Chapter 6
Reproduction in Euphausiacea

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6.1 Introduction

In the group Euphausiacea, females either retain mature eggs in a brood pouch until they hatch, or release the eggs directly into the water column. All the species currently being commercially harvested, however, are broadcast spawners (Nicol & Endo, 1997). The focus of our discussion of the reproduction patterns and strategies of euphausiids is on those species that are of commercial interest, e.g. *Thysanoessa inermis, T. raschii, Meganyctiphanes norvegica, Euphausia pacifica, E. nana* and *E. superba*. However, we assume that certain reproductive characteristics are common to the entire taxonomic group. Our understanding of the reproductive cycle will be enhanced by including studies of non-harvested species, e.g. *E. lucens, Nyctiphanes australis, N. couchii* and four additional Antarctic species, *E. crystallorophias, T. macrura, E. frigida* and *E. triacantha*.

The emphasis in this chapter is on reproductive patterns and population fecundity in euphausiids. Both are critical to our understanding of the pattern and level of fishing effort a population can withstand over the long term. Reproductive patterns include topics such as age and size at first spawning, initiation and duration of the spawning season, and the distribution of spawning populations. Oöcyte maturation and the use of sexual development stages to identify seasonal patterns of ovarian development are emphasised. We address also the topics of multiple spawning, batch size, and embryo size. The implications of these reproductive characteristics and strategies for fisheries management are briefly discussed.

6.2 Reproductive cycle

The patterns of reproduction in euphausiids show trends with latitude in timing and duration of the spawning season. However, the exceptions yield clues about the environmental conditions that support successful reproduction.

Patterns of reproduction – age and size at first spawning

Euphausiids are relatively long-lived crustaceans, with life-spans that range from slightly more than a year to seven years (Table 6.1). Smaller species and populations

Table 6.1 Reproductive patterns in euphausiids. Size and age at maturity, maximum size and lifespan, type of reproductive season (continuous, intermittent, limited), number of months spawn during year, number of years an individual spawns; dur, duration; pk, peak.

Species	Mat size (mm)	1st Spawn (yr)	Max size (mm)	Lifespan (yr)	Reproductive season	Months spawning	Years spawning
E. crystallorophias	21	2+	33	4–5	limited	1	3–4
E. lucens	11	0.5	~18	1–1.2	continuous	8–10	1
E. nana	–	–	12	<1	–	–	–
E. pacifica	12	1+ 0.5	25	<1.5 to >2	limited or intermittent	1.5–2	1
E. superba	33 or 35	2+ or 3+	65	5–7	limited, usually no pk	1–3	3–6
M. norvegica	25	1+	40	2.5	limited (long dur or 2 pks)	variable	⩾2
N. australis	11	0.75–0.8	21	~1	continuous, occ regression	8–10	1
T. inermis	22	F 2+ M 1+	30	2+	limited	1–3	1
T. raschii	–	1	25	2+	limited, 2 pks poss	1–2	2

Sources of information listed by species. E. c.: Harrington & Ikeda (1986); Siegel (1987). E. l: Pillar & Stuart (1988). E. n.: Nicol & Endo (1997). E. p.: Brinton (1976); Ross *et al.*, 1982; Nicol & Endo (1997). E. s.: Cuzin-Roudy (1987); Siegel (1987); Siegel & Loeb (1994); Nicol & Endo (1997). M. n: Nicol & Endo (1997). N. a.: Hosie & Ritz (1983); Nicol & Endo (1997). T.i.: Nicol & Endo (1997). T. r.: Nicol & Endo (1997).

of a species living in lower latitudes, e.g. *N. australis* and *E. pacifica*, tend to have life-spans between 1 and 1.5 years, whereas larger species and those in subarctic regions live to about 2.5 years, e.g. *M. norvegica*, *Thysanöessa* spp. The two largest polar euphausiids, *E. crystallorophias* and *E. superba*, have life-spans of over 4 years. Euphausiids usually reach maturity when they measure about half of their maximum total length, and have reached 30 to 60% of their life-span (Table 6.1). In several species of euphausiids, female maturity may be delayed beyond the point of 60% of the life-span. In *T. inermis* near Iceland, females mature at two years of age, towards the end of their life-span, and a small percentage survive to breed in a second reproductive season (Einarsson, 1945; Astthorsson, 1990). Siegel & Loeb (1994) suggested that Antarctic krill, *E. superba*, shows 'knife edge' maturity, i.e. reaches maturity within a single age group. However, the high percentage of immature females of this species in size classes > 40 mm in some summers suggests that under some conditions reproduction may be postponed until the fourth summer (Shaw, 1997).

Life-span and the age of first reproduction are not always the same for male and female euphausiids. When there is a difference, males have a shorter life-span. In the case of *E. pacifica* off Japan, females live 2+ to 3 years, whereas males live less than 2 years (Nicol & Endo, 1997). A similar difference appears to hold for *E. crystallorophias* in the Indian sector. Males live for 3+ years compared to the females' 4+ years (Pakhomov & Perissinotto, 1996). Although the life-spans are different, the growth rates and age of first reproduction (2+) of male and female *E. crystallorophias* are the same (Siegel, 1987). The implication for both species is that males participate in one less reproductive season than females. In other species males and females mature at different ages. Male *T. inermis* near Iceland, for example, mature a year before the females, when they are one year old not two (Astthorsson, 1990; Einarsson, 1945). However, *T. raschii* males and females from the same area mature at the same age (Astthorsson, 1990).

A common assumption is that the energy costs of spermatophore production are insignificant, and that female euphausiids expend more energy during the reproductive season than males. However, there are several lines of evidence that this assumption does not hold for *E. superba* (Virtue *et al.*, 1996), and thus may not hold for other species. For *E. superba*, large mature males had higher mortality rates than females, and lower total lipid and triacylglycerol stores. In addition, the sex ratio decreased with increasing size, with the percentage of males decreasing sharply in the size range 51–55 mm. Either the growth rates of males and females are significantly different, or mortality rates are different. In either case, the cost of reproduction is one possible explanation for the differences observed. Little is known about differences in male versus female growth or mortality rates for other species, although Pillar & Stuart (1988) suggested that the retarded growth rates in male *E. lucens* may be due to the allocation of energy to spermatophore production throughout most of the year.

Reproductive patterns

Patterns of reproduction in euphausiids can be classified as continuous, intermittent or limited (Table 6.1). With continuous reproduction there is no regression to a spent stage once maturity is reached, although the intensity of spawning is higher during some parts of the year. Continuous reproduction is primarily confined to species inhabiting the mid-latitudes and equatorial regions. *E. lucens* is characterised as a continuous spawner, with spawning most intense in late winter and early spring, just prior to upwelling and bloom (Pillar & Stuart, 1988). In a few species, reproduction is intermittent, with a cycle of maturation and regression more than once in one season, resulting in multiple cohorts (generations) per year. Intermittent reproduction was confirmed in *N. australis*, a species which produces three cohorts per year (Ritz & Hosie, 1982), and *E. pacifica* in some regions (Brinton, 1976). Intermittent reproduction was inferred in two other species in the north-east Atlantic which produce more than one generation per year, e.g. *N. couchii*, three to four per year (Lindley, 1982), and *T. longicaudata*, two per year (Lindley, 1978).

Limited reproduction means that there is a limited spawning season, with a cycle of ovarian maturation and regression once a year. Egg production is limited to a 1.5 to 3 month season, alternating with a longer period of gonadal rest. Several peaks in egg production can occur within this limited season, sometimes separated by periods of weeks; such a pattern could lead to multiple cohorts in a single year class. Limited reproduction is usually found in polar and subpolar species, e.g. the Antarctic euphausiids, *Thysanoessa* spp., *M. norvegica* (Table 6.1). However, the pattern of reproduction in a species is flexible. The reproductive season is limited over most of the range of *E. pacifica*, a temperate and subarctic species, but intermittent in the upwelling regions off Southern California (Brinton, 1976) and in some parts of Puget Sound, Washington (Ross *et al.*, 1982).

Timing and duration of spawning

From the early review of Mauchline & Fisher (1969), the timing and duration of spawning were known to vary, both between populations of the same species living in regions at similar latitudes, and among species at the same latitude (Fig. 6.1 and Fig. 6.2). As a general rule, earlier and longer spawning occurs at lower latitudes. These observations led to the hypothesis that timing and duration of spawning are keyed to the period of elevated food production, i.e. earlier in the year and longer at lower latitudes. In addition, spawning has been observed to coincide with the spring bloom, e.g. *T. inermis* and *T. longicaudata* in the Barents Sea (Dalpadado & Skjoldal, 1996), or times of high phytoplankton concentrations, e.g. *E. pacifica* in areas of intermittent reproduction (Nicol & Endo, 1997).

The premise underlying the hypothesised link between food production and spawning is that food must be available at the right time and in the right amounts to satisfy the energetic demands of reproduction. Initiation of ovarian development
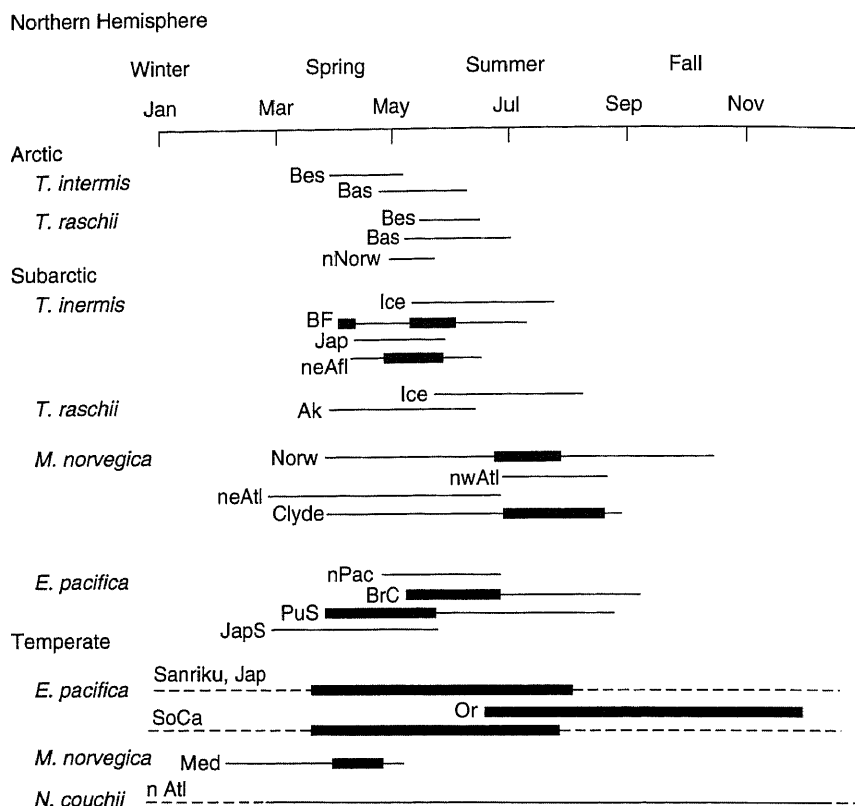
Northern Hemisphere

| Winter | Spring | | Summer | Fall | |
| Jan | Mar | May | Jul | Sep | Nov |

Arctic
  T. intermis   Bes ———
                         Bas ———
  T. raschii   Bes ———
                       Bas ———
                     nNorw ——
Subarctic
  T. inermis   Ice ———
                   BF ■———■———
                   Jap ———
                   neAfl ■———
  T. raschii   Ice ———
                   Ak ———

  M. norvegica   Norw ——————■———
                             nwAtl ———
                neAtl —————————
                   Clyde—————■———

  E. pacifica   nPac ———
                       BrC ■———
                   PuS ■———
                   JapS ———
Temperate
  E. pacifica   Sanriku, Jap ———■———————
                   SoCa ———■——— Or ■———————
  M. norvegica   Med ———■———
  N. couchii   n Atl ————————————

Fig. 6.1 Initiation, duration and intensity of spawning season for euphausiid species in different regions in the Northern Hemisphere. BeS, Bering Sea; BaS, Barents Sea; nNorw, northern Norwegian fjords; Ice, Icelandic fjords; BF, Bay of Fundy, Canada; Jap, Japan; ne- or nw, northeast or northwest: Atl, Atlantic Ocean; Ak, Auke Bay, Alaska; Clyde, Firth of Clyde, Scotland; nPac, north Pacific Ocean; BrC, British Columbia; PuS, Puget Sound, Washington; JapS, Japan Sea; Or, Oregon coast; SoCa, southern California coast; Med, Mediterranean Sea. Sources of information listed by species. T.i.: Kulka & Corey (1978); Hanamura *et al.* (1989); Astthorsson (1990); Einarsson (1945); Smith (1991); Nicol & Endo (1997). T.r.: Falk-Petersen & Hopkins (1981); Astthorsson (1990); Paul *et al.* (1990); Einarsson (1945); Timofeyev (1994); Smith (1991); Nicol & Endo (1997). M.n.: Lindley (1982); Boysen & Buchholz (1984); Nicol & Endo (1997); Cuzin-Roudy (1993); Cuzin-Roudy & Buchholz (1999). E.p.: Ponomareva (1966); Smiles & Pearcy (1971); Brinton (1976); Heath (1977); Ross *et al.* (1982); Bollens *et al.* (1992); Iguchi *et al.* (1993); Nicol & Endo (1997). N.c.: Lindley (1982).

may be keyed to a seasonal cue such as photoperiod, but actual spawning (release of eggs) will depend on the rate of ova maturation, and thus the rate of energy input prior to spawning. In some species energy is stored from the previous season for ovarian development, in others ovarian development is dependent on immediate food supplies. If reproduction is iteroparous (Section Population fecundity), the rate of production and number of subsequent batches of eggs is likely to depend on both energy input prior to spawning, and on food availability during the spawning season.
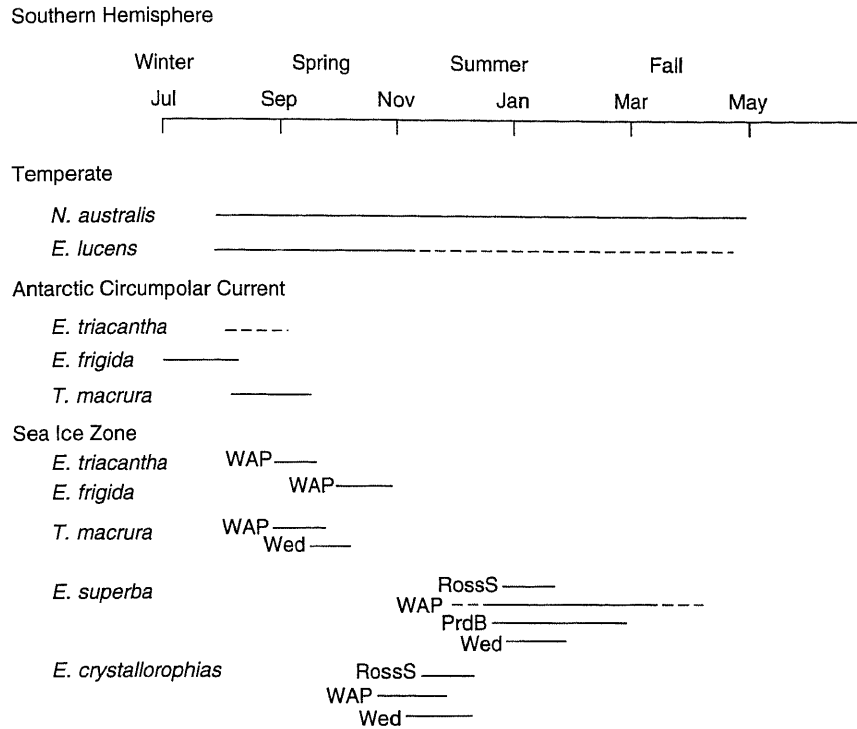
Fig. 6.2 Initiation, duration and intensity of spawning season for euphausiid species in different regions in the Southern Hemisphere. Wed, Weddell gyre; WAP, western Antarctic Peninsula; RossS, Ross Sea; PrdB, Prydz Bay and Lasarev Sea. Sources of information listed by species. N. a.: Blackburn (1980); Ritz & Hosie (1982). E. l.: Pillar & Stuart (1988); Stuart & Pillar (1988). E. t.: Baker (1959). E. f.: Makarov (1977); Siegel (1986); Makarov *et al.* (1990); Men'shenina (1992). T. m.: Stepnik (1982); Makarov *et al.* (1990); Men'shenina (1988, 1992); Makarov & Men'shenina (1992). E. s.: Makarov *et al.* (1985, 1990, 1991); Hosie & Cochran (1994); Makarov & Men'shenina (1992); Ross & Quetin (1983); Quetin *et al.* (1994). E. c.: Fevolden (1980); Makarov *et al.* (1990, 1991); Brinton & Townsend (1991); Makarov & Men'shenina (1992); Harrington & Thomas (1987).

The sequence of spawning for Antarctic euphausiids illustrates the latitudinal trend. In general, production cycles in the northern areas start earlier, and finish later, than further south (Hart, 1942; Foxton, 1956). Matching this cycle, oceanic species at lower latitudes reproduce in the early spring, whereas the shelf and coastal species at higher latitudes spawn one to two months later (Fig. 6.2). The exception is the coastal species, *E. crystallorophias*, which reproduces before *E. superba* (Fig. 6.2). Also, at higher latitudes where the period of elevated production is longer, spawning seasons are longer, e.g. west of the Antarctic Peninsula compared to the Ross Sea, and the Scotia Sea compared to the Lasarev Sea. Spiridonov (1995) confirmed this pattern for *E. superba* in a study of reproduction with data from both the Weddell Sea and waters west of the Antarctic Peninsula. He identified five habitats based on the timing of initiation, duration and intensity of

spawning. In the northern most habitat, at the fringe of the extent of seasonal sea-ice, spawning was early (late November–early December), and tended to be long (3–3.5 month) but variable in duration. In contrast, in coastal areas at higher latitudes, spawning began later and was of shorter duration (~ 1.5 month).

Understanding this link between food production and spawning allows us to reconcile what appear to be conflicting views of the influence of seasonal sea-ice dynamics on the spawning season of *E. superba* (Spiridonov, 1995; Siegel & Loeb, 1995; Makarov & Men'shenina, 1992). For Antarctic krill living at the tip of the Antarctic Peninsula, Siegel & Loeb (1995) found that low sea-ice extent in winter and/or early sea-ice retreat led to a delay in spawning. In contrast, Spiridonov (1995) concluded that low sea-ice extent resulted in early spawning, and a slow (late) retreat resulted in a delayed spawning season that was not intensive. In coastal waters in the Weddell Sea, when polynas open early in the spring, i.e. simulating an early retreat, reproduction starts earlier than in waters to the north which are still covered with ice. Makarov & Men'shenina (1992) called this phenomenon the polyna or 'oasis' effect, and it can reverse the normal north–south gradient in timing of reproduction for both *E. superba* and *T. macrura*.

Can we reconcile these disparate views of the influence of seasonal sea-ice on the timing and intensity of spawning of Antarctic krill? The retreat of sea-ice impacts food availability in spring because the melting sea-ice conditions the water column for ice edge blooms. Without this conditioning, phytoplankton blooms are delayed until late spring or early summer. Since Antarctic krill do not come into reproductive condition under the ice (Cuzin-Roudy & Labat, 1992), the extent and timing of these ice edge blooms will play an important role in the rate of ovarian development and thus the timing of spawning. Sea-ice extent represents the areal extent of conditioning and thus enhanced food availability in spring; the timing of retreat represents when conditioning occurs and thus the timing of the blooms. The timing of sea-ice retreat is region-specific, that is, 'early' retreat for northern regions is likely to be earlier in the spring than in southern regions. 'Early' in one region may lead to blooms prior to the peak demand for food for ovarian development, whereas in another region 'early' retreat may create ideal conditions. In the Elephant Island area (Siegel & Loeb, 1995), at the northern edge of the influence of seasonal sea-ice, if sea-ice in winter is low little of the region will be conditioned for an ice edge bloom, and the area of enhanced food availability will be small. With an early retreat, bloom conditions may occur prior to the time of maximum need for food for ovarian development. Thus low winter sea-ice extent and/or early retreat mean lower food availability in the spring, and these environmental conditions will be associated with slow ovarian maturation, and delayed spawning. However, when polynas open early in the spring in the higher latitude coastal waters of the Weddell sea, ice edge blooms create a source of food at a time of prime need. Polynas allow the cycle of food production to start earlier in the spring at higher latitudes than in the ice-covered seas at lower latitudes; food is available for ovarian maturation, and thus spawning can start earlier. The reverse will be found with a 'late' retreat. The

two viewpoints can be reconciled by assuming that sea-ice mediates the areal extent and timing of spring food for ovarian development.

The Antarctic species are not the only euphausiids to show inter-annual and geographical variability in reproduction within a species, even among locations that differ only in food availability and not in either temperature or photoperiod. The reproductive season for the Northern krill, *M. norvegica*, begins in the spring in all areas but the north-west Atlantic off Canada where the influence of the cold Laborador Current delays the onset of net primary production, and spawning does not begin until summer (Lindley, 1982). For the smaller *E. pacifica*, the population in Puget Sound begins to spawn in the spring, continuing through summer in some areas of Puget Sound but not others (Ross *et al.*, 1982; Bollens *et al.*, 1992). However, *E. pacifica* off the coast of Oregon does not spawn until late summer and early fall (Smiles & Pearcy, 1971) (Fig. 6.1). Peaks in chlorophyll a occur in April and May in Puget Sound, but off Oregon appear later in the year and are associated with the summer upwelling regime. A link between the phytoplankton bloom and the length and intensity of spawning has also been suggested as the source of the inter-annual differences in the duration of the period of high egg concentrations of *T. raschii* in Auke Bay, Alaska (Paul *et al.*, 1990).

Spawning is not usually synchronous among species where their ranges overlap. In the arctic and subarctic North Atlantic, *T. inermis* spawns earlier than *T. raschii*, which in turn spawns earlier than *M. norvegica* when that species is present (Astthorsson, 1990). Such differences may reflect the extent to which reproduction depends on that season's primary production, whether directly or indirectly, versus stored reserves from the previous season. Omnivores or carnivores may show an indirect dependence on primary production through food web links. If the populations of prey increase in response to seasonal phytoplankton blooms, food availability for the omnivores and carnivores is indirectly dependent on periods of primary productivity. In some species, initiation of ovarian maturation may be keyed so spawning occurs before the spring bloom or period of upwelling. With this strategy, stored reserves provide the energy to initiate reproduction, and seasonal production benefits the larvae. If reproduction is in response to the spring bloom or period of upwelling, the implication is that stored reserves are not adequate to fuel reproduction. The degree of inter-annual variability in the initiation of the spawning season is thus apt to vary with the degree of reliance on stored reserves versus that season's food production. In a recent comparison of the lipid biochemistry of the six most abundant species of Arctic and Antarctic euphausiids, Falk-Petersen *et al.* (August 1999) found that neutral lipid deposits are primarily accumulated for reproduction. Four species, *T. inermis*, *T. longicaudata*, *T. macrura* and *E. crystallorophias*, depend primarily on lipid reserves for spring reproduction. *T. raschii* and *E. superba* rely on food availability in the spring for final gonad maturation. *E. superba* is the single Antarctic euphausiid with a reproduction season in summer, and a recent study (Shaw, 1997) suggests that the initiation and duration of the spawning season is dependent on both spring and summer food sources.

Mating and spawning

In euphausiids, males tend to mature several months earlier in the season than females. For example, in the northern Baltic, immature male *M. norvegica* are distinguishable in October whereas immature females cannot be distinguished until January; the males also have fully developed spermatophores at nine months (Boysen & Buchholz, 1984). Mating behaviour begins up to 1–2 months prior to spawning and continues throughout the spawning season (Table 6.2). Thus transfer of the spermatophore occurs a considerable time before spawning, and one cannot assume that the presence of spermatophores on a female indicates that the female is gravid. Euphausiids lose the sperm mass held in the thelycum when they moult. Since euphausiids moult on a time-scale of weeks throughout their lives, mating must continue throughout the reproductive season to ensure that eggs are fertilised. Males with mature spermatophores in the ejaculatory ducts are found throughout the spawning season (Bargmann, 1937; Boysen & Buchholz, 1984; Astthorsson, 1990).

Table 6.2 Relative timing of mating behaviour and initiation of spawning.

Species	Mating begin	Spawning begin	Reference
E. superba	Nov	late Dec	Bargmann (1945)
M. norvegica	Jan	Apr–Oct	Falk-Petersen & Hopkins (1981) Boysen & Buchholz (1984)
T. inermis	late Feb	mid–late Apr	Hanamura *et al.* (1989)
T. inermis	Feb	Apr	Astthorsson (1990)
T. raschii	Apr	May	

Mating behaviour has been observed in *E. superba* in the ice edge zone in December (Naito *et al.*, 1986). Bargmann (1937) described the exchange of spermatophores in *E. superba*. A sequence of chase and contact behaviour between male and female *E. superba* believed to be part of mating behaviour has also been observed in large aquaria in the laboratory (Fig. 6.3) (Ross *et al.*, 1987). Durations of chases were about 5 sec, and the contact or close times 10–30 sec. In the tanks males appeared to perceive a chemical trail within 8–10 cm of the female, and turn in pursuit.

Surface aggregations have often been described as facilitating mating behaviour (Ritz, 1994). These aggregations tend to occur in the late winter or early spring, prior to reproduction. In five species, mature breeding individuals predominated in daytime surface aggregations (Table 6.3). The aggregations thus contain mature euphausiids in the close proximity necessary to initiate a pursuit sequence at a time in the cycle when finding a mate is critical. The sex ratios in these surface swarms were sometimes (Nemoto *et al.*, 1981, *E. superba*; Nicol, 1984, *M. norvegica*), but not
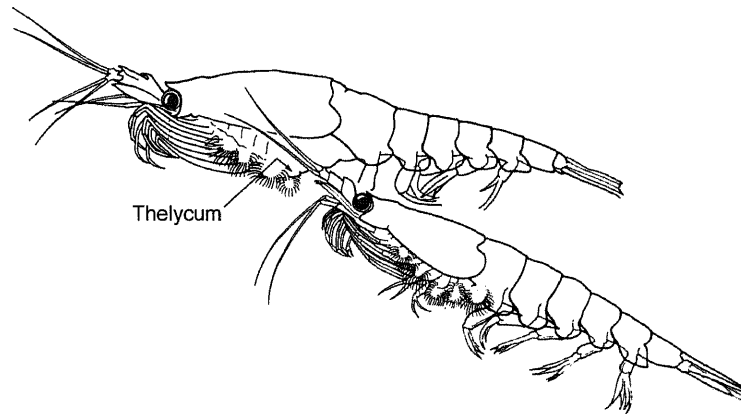
Fig. 6.3 Relative positions of the male (on the bottom) and female adult *Euphausia superba* during the chase and contact sequence of mating behaviours.

Table 6.3 Observations of daytime surface aggregations dominated by mature individuals. See Fig. 6.1 for the key.

Species	Months, or Location	Dom sex or Size	Reference
E. pacifica	Mar–Apr, Japan nw	female >14 mm	Endo (1984) Odate (1991) cited in Nicol & Endo (1997)
	May–June, nPac		Kotori (1995)
E. superba	Dec in ice zone	mating	Naito *et al.* (1986) Nicol *et al.* (1987) O'Brien (1988)
M. norvegica		female	Nicol (1984)
T. spinifera		–	Smith & Adams (1988)
T. inermis	Feb–Apr	female	Hanamura *et al.* (1989)
T. raschii	Barents Sea	female	Timoteyev (1994)

always extreme (O'Brien, 1988, *N. australis*). In another study of aggregation characteristics in *E. superba*, population composition was often skewed, with mature males and gravid females dominating some aggregations, and immature individuals dominating others (Watkins *et al.*, 1992). However, there was a positive correlation between the presence of mature males and mature females with developing ovaries (Watkins *et al.*, 1992). Such an association would be necessary for the continuing transfer of spermatophores to females throughout the reproductive season. There also appears to be spatial segregation on small scales. Off Japan, male and female *E. pacifica* may separate after mating. Males dominate the surface swarms during the day, with females at depths below 15 m (Nicol & Endo,

1997). Sex ratios in catches of *M. norvegica* also vary (Hollingshead & Corey, 1974), with surface and deep aggregrations showing different population structures that suggest that mated and ready-to-spawn females separate from the rest of the population (Nicol, 1984; Cuzin-Roudy & Buchholz, 1999).

Although information is scarce, the distribution of spawning populations of euphausiids does not appear to be homogeneous. The concept of spatial and geographical succession in Antarctic krill developmental stages has been described by several authors (Makarov & Sysoyeva, 1985; Siegel *et al.*, 1990; Lascara *et al.*, 1999). Gravid female *E. superba* are generally found in the vicinity of the continental slope (Siegel, 1992), and in waters overlying Circum-Polar Deep Water (CDW) (Hofmann *et al.*, 1992). Release of eggs over CDW is thought to be part of a reproductive strategy to enhance survival of the larvae. During the season, as the females progressively mature, their distribution changes. Less advanced stages of female *E. superba* are found on the inner shelf (Shaw, 1997) or closer to the ice edge (Cuzin-Roudy & Labat, 1992; Quetin *et al.*, 1992). Females in vitellogenesis and spawning are first found in open waters. Spawning in several other species appears to be spatially restricted. Spawning zones for *T. macrura* are found in the Antarctic Convergence, and the Secondary Frontal Zone (Men'shenina, 1988). There is a single spawning centre for *T. inermis* in the waters south of Spitzbergen, with eggs and larvae transported elsewhere (Timofeyev, 1994). And lastly, the percentage of gravid female *E. lucens* increases offshore (Pillar & Stuart, 1988). Thus, in these four cases, spawning is not randomly distributed within the species' range. The advantages to this heterogeneity are not apparent for all species, but the patterns are clear. Such distributions may enhance retention of larvae in favourable regions as has been found for fishes or enhance hatching success or reduce predation on the vulnerable early life history stages.

The concept of 'pseudopopulations' or non-breeding populations should also be mentioned in the context of the distribution of maturity stages of euphausiids. Although most species breed throughout their range of occurrence, there are exceptions. *T. inermis*, for example, does not breed north of 65–70°N (Nicol & Endo, 1997), thus the population of *T. inermis* in the southern Barents Sea (Zelikman *et al.*, 1980) is believed to be non-reproducing. There is also some debate over whether populations of *E. superba* around South Georgia are non-reproducing. Although abundances can be high, the lack of eggs and young larvae in these regions is cited as evidence for populations that are not successfully reproducing.

Ovarian maturation cycle

Ovarian development and maturation occurs over a period of several months prior to spawning. In *T. inermis*, ovaries mature over the three month period between mid-January and mid-April, prior to spawning in the spring. Ovarian development in *T. raschii* in the north-east Pacific (Zelikman, 1958), *M. norvegica* in the north-east Atlantic (Zelikman, 1958), and *E. superba* in the Antarctic (Bargmann, 1945)

also takes about three months. Maturation of testes in males generally is more rapid, about 1 month in *T. inermis* (Kulka & Corey, 1978) and 2+ months in *M. norvegica* (Mauchline, 1968; Hollingshead & Corey, 1974).

General progression

The details of ovarian maturation help us to understand where environmental variability is most likely to impact rates of ovarian maturation. Ovarian maturation in crustaceans is characterised by a progression in ova development that is found in all species (Nelson, 1991). First, during oogenesis the oögonia (og) multiply in the germinal zones (GZ) of the ovary. When the oögonia leave the germinal zone, they are characterised as primary or young oöcytes (yoc). The yocs represent multiple batches of eggs in the sense that groups of eggs will develop in sequence, not simultaneously. At this point the female may enter a resting phase. Upon leaving the resting phase, groups of yoc accumulate glycoproteic yolk synthesised within the oöcyte in a process called primary or pre-vitellogenesis. At this point the ovary is increasing in size and mating may occur, but the female euphausiid is not swollen. Mating has occurred when either the thelycum is full or spermatophores are attached. The growing type 1 oöcytes (oc1) may accumulate at a second plateau before they enter vitellogenesis. During vitellogenesis, or lipidic yolk accumulation in type 2 (oc2) and type 3 (oc3) oöcytes, the oöcytes rapidly enlarge, increasing the cytoplasm to nucleus ratio. The source of the lipidic yolk is outside the oöcyte, likely the 'fat body' (Cuzin-Roudy & Buchholz, 1999). Final egg maturation occurs after vitellogenesis is complete, the nucleus moves to the periphery and loses its membrane, and meiosis occurs in the type 4 oöcyte (oc4). Another plateau can occur at this point. Ovulation, fertilisation and release of the embryos are the final steps.

The plateaus are assumed to occur at points during ovarian maturation when additional resources or environmental cues such as photoperiod are needed for further development. The cue for the second plateau is suggested to be a threshold accumulation of 'lipid' in the 'fat body', enough to complete the development of one group of oöcytes. Evidence for the existence of a 'fat body' in euphausiids is emerging for two species, *E. superba* and *M. norvegica* (Cuzin-Roudy & Buchholz, 1999).

Maturity keys based on physiological state

As oöcytes move through the succession of physiological steps of ovarian maturation as described above, they show characteristic morphological (Fig. 6.4) and biochemical changes. Keys for stages of female sexual development for two euphausiids, *E. superba* (Table 6.4, Cuzin-Roudy & Amsler, 1991) and *M. norvegica* (Cuzin-Roudy, 1993) have been developed based on both external secondary sex characteristics and the types of oöcytes in the ovary as characterised with the 'squash' technique. External secondary sex characteristics include the development
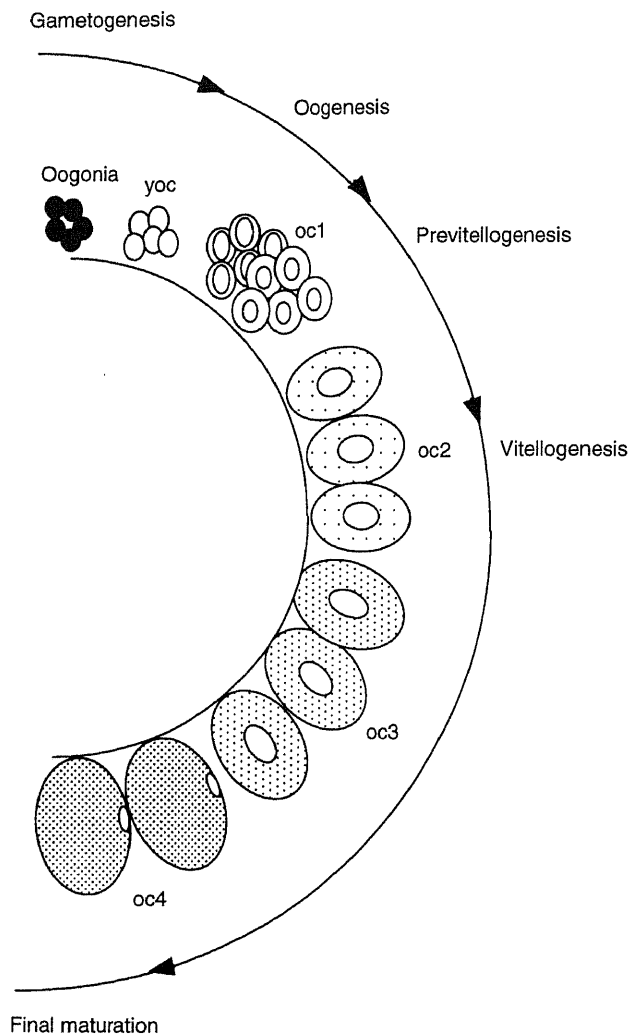
Fig. 6.4 Relative size of oöcytes and nucleus/cytoplasm ratio in the cycle from gametogenesis to final maturation. yoc, young oöcytes or primary oöcytes; oc1, stage 1 oöcytes; oc2, stage 2 oöcytes; oc3, stage 3 oöcytes; oc4, stage 4 oöcytes. Nucleus is clear. Cytoplasm becomes increasingly speckled as lipidic yolk accumulation proceeds.

of the thelycum, the size of the ovary as seen through the carapace, and the degree of swelling of the thorax. During gametogenesis the thelycum is not yet present, and the ovary is composed of germinal zones and oögonia, small non-descript cells. During oogenesis the thelycum is immature, and although the ovary is still small, some of the oögonia have transformed into the slightly larger yoc. During pre-vitellogenesis the thelycum is completely developed. The ovary grows considerably during this phase, but the thorax is not swollen. The oöcytes (oc1) accumulate

Table 6.4   Definitions of sexual development stages (SDS) for female *Euphausia superba* (Cuzin-Roudy & Amsler, 1991).

SDS	Dev phase	Thelycum	Ovary and oöcytes
1	Gametogenesis	Absent	Ovary small. Germinal zone (GZ) and primary and secondary oögonia (og 1, og 2)
2	Oogenesis	Present, sternal and coxal plates not fully grown	Ovary small. Og 2 developed into yoc
3	Previtellogenesis	Mature thelycum	Thorax not swollen. Oc1 up to 200 μm
4	Previtellogenesis	Mature thelycum, may be red. May be mated	Thorax not swollen. Developing ovary visible. Oc1 up to 450 μm
5	Vitellogenesis	Mature thelycum, red. Mated	Ovary obvious. Oc2 present
6	Vitellogenesis	Mature thelycum, red. Mated	Thorax conspicuously swollen. Ovary full of oc3; may have various combinations of GZ, oc1, oc2 and oc3
7	Oöcyte maturation	Mature thelycum, red. Mated	Ovary in live krill opaque or bluish, full of oc4; may have various combinations of GZ, oc1, oc2, and oc4
8	Oviposition	Mature thelycum, red	Thorax swollen, but ovary reduced in size and lobes contracted. May have various combinations of GZ, oc1, oc2 and residual oc4 (continuing) or only GZ and residual oc4 (final or post spawn)
9	Ovarian reorganization	Mature thelycum, red	Thorax not swollen. Ovarian lobes irregular and lumpy, contain GZ with og1, og2 and yoc, plus residual oc4
10	Ovarian reorganization	Thelycum regressing to more juvenile form	Thorax not swollen. Ovarian lobes irregular and lumpy, contain GZ with og1, og2 and yoc, possibly residual oc4

glycoproteic yolk, and are translucent with a nucleus/cyctoplasm ratio of about 60%. Mating occurs during previtellogenesis, and a sperm mass often fills the thelycum. During vitellogenesis, the oöcyte grows, and the accumulation of lipidic yolk gives the cytoplasm in the oöcyte a cloudy or grainy appearance (oc2s and oc3s). Opaque oöcytes overlapping the size of oc1s but with a cloudy appearance are oc2s; larger oöcytes with a lower nucleus/cytoplasm ratio and a more granular appearance are

oc3s. The nucleus is large and distinct in both oc2s and oc3s. Externally the ovary is now conspicuous, and the thorax swollen. Ovaries with mature oöcytes (oc4) appear opaque or even bluish gray, e.g. *E. crystallorophias* (Harrington & Thomas, 1987), *E. pacifica* (Ross *et al.*, 1982), *E. superba* (Ross & Quetin, 1983), and *M. norvegica* (Cuzin-Roudy & Buchholz, 1999). Oc4s have completed vitellogenesis, lack a large central nucleus, and meiotic figures can be seen under high magnification. The small nucleus without a membrane is in the peripheral cytoplasm (Fig. 6.4). After the mature oöcytes (oc4s) are released, the thorax remains swollen, and the female is considered post-spawn. However, the female may not have completed the reproductive season. In both *E. superba* (stage 8_c = 8 continuing) and *M. norvegica* (stage 5_1) the presence of oöcytes in earlier stages indicates that another group or batch of oöcytes will mature and another spawning will occur that season. When the ovary in a post-spawn female contains only the germinal zone and oogonia, the reproductive season is complete for that individual, and she enters a period of reorganisation and reproductive rest.

The sexual development stages (SDS) for *E. superba* (Table 6.4) have been slightly simplified for use with *M. norvegica* (Cuzin-Roudy, 1993). For *M. norvegica*, no stage is defined for gametogenesis, and there is only one stage each for previtellogenesis and vitellogenesis. The distinction between post-spawn females that will recycle and those that have completed egg production for that season is retained (see comparison in Table 6.5). Similar keys could be used for other species, since all euphausiids move through the same stages during ovarian maturation.

Table 6.5 Sexual development stages of euphausiids and the relationship to known physiological phases of ovarian development.

Physiological phases of ovarian development	*Euphausia superba* (Cuzin-Roudy & Amsler, 1991)	*Meganyctiphanes norvegica* (Cuzin-Roudy, 1993)
Immature or resting	2 and 10	1
Oogenesis		
ONSET		
Oöcyte development		
• previtellogenesis; mating activity	3 and 4	2
• vitellogenesis	5 and 6	3
Oöcyte maturation and egg release		
• ready to spawn	7	4
• post-spawn, may recycle	8_c and 8_f	5_1 and 5_2
END		
Spent females, ovary in regression	9	6

Unlike earlier keys, these two keys distinguish physiological stages of ovarian development, not just external secondary sex characteristics. The difference allows for more detailed analysis of the reproductive cycle. For example, the key of Makarov & Denys (1980), commonly used for *E. superba*, does not distinguish between females in previtellogenesis and those undergoing ovarian reorganisation, i.e. females at the beginning and end of their reproductive cycle. Nor do they separate females in late vitellogenesis from females in the final stages of egg maturation. Finally the Makarov & Denys key does not distinguish females continuing to produce eggs after a spawn from those at the end of their reproductive season.

Analysis of sexual development stages in the populations of *E. superba* west of the Antarctic Peninsula and *M. norvegica* in the Ligurian Sea in the Mediterranean has led to an understanding of the timing and duration of the different stages of ovarian maturation (Fig. 6.5). The pattern of ovarian development in the two species is basically similar. In both species previtellogenesis occurs in the whole ovary prior to the start of the reproductive season, January to late February in *M. norvegica*, and for a longer period from September through November in *E. superba*. Vitellogenesis in both species is cyclical, with successive batches of oöcytes brought to maturity and released throughout the reproductive cycle in the spring for *M. norvegica* or summer for *E. superba*. The energy source appears to be different during the two phases of yolk accumulation. In *E. superba*, previtellogenesis cannot continue without an outside source of energy because this species does not store enough lipid for this process. In both species, the fat body in previtellogenic krill becomes progressively better developed (Cuzin-Roudy, 1993). Since vitellogenesis and egg maturation continue even with poor food, the 'fat body' may be a source of lipid during this time and reduce dependence on immediately available food during vitellogenesis. The limited period of egg production alternates with a longer period of gonadal rest.

However, there are some differences between the two species. In *M. norvegica*, the ovary continually produces new yoc throughout the season, and oöcyte development is progressive; this strategy leads to rapid successive cycles of small batches of embryos. In *E. superba*, production of yoc is not constant. The yoc at the start of ovarian maturation mature in successive batches, with the possibility of four different stages of oöcytes (mature, vitellogenic, previtellogenic, and yoc) simultaneously in the ovary. The strategy is one of pulses of oöcyte production in spawning episodes with large batches of eggs at the individual level. At the population level, both strategies lead to more even egg production over a 2 to 4 month period. This dispersal of eggs and larvae in time and space will enhance survival of the young in variable environments. A similar cycle was inferred for *T. inermis* in the Bay of Fundy from descriptions of oöcyte types and combinations in the ovary throughout the season (Kulka & Corey, 1978). We suspect that this general pattern is common to all euphausiids, but additional studies of the sexual development stages of other species will be necessary.
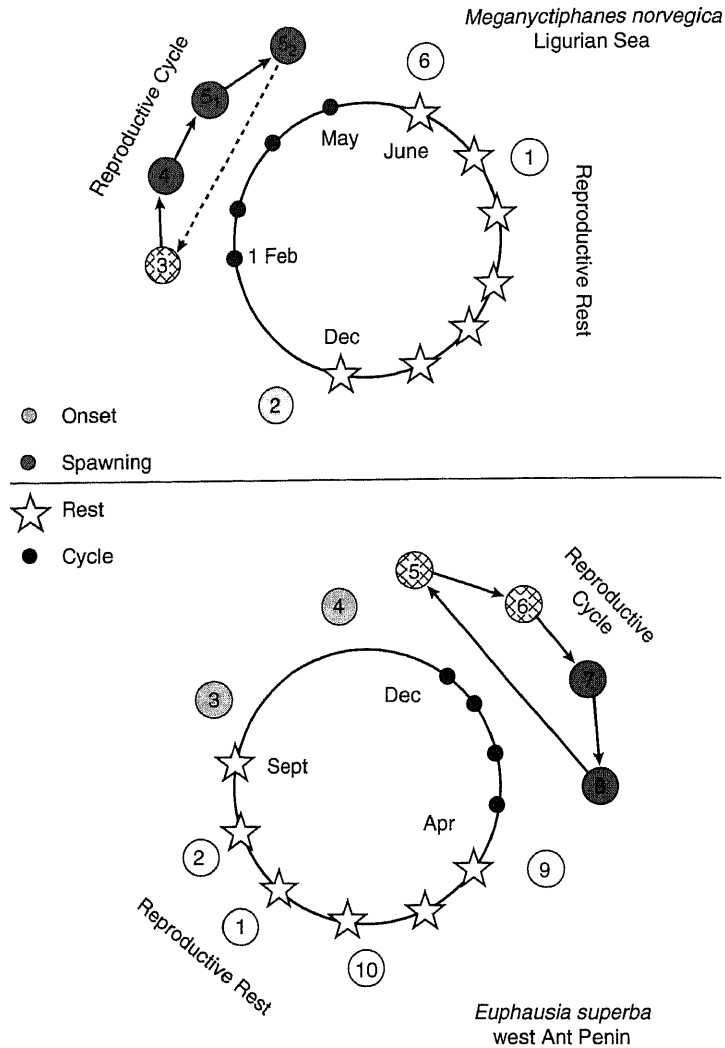
Fig. 6.5 Alternation of reproductive cycle (black circles) and resting phases (pale grey stars) throughout the year for (a) the Northern krill, *Meganyctiphanes norvegica*, in the Ligurian Sea of the Mediterranean, redrawn from Cuzin-Roudy & Buchholz (1999); and (b) the Antarctic krill, *Euphausia superba*, from samples west of the Antarctic Peninsula (data of Quetin & Ross). Numbers in circles refer to sexual development stages as described in Tables 6.4 and 6.5. Onset means onset of ovarian maturation or previtellogenesis. Spawning is period when eggs are released. The arrows indicate stages involved in ovarian cycling.

Population fecundity

Population fecundity, i.e. total rate of egg production of the population in a region, and early larval survivorship are the two main factors affecting recruitment in a region. Population fecundity in euphausiids is a product of female abundance, the percentage of females reproducing that season, the number of spawning episodes, and the number of eggs per spawning episode. The number of spawning episodes is a function of the duration of the spawning season and how often the ovary recycles during that period, i.e. the length of time between spawning episodes.

Percentage population reproducing

The assumption has been that all females, once they are the size of a mature individual, will reproduce during that reproductive season, i.e. Siegel & Loeb (1994) for *E. superba*. An examination of the sexual development stages present in the population is a test of that assumption. If all females larger than the size at maturity (Table 6.1) are in late previtellogenesis, vitellogenesis or maturation during the reproductive season, then the entire population is reproducing. However, if a percentage of the population is in a resting stage, then not all females will reproduce that season. The assumption has been verified for *M. norvegica* in the Ligurian Sea (Cuzin-Roudy & Buchholz, 1999), but refuted for *E. superba* west of the Antarctic Peninsula (Shaw, 1997). In the case of *E. superba*, the percentage of the population reproducing varies from less than 20% to nearly 100%. The percentage is the proportion of females in the reproductive cycle or having just completed the reproductive cycle of the total population of subadult and adult females in January. Thus for *E. superba* the number of seasons that an individual reproduces is an important variable. For a species that is long-lived, and which can reproduce for several seasons, the strategy of delayed reproduction or putting energy into growth instead of reproduction for a season can potentially enhance the total number of offspring produced. However, most euphausiid species only reproduce during one year (Table 6.1), with a small percentage surviving to reproduce over a second season, so this phenomenon is probably rare.

Individual fecundity

Based on the results of spawning frequency experiments with *E. pacifica* in Puget Sound, Ross *et al.* (1982) first proposed multiple spawning episodes in an individual euphausiid. Subsequently, studies of ovarian cell structure and development, and experiments with live female euphausiids of many species have established that multiple spawning episodes or batches of eggs are common in euphausiids (Table 6.6). Multiple spawning episodes in a single season theoretically increases the probability of reproductive success in a fluctuating environment.

Table 6.6 Euphausiid species with multiple broods in a reproductive season, confirmed or inferred from experiments or histological examination of the ovary or for *N. couchii* inferred from number of cohorts per year.

Species	Expt	Histology	Reference
E. crystallorophias	X		Harrington & Thomas (1987)
E. hanseni	X	X	Stuart & Nicol (1986); Stuart (1992)
E. lucens	X	X	Stuart & Nicol (1986)
E. pacifica	X		Ross *et al.* (1982)
E. superba	X	X	Ross & Quetin (1983); Cuzin-Roudy (1987)
M. norvegica	X	X	Cuzin-Roudy (1993); Cuzin-Roudy & Buchholz (1999)
N. australis	X	X	Hosie & Ritz (1983)
N. capensis		X	Stuart & Nicol (1986)
N. couchii		infer	Lindley (1982)
T. inermis		X	Kulka & Corey (1978)

The number of spawning episodes per female is a function of the duration of the spawning season and the interbrood period, itself a function of the rate of oöcyte development. For those species for which we have estimates, the interbrood period ranges from a few days to 30 days (Table 6.7). Because of its dependence on oöcyte development rate, the interbrood period (number of spawning episodes) is likely to be a function of food availability, and thus will vary inter-annually and geographically. For *E. superba*, the interbrood period varies with location and year (Quetin *et al.*, 1994), with a minimum of 6 days and a maximum of 50 days in mid-summer. With data on the duration of the spawning season, and estimates of interbrood periods from spawning frequency experiments, estimates of the number of spawning episodes per season for a reproducing *E. superba* range from 3 to 9 per season (Table 6.7). Observations of individual spawning females held in the laboratory for more than several days must be qualified with the possibility that spawning frequency is impacted by the nutritional conditions in the laboratory. However, these observations do suggest that individuals and populations may not show the same patterns. For *E. superba* (Harrington & Ikeda, 1986; Nicol, 1989), not all females produced second or third batches of embryos. Also the interval between broods was often shorter than predicted from the spawning frequency of a group of females (6–12 days, Harrington & Ikeda, 1986). In *M. norvegica* (Cuzin-Roudy & Buchholz, 1999), spawning events in individuals were only separated by 1–2 days, but spawning was confined to a restricted part of the moult cycle, which would increase estimates of population interbrood periods. In a detailed study of the relationship between spawning and moulting cycles, Cuzin-Roudy & Buchholz (1999) showed that *M. norvegica* released a complete batch of eggs (one vitellogenic

Table 6.7 Size of egg and individual fecundity estimates for euphausiid species: number of spawning episodes (SPE) per season, interbatch period, average number of eggs per female per SPE or ovarian eggs (OvEggs, E.s.) or vitellogenic cycle (M.n.), range in number of eggs per SPE or equation relating number of eggs (either per SPE or OvEggs) and total length (TL). I = intermittent range, L = limited range for E. p.

Species	Size egg μm	No. SPE per season	InterBat period	Av no. egg per fem per SPE	Range no. egg per SPE
E. crystalloophias	673, 650		6–10 d	187	
E. lucens	728	3–10 per life vs 135 per life	– 2 d	17–138 14–28 d^{-1} fem^{-1}	No = 0.00064TL$^{4.25}$ 2–80
E. pacifica	580, 460	I: 2–6 L: 11–30	2–10 d	<16 mm, 60; >19 mm 132	12–296 No = 39.07 + 7.87 DWT
E. superba	600 (555–630) 556–803 3 sites [560–590]	if repro, 3–9	5–33 d	1309 1417 2809 1372 45 mm–2469; 50 mm–3588 45 mm–2900 OvEggs '82 45 mm–1700 OvEggs '78	1140–1688 627–3115 89–6167 263–3662 500–8000 OvEggs = −15770 + 415.1 (TL) '82 OvEggs = −7224 + 198.5 (TL) '78
M. norvegica	722, 740	2 to 4 vit cycle	2–3/IMP	650 per vit cycle	3 loc: 513, 681, 735
N. australis*	378–405	8–10 per life	30 d		49–193

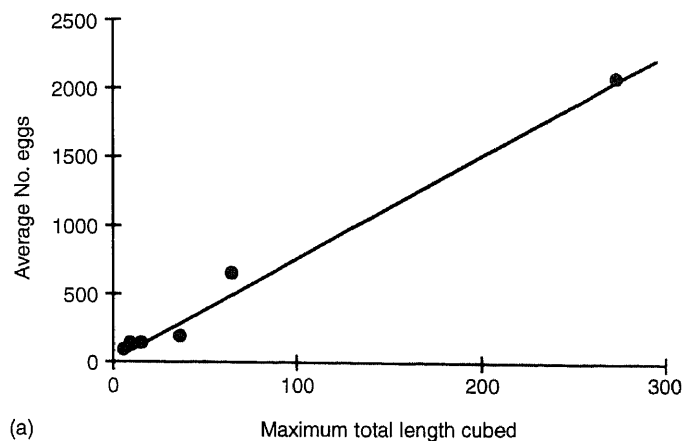*egg size in ovisac

Sources of information listed by species initials. E. c.: Harrington & Thomas (1987), Ideda (1986). E. l.: Pillar & Stuart (1988) lower estimate of SPE per lifespan, Stuart & Nicol (1986), Stuart (1992) higher estimate of SPE per lifespan. E. p.: Brinton (1976), Ross et al. (1982), Suh et al. (1993), Iguchi & Ikeda (1994). E. s.: Cuzin-Roudy (1987), Kikuno (1981), Kikuno & Kawamura (1983), Siegel (1985), Harrington & Ikeda (1986), Ross & Quetin (1983), Nicol (1989). M. n.: Marschall (1983), Cuzin-Roudy & Buchholz (1999). N. a.: Hosie & Ritz (1982, 1983).

cycle) in two main and usually one residual spawning event during the premoult period. In the Ligurian Sea, spawning moult cycles alternate with vitellogenic moult cycles. This pattern may not hold throughout its distribution range; in areas of low food availability, an extended period of reorganisation of the ovary may be necessary before a new cycle of egg production begins. Furthering our under-standing of what drives this variability is critical to understanding reproductive success in euphausiids.

The number of eggs released per spawning episode varies significantly both within and between species (Table 6.7). Although an increase in fecundity with female size is predicted, the correlation with total length is usually quite low (i.e. *E. superba* as cited in Ross & Quetin, 1983; Harrington & Ikeda, 1986; Nicol *et al.*, 1995). Most investigators have inferred that the number of eggs released per spawning episode is influenced by factors other than body size. Somers (1991) examined five different regression models for the relationship between fecundity and female size for crustaceans. He concluded that the allometric model (log-transformed fecundity versus log-transformed female length) was the better choice, primarily because of the relative scale independence and the ability to make comparisons among taxa. From general allometric concepts, the relation between fecundity and female volume (expressed as length cubed) should be linear (i.e. two volume measures), as has been shown for the relationship between wet weight and ovarian oöcytes in *E. superba* and *M. norvegica* (Xuefeng & Rong, 1995; Cuzin-Roudy, 2000). The relationship between fecundity and size may also show high variability because the numbers of eggs released by the same female in successive spawning episodes are not equal, as seen in both *M. nor-vegica* and *E. superba* (Harrington & Ikeda, 1986; Nicol, 1989; Cuzin-Roudy & Buchholz, 1999). In fact, if all mature or maturing oöcytes (oc4) in the ovary are counted, the relationship between the number of eggs and the size of the euphausiid improves significantly for both *E. superba* (Siegel, 1985; Xeufeng & Rong, 1995; Cuzin-Roudy, 2000) and *M. norvegica* (Cuzin-Roudy, 2000). The implication is that a batch of eggs is released over a period of days in several spawning episodes, and that the sum of the eggs released in this suite of suc-cessive episodes correlates well with body size. Batch size or number of eggs per spawning episode can also vary among geographical sites (Harrington & Ikeda, 1986) or between years (Siegel, 1985; unpublished data, Ross & Quetin). Pre-sumably the nutritional conditions prior to and during the spawning season also affect the size of the batches.

Mauchline (1988) found that the relationship between brood volume and body volume for 13 species of brooding euphausiids was logarithmic, with a correlation of 0.871. The slope was slightly greater than 1, implying that larger species tended to produce larger broods, but the increase was small, from 10 to 15% of body volume. For six species of epipelagic euphausiids, the relationship between the average number of eggs per spawning episode or vitellogenic cycle and the volume (max-imum total length cubed) was linear, with $r^2 = 0.987$ (Fig. 6.6a).
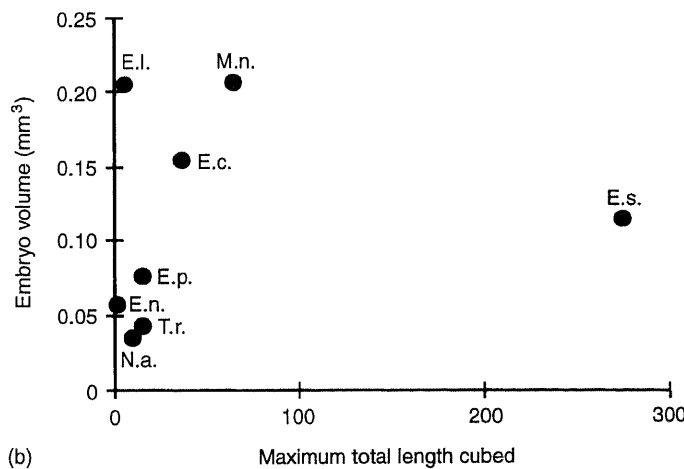
Fig. 6.6 Intraspecific comparison of euphausiid volume (expressed as the cube of total maximum length, Table 6.1) and (a) average number of eggs per spawning episode, Table 6.7; and (b) average diameter of the egg, average of values shown in Table 6.7 plus E. n. from Hirota *et al.* (1984). Initials on points are the first letter of the genus and species of euphausiid. The line shown in (a) is average number of eggs = 32.4 + 7.58 • TL^3; n = 6, r^2 = 0.987.

Embryo size

Embryo size also varies within and between species. Inter-annual and geographical differences in embryo size are well documented for euphausiids (Mauchline & Fisher, 1969). Such differences have implications for the energy reserves available for the non-feeding larvae, and may impact survivorship of early life history stages.

No studies have explicitly addressed this question, but variation in parental input into the oöcyte before release and its impact on inter-annual variability in recruitment should be investigated.

Mauchline (1988) compared average egg volume and body volume for a suite of 16 epipelagic euphausiids, 7 brooders and 9 broadcast spawners. The relationship was allometric, with r = 0.833:

$$\text{log egg volume (ml)} = 0.301 \text{ log body volume (ml)} = 4.165$$

The exponent less than unity suggests that large euphausiids have larger eggs than small euphausiids, but that egg size relative to body size decreases. From a slightly different perspective, however, the conclusions are somewhat different. A plot of egg volume against body volume (maximum TL cubed) shows that egg volume does increase with body volume for six of the eight species of euphausiids plotted. However, the egg of *E. lucens* is larger than would be predicted, and that of *E. superba* much smaller than would be predicted. Some interesting differences were obscured by the use of a log-log plot.

Mauchline (1988) suggested that there was a minimum viable size of egg to explain the decrease in relative egg size with increasing body size. The hypothetical minimum egg size also has implications for individual fecundity. Euphausiids can increase their total fecundity either by producing successive broods, as has been shown to be true for most euphausiids, or by decreasing egg size relative to body size in order to increase the number of eggs per spawning episode. In the case of *E. superba*, it appears as if the overall reproductive strategy includes both mechanisms.

6.3   Development

Eggs from different species vary not only in absolute size but also in the size of the perivitelline space (PVS), the space between the vitelline membrane and the capsule. The duration and extent of the ontogenetic migration during the early life history of euphausiids is influenced by the size of the PVS, and sinking rate and development rate of the embryo exposed to characteristic hydrographic conditions (Ross & Quetin, 1991; Hofmann *et al.*, 1992). Many investigators have suggested that a strong developmental descent and ascent is characteristic of oceanic euphausiids (Makarov, 1979, 1983; Mauchline, 1980; Marr, 1962; Hempel *et al.*, 1979; Williams & Lindley, 1982). These species would have small PVS. Neritic species, on the other hand, would have a large PVS, and would be either neutrally buoyant or have slow sinking rates. The vertical extent of the developmental descent and ascent would be small. The larger vertical extent in oceanic euphausiids would reduce intraspecific predation, whereas the small vertical extent in neritic euphausiids would reduce the extent of benthic predation. The data to date (Table 6.8) do not clearly support this hypothesis. For *M. norvegica* and *T. raschii*, both

Table 6.8   Perivitelline space (PVS) as percentage volume of embryo and qualitative characterisation, sinking rate and reference.

Species	PVS % vol	Qual char of PSV	Sink rate (m d^{-1})	Reference
Neritic				
E. crystallorophias	–	'larger than E. superba	'neutral'	Harrington & Thomas (1987)
M. norvegica	78		61–104	Marschall (1983)
		'med-large'	132–180	Mauchline & Fisher (1969)
T. raschii	52		42–67	Marschall (1983)
		'large'	132–180	Mauchline & Fisher (1969)
Oceanic				
E. pacifica	–	small	Sink	Bollens *et al.* (1992)
E. superba	9	small	203–231	Marschall (1983)
			175	Quetin & Ross (1984)
E. nana	–	small	–	
T. longicaudata	–	'very small'	–	Williams & Lindley (1982)

slow and fast sinking rates have been measured (Mauchline & Fisher, 1969; Marschall, 1983). For some species with a small PVS, high sinking rates but fast development rates still yield a small vertical excursion, as seen in *E. pacifica* in Dabob Bay (Bollens *et al.*, 1992). More research is clearly warranted.

6.4   Implications for fisheries management

The goal of management of euphausiid fisheries, as for all fisheries, is to ensure that recruitment to the adult population is adequate to compensate for the stock that is harvested. The harvest rate must depend on the rate of recruitment into the adult population that in turn depends on the population fecundity. Thus reproduction (egg production) and its impact on recruitment should be a critical aspect of management of crustacean fisheries (Botsford, 1991). However, although recruitment depends on egg production through the relationship between stock and recruitment, the impact of variation in egg production is subsequently modified by the impact of the fluctuating pre-recruitment environment on the survival of the early life history stages.

At present we know very little about stock-recruitment relationships in crustaceans (Botsford, 1991). Data necessary to establish the relationship between spawning stock and reproductive output in euphausiids are scarce. The time series needs to be long, and both stock and recruitment must be measured on relevant time and space scales. One critical issue is whether the stock measured is the one that produced the larvae recruited to that adult population, or if the eggs and larvae were transported by currents prior to recruitment to the adult population.

Zelikman *et al.* (1980) suggested that the lack of correlation between stock and

recruitment in euphausiids supported the concept of a 'self regulating' population, i.e. density dependent mechanisms regulating recruitment. The amount of uncertainty about the relative importance of egg production and early larval mortality on recruitment, however, suggests that this conclusion may be premature. The effects of egg production on recruitment may be hidden by processes occurring during the early life history stages, i.e. the effects of abiotic and biotic factors in the pre-recruitment environment. In the case of *E. superba*, we know that interannual variability in recruitment success of *E. superba* is high (Siegel & Loeb, 1995). Although the mechanism proposed is the over-winter survival of the larvae (Ross & Quetin, 1991; Quetin *et al.*, 1996; Siegel & Loeb, 1995), the role of reproductive output has not been thoroughly evaluated.

An alternative explanation for the lack of correlation between stock and recruitment is that population fecundity is complex and varies greatly with stock. Emerging evidence for euphausiids suggests that the number of eggs produced per female may show large inter-annual variation due to the effect of nutritional history on factors such as the percentage of the population reproducing, variation in numbers of spawning episodes and batch size. Early larval survival may also be affected by the amount of reserves in the embryo. Variation in embryo size for euphausiids is well documented, and this variation implies that the amount of reserves also varies.

Given our uncertainties about the relative roles of egg production and larval survivorship in recruitment, the conservative management tactic would be to guard egg production. Botsford (1991) presents the argument that such a management tactic does not always create the highest yield, but that the population will be maintained. To achieve this goal of guarding egg production, restrictions may be placed on the timing or spatial occurrence of commercial harvesting, or on the part of the population that can be fished. One common tactic when reproduction is concentrated in one part of the year is a limited season for harvesting after the reproductive season. With the species of euphausiids currently harvested, the limited reproductive seasons would allow this tactic.

The restricted distribution of spawning populations would allow the use of a somewhat different policy, basically to prohibit the harvesting of gravid females, analogous to prohibiting 'berried' lobsters and crabs from being kept. Fishing pseudopopulations, for example, would have no immediate impact on population recruitment. We also know that swarming is often correlated with reproductive activity, so fishing surface swarms may selectively harvest the portion of the population that we most want to guard. On the other hand, if we understand the behaviour of individuals in the surface aggregations better, we may be able to take advantage of differences in the behaviour of mated females in terms of timing of spawning or diel distribution.

A more complex management tactic would be based on the fact that population fecundity will depend on the size–age structure of the population, which in turn depends on harvest policies. Larger females produce the greater number of eggs.

The goal would be to prevent the overfishing of the large egg-producing females and the males needed to mate with those females throughout the season. In some crustacean fisheries, a size limit is set for a single sex fishery (e.g. males below a certain size, or females above a certain size), but this tactic would not be possible with most euphausiids. Even though catches often show a skewed sex ratio (Watkins *et al.*, 1992) throwing back the 'wrong' sex would not be feasible. Once caught, large individuals would not survive if thrown back. In summary the best options for management tactics based on our knowledge of euphausiid reproduction appear to be restrictions of the fishery in time and space to guard the large egg-producing females.

Acknowledgments

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