Chapter 8 in this volume for a full chapter on migration in crustaceans).

Exoskeleton and Molting

An exoskeleton that is molted as the organism grows is one of the central and unifying characteristics of crustaceans and all arthropods. Some consequences of a molt are not related to an increase in body size but still have implications for semelparity and iteroparity. For instance, Tarling and Cuzin-Roudy (2008) have shown that frequent molts allow adult Antarctic krill (*Euphausia superba*) to remove ectoparasites. Molts are energetically costly and make individuals vulnerable, but in this case, they would potentially increase adult survival and reduce aging (mortality rate that increases with age, to which gradual accumulation of ectoparasites could contribute). These molts could then, independently of impacts on body size, select for iteroparity through increased survival. Other studies have found that under limited food conditions body size increments between molts are considerably reduced (Hartnoll 2001). This also suggests advantages of molts for future reproduction, beyond increased size and fecundity.

Many crustaceans are known for their ability to regenerate lost limbs (Savage and Sullivan 1978). In decapods, losing limbs mean decreased foraging ability or increased risk of being killed by a predator (reviewed in Juanes and Smith 1995) as well as loss of dominant status (Sekkelsten 1998). Consequently, molts that make regrowth of limbs possible (see Hopkins and Das 2015) increase survival and reproduction chances and thereby allow for iteroparity.

Many Decapoda, Ostracoda, and Copepoda do not grow after maturation and have a terminal molt (Hartnoll 1984). A terminal molt does not mean death, as for strict semelparity. Ectoparasite accumulation and poor regeneration is, however, expected to cause increased postbreeding mortality (Drouineau et al. 2013), which causes selection toward semelparity. The molt schedule in crustaceans is under endocrine control (Hartnoll 2001) and is consequently a potential proximate

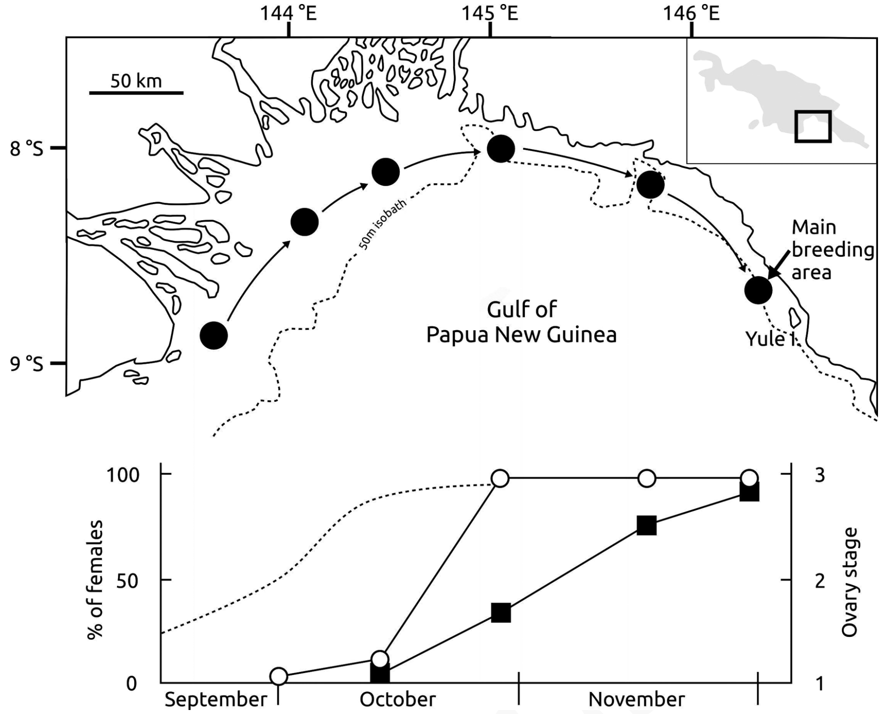

Fig. 4.6.
Annual breeding migration of the spiny lobster *Panulirus ornatus* in the Gulf of Papua (Papua New Guinea). Mating and oviposition takes place during the migration. Specimens of *P. ornatus* were collected at different sites (black dots in the map; locations are approximate), and the relationship between mating (circles) and oviposition (squares) was examined. The dotted line in the graph represents the mean stage of ovary development of females. During early September, about 50% of females had their ovaries developed to stage 2. Mating took place between mid to late October, and 80% had ovaries developed at stage 3 at that time. Oviposition occurred mostly during November. The breeding season mainly lasts from November to February, with up to three broods produced and large postspawning mortality in adults. There is variation between seasons and between different migratory waves of the same season (see MacFarlane and Moore 1986 for details). Modified from MacFarlane and Moore (1986), with permission from CSIRO Publishing.

mechanism for regulation of investment in future reproduction through growth (see Webster 2015 for a full chapter on the endocrinology of molting). From this perspective, the terminal molt, often seen as an internal developmental constraint, should perhaps rather be seen as an adaptation linked to favoring current reproduction over adult survival and growth.

Indeterminate Growth

Many crustaceans are indeterminate growers (i.e., species in which adults grow after maturation). The adaptive value of indeterminate growth is a central topic in life history theory (Heino and Kaitala 1999, Ejsmond et al. 2010) and much discussed in Crustacea (Hartnoll 2001, see also Chapter 2 in this volume).

Increased size translates to a range of ecological consequences, but the most general and important effect of a larger body is higher potential fecundity (Hines 1982, Corey and Reid 1991, Kiørboe and Sabatini 1995), with increased dominant status also being central in many cases (van der Meeren 1994, Duffy and Thiel 2007). To reach a large size, reproduction must be postponed. This is the classic evolutionary dilemma between benefits of investments in current versus future reproduction (Williams 1966). Investment in future reproduction through growth must be discounted by the chances that the organism dies before reproduction (Kozłowski 2006). Growth after maturation is therefore expected if organisms have relatively high chances of surviving to later reproductive events (Kozłowski and Teriokhin 1999, Ejsmond et al. 2010). Consequently, organisms with a short life span and a life history toward semelparity should not grow after reproduction but rather invest more in current reproductive efforts (e.g., Fig. 4.3B).

Importantly, growth after maturity is a strong sign of iteroparity. Gammaridean amphipods represent a full spectrum from semelparity to iteroparity (Sainte-Marie 1991). At the long-lived and iteroparous end, a good illustration is provided by the indeterminately growing *Eurythenes gryllus,* which matures at around 9 years of age and with an asymptotic size of about 14 cm and produces successive broods interspaced by molting and growth (Ingram and Hessler 1987). On the contrary, lack of growth after maturation cannot be used to conclude semelparity, as evident from the many iteroparous crustaceans that are determinate growers (e.g., the snow crab *Chionoecetes opilio* or the copepod *Calanus hyperboreus*).

Parental Care

Levels of parental care vary between and across crustacean taxa. For example, there are both egg-carrying and free-spawning copepods (Kiørboe and Sabatini 1994); there are long-lived decapods in which females carry the eggs for nearly a year, such as in the two commercially harvested lobsters *Homarus gammarus* and *H. americanus* (Phillips 2008); and there are crayfish where even the two first juvenile stages are carried by their mother (Vogt and Tolley 2004). Furthermore, broods are incubated in the marsupium by all (aquatic and terrestrial) amphipods (Sainte-Marie 1991, Thiel 1998). A link between parental care and semelparity has been suggested for insect species, where parental care has been predicted to be associated with reproduction that terminates life (Tallamy and Brown 1999). This link, however, has not been confirmed by comparative analyses. Only about 24% of the well-studied insect species with parental care were found to be semelparous (Trumbo 2013).

Parental care such as brood carrying can sometimes be viewed as an overhead cost of reproduction. For the evolution of semelparity, the nature of this cost is crucial. Importantly, it is not the brood carrying itself that triggers evolution of semelparity. With increasing parental care, juvenile survival increases and adult survival often decreases (Clutton-Brock 1991, Thiel 1999, Lewis and Loch-Mally 2010). Parental care therefore changes the relationship between adult and juvenile survival in a direction that favors a shorter adult phase with semelparity at the extreme. Semelparity is strongly selected for if chances for future reproduction (including mortality risk) are equal or lower than chances that a juvenile enters the adult phase (Charnov and Schaffer 1973). Even if various biological aspects might affect the threshold condition derived by Charnov and Schaffer (1973), semelparity will not be selected if survival of adults is orders of magnitude higher than juvenile survival. Therefore, intensive and long parental care can be expected to correlate with semelparity, but only for species with short life expectancy.

Semelparity is therefore relatively frequent in groups of short-lived crustaceans in which females care for the offspring by carrying embryos in the marsupium, a ventral brood pouch. In almost 200 species of gammaridean amphipods, a group with parental care (brood incubation in the marsupium), the great majority has short (< 2 years) life expectancy (see Appendix 1 in Sainte-Marie 1991) and almost 20% of the reviewed species were classified as semelparous (Sainte-Marie 1991). Even without control of the absolute measures of mortality in adults and juveniles, comparative studies show evidence consistent with this prediction. A clear example of extensive parental care and semelparity (suggested by death after one brood only) is the mud-dwelling amphipod *Casco bigelowi* (Thiel 1998). Within insects that care for offspring, semelparity was rare (12% of species) in species in which parental care is associated with creating structures that decrease mortality of juveniles but likely also adults (e.g., nests, burrows; Trumbo 2013). In contrast, for species that guard offspring in the open, semelparity was more common (45%; Trumbo 2013). What are the patterns for Crustacea? We are not aware of such an analysis, but observed variability in parental care provides a good starting point. Investigations should take into account the absolute differences between survival of adults and juveniles, and not only analyze the relative consequences of parental care.

Sex-Specific Strategies

Semelparity can be sex-specific, as observed and predicted for some fish species (Huse 1998). It is common that males display greater tendency toward semelparity than females. Crustacean examples of males, but not females, dying shortly after reproduction include some copepods (Miller et al. 1984, Boxshall et al. 1997) and amphipods such as *Monoporeia affinis* (Jacobson and Sundelin 2006). Loss of feeding appendages in males, but not females, is a clear sign of sex-specific semelparity, such as in the copepod *Euchaeta rimana* (Boxshall et al. 1997). Females may still be semelparous in the sense of breeding once or during one season, but live longer than males for reasons such as parental care (e.g., brood carrying in amphipods) or fertilization and egg production over some time using stored sperm (Titelman et al. 2007). In the copepod species *Eucalanus bungii*, there is evidence for true iteroparity in females, whereas males are semelparous and alive during a shorter time window than females (Miller et al. 1984). Similar observations exist for other calanoid copepods (Kosobokova 1999), as also discussed by Varpe (2012). In some species and breeding systems, however, it may be the females that are strictly semelparous and the males that breed for longer. An example is the alpha males of the isopod *Paracerceis sculpta* that mate with multiple females (where females reproduce only once) and also guard the females from other males (Fig. 4.1B; Shuster 1987). These alpha males can be active for a period corresponding to several female gestations (Shuster 1987).

For comparison, detailed studies on suicidal reproduction in mammals suggest that lethal effort of males is selected for under short and predictable conditions favorable for breeding, short and intensive period of mating, and intensive postcopulatory sexual selection (e.g., sperm competition; Fisher et al. 2013). We can predict that if the mating period is intensive and energetically costly, then males in particular are selected toward shorter life spans and semelparity.

Dormant Eggs and Seed Bank Implications

The theoretical studies on evolution of semelparity that we have reviewed previously assume (for simplicity) immediate recruitment of produced offspring. This is partly the reason that it is sometimes argued that annual reproduction (with nonoverlapping generations, and in many cases semelparous) is a strategy unable to persist over evolutionary time because any year with no offspring recruitment would lead to extinction. This argument is also used to explain why iteroparity is common. However, it ignores adaptations of many annual and semelparous organisms that make them resistant to year-to-year fluctuations in environmental conditions. A well-known example is annual plants with seeds produced during one season but germinating over several years (Cohen 1971). This "seed bank" strategy has also evolved among many annual or semelparous animals, including the resting egg solution of many crustaceans (Hairston 1996, Marcus 1996, Brendonck and de Meester 2003). The survival of resting eggs can be high, and emergence can take place over many years (Moritz 1987, Hairston et al. 1995, Hairston 1996). For instance, many freshwater cladocerans produce resting eggs that survive the winter and that form egg banks (Weider et al. 1997). Resting eggs are also the solution to other harsh periods, such as the dry stages of rock pools (e.g., in the fairy shrimp *Branchipodopsis wolfi*; Brendonck and Riddoch 2000). Resting eggs with differential emergence is a bet-hedging strategy similar to the way iteroparity is about "putting eggs in more than one basket." From a demographic point of view, the strategy of a univoltine (i.e., having one generation per year) crustacean (e.g., *Cyclops abyssorum* and *Leptodiaptomus minutus* in a high-latitude lake ecosystem; Antonsson 1992) dying at the end of the reproductive season is closer to an iteroparous perennial than a strictly annual and semelparous organism, because produced eggs recruit to the population over several years (cf. Orzack and Tuljapukar 1989; see Chapter 5 in this volume for a full discussion of voltinism). Another example is the "prolonged diapause" of larvae (i.e., diapause that in some individuals may last several years, as observed in several insect species; Menu and Debouzie 1993).

Egg bank strategies that allow recruitment to be prolonged for several years after reproduction show that recruitment does not have to follow the pulsed reproduction expected under semelparity. Several theoretical studies have investigated the adaptive value of prolonged diapause or seed banks (e.g. Cohen 1971, Menu et al. 2000). Interestingly, the model by Tachiki and Iwasa (2013) has suggested that prolonged diapause is an effect of coevolution with a fluctuating food resource. However, these models assumed either semelparity or iteroparity. For models on parity, however, it would be instructive if reproductive life span could emerge in parallel with the diapause and recruitment strategy. Little has been done to show when iteroparity (a bet-hedging strategy in fluctuating environments) can be outcompeted by semelparity with prolonged recruitment of juveniles.

THE EMPIRICAL CHALLENGE OF INFERRING SEMELPARITY AND ITEROPARITY

Several types of observations lead researchers to conclude that an organism is semelparous, but few are based on direct observations of adult mortality following a big-bang reproductive episode, as for instance in females of the isopod *Paracerceis sculpta* (Shuster 1991). Instead, several indirect methods are predominantly used when seeking evidence of semelparity versus iteroparity. Here we look into five categories of observations and discuss their strengths as well as potential pitfalls.

Oocytes

Among the strongest indirect evidence for iteroparity is the presence of small oocytes in spawning females or two generations of oocytes in gravid females. This criterion has, for instance, been applied in studies of shrimp (Lacoursiere-Roussel and Sainte-Marie 2009), similar to its use in determining if production of multiple clutches within the same breeding season is possible for squat lobsters (Dellatorre and Baron 2008). Kosobokova (1999) used gonad morphology to conclude that iteroparity is possible in the copepod *Calanus glacialis*.

Growth or Storage After Reproduction

Continuing growth or refilling reserves after a reproductive episode is strong additional evidence for investment in future reproduction and hence iteroparity. Growth can be viewed as a long-term investment in future reproduction and storage as preparation for future survival (such as diapause) or an upcoming breeding event (Varpe et al. 2009, Ejsmond et al. 2015). However, lack of growth after maturation does not necessarily equate to semelparity. Many iteroparous crustaceans are determinate growers. For copepods, sometimes thought of as semelparous, field studies have found some evidence of a switch from current reproduction to energy storage, which should be interpreted as a sign of iteroparity (Swalethorp et al. 2011). Interestingly, these signs of iteroparity were found in *Calanus hyperboreus* and *C. glacialis*, the most long-lived and capital breeding copepods, but not in the shorter-lived and income breeding *C. finmarchicus* (Swalethorp et al. 2011).

Rapid Drop in Adult Abundance

A rapid postreproductive decline in adult abundance is a clear sign of high postreproductive mortality, as long as migrations out of the study system can be excluded. It is reasonable to conclude semelparity in such cases. Examples include the leptostracan *Nebalia daytoni* (Vetter 1996), the observed massive male death shortly after mating in the amphipod *Monoporeia affinis* (Jacobson and Sundelin 2006), and investment in only one brood combined with male and female absence during parts of the year as in the amphipod *Casco bigelowi* (Thiel 1998; Fig. 4.7.). However, some degree of synchronized timing of breeding is needed for disappearance of a whole cohort to be a useful signal of semelparity. Such synchronization is typically pronounced in seasonal environments. Furthermore, iteroparity may for many species be physiologically possible and the strategy opted for, yet realized so rarely (because of high mortality) that semelparity is concluded. The possibility of iteroparity in the copepod *Calanus glacialis* (Kosobokova 1999) illustrates this point. It is stronger evidence of semelparity when rapid disappearance of adult individuals is accompanied with signs of programmed death following reproduction. *Schizidium* females that die during parturition provide such a contrasting example (Warburg and Cohen 1991).

Body Size and Abundance Data Combined

Size structure and analyses of cohorts are frequently used for evaluating basic life cycle features of crustaceans and have been used to suggest semelparity; examples include *Mysis mixta* (Richoux et al. 2004), *Onisimus litoralis* (Nygård et al. 2010), and *Uromunna naherba* (Esquete et al. 2014). The approach helps determine at which time of the year juveniles mature into adults and the time (age) needed to reach size of first reproduction. If adults continue to grow after first reproduction and form cohorts of different adult size, then iteroparity is the likely explanation. For instance, for *Onisimus litoralis*, for which Nygård et al. (2010) concluded semelparity, Węsławski et al. (2000) noted some particularly large females indicative of a second breeding season for a minority of the population. Similarly, Vetter (1996) concluded semelparity for *Nebalia daytoni* and iteroparity for *Nebalia hessleri*. However, if growth is deterministic, individuals may remain in the same size category and reproduce multiple times. That would be iteroparity (potentially combined with a terminal molt) but could be mistaken for semelparity, particularly if adult mortality is high and few would survive to their second breeding attempt.

Nonfeeding Adults

The absence of feeding appendages in the adult stage is a strong correlate of semelparity. It is then hardly possible (or beneficial) to prepare for a second breeding event. Crustacean examples include the copepods *Neocalanus* spp. (Miller et al. 1984, Fig. 4.4) and some sphaeromatid isopods (Harrison 1984, Shuster 1991). Interestingly, the lack of functional feeding appendages in adults is sparsely distributed among crustaceans when compared to insects where large taxonomic groups are characterized by no feeding in the adult stage. For instance, in mayflies (Ephemeroptera), adults do not feed and only live for hours or up to a few days (Brittain 1982), and similarly, a nonfeeding adult stage is common in several groups within Lepidoptera (Tammaru and Haukioja 1996).

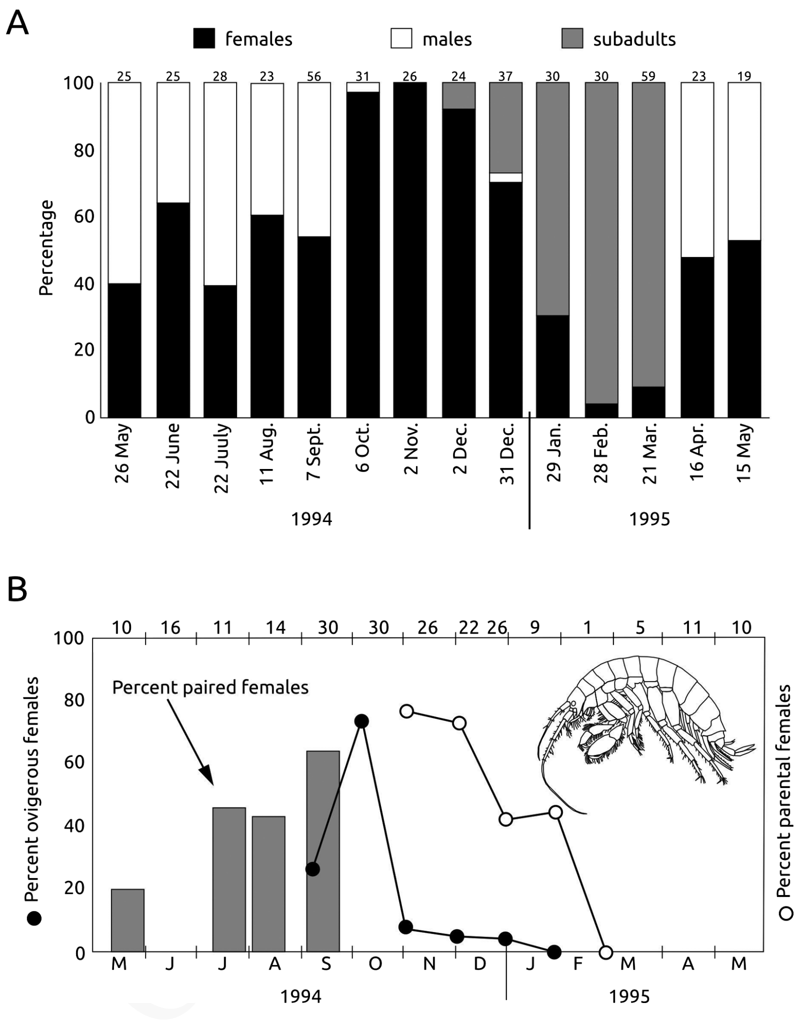

Fig. 4.7.
Inferring semelparity and iteroparity from empirical observations is often based on indirect evidence such as abundances and reproductive states of adults over time. The case of the deposit-feeding amphipod *Casco bigelowi*, studied by Thiel (1998), can illustrate this. Examination of (A) concurrent seasonal changes in relative abundance of females, males, and subadults (number of individuals collected on each sampling date is given on top of bars) and (B) reproductive status of females as seasonality of the percentage of paired females, ovigerous females, and parental females (number of adult females found on each sampling date is given on top of abscissa) shows that the proportion of females that are paired with males slowly builds up during the summer and the proportion of ovigerous females peaks, at the same time that males disappear from the population. Females care for offspring in their burrows for several months before they also disappear, probably dying. Consequently, subadults dominate the population during winter. These seasonal population dynamics illustrate that this species follows an annual life cycle, and in this case is also strictly semelparous, as it can be inferred from the population demographics that *C. bigelowi* produces only one brood during its lifetime (Thiel 1998). Other species in the same habitat, *Leptocheirus pinguis* and *Dyopedos monacanthus*, have multiple broods within the one breeding season (Thiel 1998). Modified from Thiel (1998), with permission from Springer. Inset of *C. bigelowi* modified from Bousfield (1973), with permission from NRC Research Press.

CONCLUSIONS AND FUTURE DIRECTIONS

Evolution of semelparity is directly related to the very central trade-off of current versus future reproduction (Williams 1966, Stearns 1992). Before asking where in the landscape of semelparity and iteroparity a species belongs, it is wise to first think about juvenile and adult reproductive value by mapping adaptations, behavior, and traits of a species on two life history axes: current versus future reproduction and juvenile versus adult survival. The theory of life history evolution, reviewed above, provides several hints and predictions regarding how the results of that mapping would relate to semelparity versus iteroparity, and the theory helps formulate ultimate explanations and project further evolutionary changes in reproductive life span.

In this chapter, we divided theoretical studies on evolution of semelparity into three groups: (1) bet-hedging in fluctuating environments, (2) age-specific birth and death rates in deterministic environments, and (3) fitness consequences of explicitly formulated life history trade-offs (optimal allocation of resources). Each provides important insights and suggests future directions for studies on evolution of semelparity. Models of fluctuating environments show that iteroparity is a bet-hedging strategy preventing complete recruitment failure in adverse years. However, semelparous crustaceans with resting eggs that recruit in several following years are also well adapted to fluctuating conditions. An important future direction would be to determine the critical conditions that select toward either iteroparous or semelparous reproduction with delayed recruitment. We would further argue that the demographic approach focused on deterministic environments, in which birth and death rates are assumed, should develop toward a more mechanistic approach, where birth and death rates emerge from life history trade-offs that are explicitly incorporated and linked to fitness. A very important future direction is to determine mechanisms underlying the trade-off between rate of reproduction and postbreeding survival in animals. Without this step, generalizations about the evolution of semelparity, similar to those invented for plant life histories, would be difficult to formulate.

Several ecological and evolutionary correlates discussed in this chapter generate interesting directions for future studies. For instance, signs of growth or renewing of storage after reproduction is a clear sign of iteroparity. Determinate growth, on the other hand, could be optimal also in long-lived perennial iteroparous species, and there is no reason to assume that determinate growth is a sign of semelparity. In both theoretical and empirical scientific literature, relatively little attention is given to the evolutionary connection between capital breeding and semelparous versus iteroparous reproduction. Whereas semelparity in a majority of cases should be combined with capital breeding, many perennial iteroparous species in Crustacea and other taxa are capital breeders. We see this variability as a fruitful direction for further investigation. Also, from the perspective of optimal resource allocation, we see a great potential in investigations of the adaptive value of the terminal molt in Crustacea. The terminal molt is routinely seen as a constraining factor and its adaptive value should be investigated more often. Finally, and inspired by recent work on plant reproduction (Hughes and Simons 2014), we would recommend greater attention to within-species variability in semelparity and iteroparity, particularly toward the semelparity end of the continuum where phenotypic plasticity would be expected to cause observed variability in reproductive life span.

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