

REVIEW

Juvenile mortality in benthic marine invertebrates

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ABSTRACT: Thirty years ago, Thorson (1966; *Neth J Sea Res* 3:267–293) calculated that juvenile mortality in marine bivalves could exceed 98.6%. Subsequently, juvenile mortality rates have been assumed to be high and to influence the evolution of life history traits. However, there have been no attempts to establish whether high juvenile mortality is common or to determine if interspecific trends in juvenile mortality exist. To address this issue, we reviewed 30 studies of age-specific mortality among bivalves, gastropods, barnacles, ascidians, bryozoans and echinoderms. High juvenile mortality is widespread among benthic marine invertebrates, with 20 of the 30 studies reporting levels of juvenile mortality >90%. Mortality is particularly high during the first moments of juvenile life, and can exceed 30% during the first day. Pooling survivorship data from all species revealed a general trend, with survivorship decreasing exponentially during the first days or weeks of juvenile life until, by the age of 4 mo, virtually all cohorts were reduced to <20% of their initial numbers; mortality remained low thereafter. We suggest that extreme vulnerability at the onset of juvenile life is a shared trait that is largely responsible for the survivorship trend. Natural variation within this trend would be largely due to variation in intensity of mortality factors. Predation and desiccation are well-documented causes of juvenile mortality, but the current lack of data on factors such as ultraviolet radiation, diseases, and 'internal' causes (energy depletion, developmental and physiological defects) precludes a ranking of factors as selective pressures. Methods used to quantify juvenile mortality vary considerably in the level of resolution they can achieve within the early juvenile period. Studies of early juvenile mortality should ideally monitor the fate of individuals from the onset of juvenile life, using sampling intervals ≤ 1 d. Mapping and imaging techniques can provide accurate results for sessile organisms, whereas mark and recapture can be effective for motile animals with limited dispersal. Early juvenile mortality has been shown to influence population abundance and distribution as well as community structure. Juvenile mortality is also expected to be an important determinant of age at maturity, but only among species maturing within 4 mo of postlarval life since mortality remains low after the age of 4 mo. A compilation of data on age at first reproduction in 92 species revealed a bimodal grouping of species: 22% of species maturing within 45 d after beginning juvenile life, and 60% maturing after at least 1 yr. The influence of juvenile mortality on age at maturity will differ substantially among these 2 groups and will therefore not be equal or directly comparable among all species. Given the magnitude of early juvenile mortality and the similarities in mortality patterns across diverse taxa and habitats, a better understanding of early juvenile mortality should help researchers to understand how population parameters are regulated and help elucidate the significance of traits that characterize populations and species.

KEY WORDS: Mortality factors · Survivorship · Early juvenile · Selective pressures · Population parameters · Life history traits · Age at maturity

INTRODUCTION

In a seminal paper published 3 decades ago, Thorson (1966) suggested that mortality rates could be high among newly established juvenile invertebrates. He calculated that less than 1.4% of bivalves settling on

subtidal mudflats might survive long enough to reach a size of 2 mm. At this level of mortality, the processes responsible for mortality during juvenile life could have major repercussions on population parameters such as abundance and distribution. High juvenile mortality could also constitute a driving force in the evolutionary development of a species, as postulated in models linking age at first reproduction (e.g. Stearns

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Table 1 Cumulative juvenile mortality reported for benthic marine invertebrates. Most studies focused on a selected part of the juvenile period and thus most values reported herein do not represent total juvenile mortality (to maturity). Ages at maturity of some of these species are listed in Appendix 1. 'Age' column shows age at which mortality values were obtained: onset of juvenile life = Age 0. For 'cohort monitoring', fate of cohorts rather than that of individuals was monitored

Species	Cumulative mortality	Age	Study habitat	Sampling method	Sampling interval	Source
BIVALVES						
Pooled bivalve species	≥98.6%	~2 mm length	Subtidal sand flats	Cohort monitoring	-	Thorson (1966)
<i>Crassostrea virginica</i>	64–100% / 86–100%	7 d / 1 mo	Sub- & intertidal plates	Photos	7 d	Roegner & Mann (1995)
<i>Crassostrea virginica</i>	70–99%	1 mo	Subtidal plates	Cohort monitoring	1 mo	Osman et al. (1989)
<i>Cerastoderma edule</i>	56–63% / 94–97%	28 d / 250–286 d	Intertidal mudflat	Cohort monitoring	0.5 mo	Guillou & Tartu (1994)
<i>Cerastoderma edule</i>	~80–100% / 100%	3 mo / 1 yr	Subtid. sand & mudflats	Cohort monitoring	0.25–1 mo	Möller & Rosenberg (1983)
<i>Alba tenuis</i>	30% / 98.5%	1 mo / 1 yr	Intertidal mudflats	Cohort monitoring	0.5–1 mo	Bachelet (1989)
<i>Mya arenaria</i>	~93–100% / 99–100%	3 mo / 1 yr	Subtid. sand & mudflats	Cohort monitoring	0.25–1 mo	Möller & Rosenberg (1983)
GASTROPODS						
<i>Aplysia juliana</i>	~90% / ≥99%	5 d / 25 d	Subtidal algae	Cohort monitoring	7 d	Sarver (1979)
<i>Lacuna vincta</i>	60–76% / 97–98%	1 mo / 4 mo	Intertidal algae	Cohort monitoring	1 mo	Smith (1973)
<i>Lacuna vincta</i>	87–92% / 96–99%	1 mo / 4 mo	Intertidal algae	Cohort monitoring	1 mo	Southgate (1982)
<i>Hydrobia ulvae</i>	67% / 98.4%	1 mo / 7 mo	Intertidal mud flats	Cohort monitoring	0.5–1 mo	Bachelet & Yacine-Kassab (1987)
<i>Philine gibba</i>	~24% / ~55%	1 mo / 3 mo	Subtidal mudflats	Cohort monitoring	1 mo	Seager (1983)
<i>Haliothis rubra</i>	≥95% (most cohorts)	3–5 mo	Subtidal substrata	Cohort monitoring	1–5 mo	McShane (1991)
<i>Haliothis iris</i>	90–99%	135 d	Subtidal boulders	Cohort monitoring	2–8 wk	McShane & Naylor (1995)
<i>Littorina rudis</i>	≥98%	6 mo	Rocky intertidal	Cohort monitoring	3–6 mo	Faller-Fritsch & Emson (1986)
<i>Nucella lapillus</i>	≥90%	1 yr	Rocky intertidal	Cohort monitoring	1 mo	Fearé (1970)
<i>Nucella lamellosa</i>	≥99%	1 yr	Rocky intertidal	Cohort monitoring	1 yr	Spight (1975)
<i>Nerita atramentosa</i>	insignificant	2 yr	Rocky intertidal	Cohort monitoring	2 mo	Underwood (1975)
BARNACLES						
<i>Chthamalus fragilis</i>	53–78%	1 d	Intertidal cordgrass	Mapping	1 d	Young (1991)
<i>Balanus glandula</i>	38% / 78%	1 d / 43–45 d	Rocky intertidal	Mapping	1 d	Gosselin & Qian (1996)
<i>Semibalanus balanoides</i>	~10–45% / 47–94%	1.5 d / 2 mo	Intertidal stones	Mapping	1 d	Connell (1961a)
<i>Semibalanus balanoides</i>	51–54%	6 d	Rocky intertidal	Photos	0.5 d	Wethey (1984)
<i>Chthamalus anisopoma</i>	35%	16 d	Rocky intertidal	Mapping	~9 d	Raimondi (1990)
<i>Chthamalus fissus</i>	58% / 80%	1 mo / 2 mo	Rocky intertidal	Photos	30 d	Sutherland (1990)
ASCIDIANS						
<i>Diplosoma similis</i>	50% / 90–100%	1 d / 16 d	Subtidal substrata	Marks on substratum	1 d	Stoner (1990)
<i>Podoclavella cylindrica</i>	~3–30% / ~22–89%	1 d / 30 d	Subtidal substrata	Mapping	1 d	Davis (1987)
<i>Botryllus schlosseri</i>	0–100%	22 d	Submerged plates	Photos	3 d	Osman et al. (1992)
<i>Diplosoma</i> sp.	80–88%	15–22 d	Submerged plates	Photos	3–4 d	Hurlbut (1991a)
<i>Didemnum candidum</i>	68–71%	15–22 d	Submerged plates	Photos	3–4 d	Hurlbut (1991a)
BRYOZOANS						
<i>Bugula neritina</i>	>90% / 100%	7 d / 21 d	Artificial seagrass	Marks on substratum	7 d	Keough (1986)
ECHINODERMS						
<i>Strongylocentrotus purpuratus</i>	~50–81%	24 d	Subtidal substrata	Cohort monitoring	10 d	Rowley (1990)
<i>Pisaster ochraceus</i>	~99%	1 yr	Subtidal substrata	Cohort monitoring	1 yr	Sewell & Watson (1993)

& Koella 1986) with levels of juvenile mortality. But while high juvenile mortality has been reported, there have been no attempts to establish whether high juvenile mortality is common or to identify interspecific trends in juvenile mortality.

Since Thorson's study, new information on the ecology of juveniles has revealed that the processes operating during the early part of juvenile life differ from those operating at any other time of life. Werner & Gilliam (1984), for instance, found that many aquatic animals shifted their diet and habitat use at some point during the juvenile period. More recently, detailed studies of early juvenile lobsters (*Homarus americanus*, Wahle & Steneck 1991, Cobb & Wahle 1994; *Panulirus argus*, Smith & Herrnkind 1992) and snails (*Nucella emarginata*, Gosselin 1994) have shown early juveniles to be ecologically distinct from late juveniles and adults. Early juveniles differed from individuals at other periods of life in their use of microhabitat and food resources and in vulnerability to mortality factors. Available information for other benthic invertebrates suggests the early juvenile period is an ecologically distinct phase in many species, particularly those with motile juveniles (cf. Gosselin 1994). The patterns and the effects of juvenile mortality would therefore be regulated at least in part by processes that are specific to the early juvenile period.

In this paper, we examine the significance of juvenile mortality for benthic marine invertebrates by reviewing published reports of natural levels and causes of juvenile mortality and its implications for population parameters and 1 life history trait. Given that a variety of approaches have been used to quantify juvenile mortality, we also document the uses and limitations of the most commonly employed methods. The specific objectives of this paper are to (1) document the natural levels of juvenile mortality and identify interspecific trends among benthic invertebrates, (2) critically review the methods used to quantify natural juvenile mortality, (3) identify the causes of juvenile mortality, and (4) examine the implications of juvenile mortality for population parameters and age at maturity.

CONTEXT AND FOCUS

We review 30 studies reporting age-specific mortality data for at least the early period of juvenile life in natural or near-natural field conditions. The resolution of these studies varies widely, from rough estimates based on 'snap-shot' samples to precise survivorship curves starting at the onset of independent benthic life. There is also considerable variation in the duration of the studies. Finally, biological differences add to the

complexity of the analysis, particularly differences in duration of the juvenile period among taxa. For instance, the first 2 mo after settlement constitute only a small portion of juvenile life in the seastar *Pisaster ochraceus*, which matures ~5 yr after settlement (Menge 1974), but 2 mo are sufficient for newly settled ascidians *Didemnum candidum* to reach maturity and release gametes (Hurlbut 1991a). Although direct comparisons of results from different studies are limited by these circumstances, the data are nevertheless amenable to a broader investigation of mortality patterns among benthic invertebrates, on which the present review will focus.

MAGNITUDE AND TIMING OF JUVENILE MORTALITY

Levels of juvenile mortality exceeding 90% were reported in 20 of the 30 papers reviewed herein and were observed in bivalves, gastropods, barnacles, ascidians, bryozoans and echinoderms (Table 1). Seventeen studies report cases of juvenile mortality $\geq 98\%$.

Of particular interest is the high mortality observed immediately after settlement in 3 barnacles and 2 ascidians (Table 1). In all 5 species, cases of mortality $\geq 30\%$ were recorded during the first 1 to 1.5 d after settlement. The highest first-day mortality was reported for *Chthamalus fragilis* (Young 1991): 53 to 78% of individuals settling on the cordgrass *Spartina alterniflora* did not survive the first day in their new habitat. In an elegant study, Stoner (1990) directly observed the release, dispersal and settlement of individual *Diplosoma similis* larvae on natural substrata in the field and then monitored their fate on a daily basis for the following 26 d: 50% of these settlers died during the first day after settlement. In newly settled *Balanus glandula*, 38% died during the first day after settlement (Gosselin & Qian 1996). Mortality rates in *D. similis* and *B. glandula* dropped sharply after the first day, indicating that a brief initial period as short as 24 h following the transition to independent benthic life can be a critical period for survival.

To verify the existence of general patterns in juvenile mortality, a survivorship curve was produced by pooling data from all the studies listed in Table 1. The resulting graph, which presents data for the juvenile period only, reveals a clear interspecific trend of survival as a function of age (Fig. 1). Survivorship decreased exponentially during the first days or weeks of juvenile life, and by the age of 4 mo virtually all cohorts were reduced to $\leq 20\%$ of their initial numbers. This trend might be partly due to a methodological bias (e.g. there is less data for the 2 to 12 mo age interval than for the first 2 mo). However, the coherence of the

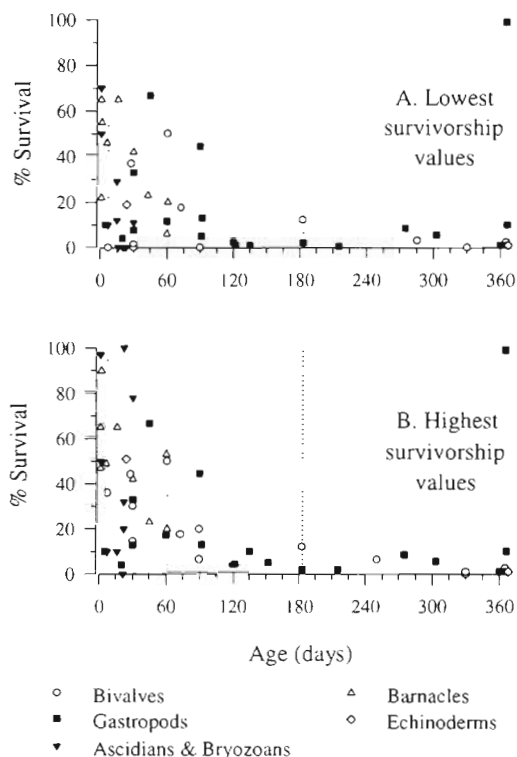


Fig. 1. Survivorship of benthic marine invertebrates during the juvenile period. Age = 0 corresponds to the onset of juvenile life. All data plotted herein were extracted from the 30 studies listed in Table 1. To integrate these results into a single figure, 4 age intervals (delimited by dashed vertical lines at ages = 7, 61, and 183 d) were subjectively determined based on age periods for which most data were available. Each study contributed a maximum of 4 data points to the figure, 1 point per age interval. Since several studies report mortality or survivorship data as a range, and occasionally for a range of ages, the data are represented in 2 graphs: (A) displays the lowest survivorship values (highest mortality, shortest age interval) reported in each study, (B) displays the highest survivorship values

data contrasts with the diversity of methods and sampling intervals, suggesting that the pattern is not a methodological artifact. We conclude that high mortality shortly after the onset of juvenile life is a common occurrence among benthic invertebrates.

The existence of this common trend in juvenile mortality is fascinating, as it suggests that juvenile survivorship across taxa and habitats could be regulated by a common set of processes. Since the intensity of most mortality factors differs widely among habitats, the trend is unlikely to be attributable to similarities in causes of death. Rather, the more basic issue of vulnerability could be the unifying element. The initial sharp decline in mortality rates over the first 1 to 2 d may result from rapid anatomical, physiological, and possibly behavioural changes at the start of juvenile life, allowing the young individual to cope with the new

environment it then faces (Gosselin & Qian 1996). Individuals generally begin juvenile life with minimal or incomplete protective structures, such as shell, carapace, or tegument. In addition, changes in mortality rates during the first hours or days may be due to a rapid elimination of individuals located in unfavourable sites. Beyond the first days of juvenile life, mortality rates could be largely dependent on body size, a major determinant of vulnerability. Growth could therefore be responsible for much of the common trend in juvenile mortality since most species begin juvenile life as meiofauna. The gradual levelling off of survivorship would be a result of the juveniles reaching critical sizes at which vulnerability to physical and biological constraints is substantially reduced (e.g. Wahle & Steneck 1992, Gosselin 1994).

Although the data in Fig. 1 reveal an upper limit to juvenile survivorship, mortality levels varied within this trend. Methodological differences undoubtedly account for part of this variation, but in many field studies substantial variation was also common among replicates for a given species, indicating that spatial and temporal variation in natural mortality is often important. Variation in intensity of mortality factors is likely to be a major cause of this natural variation in mortality. This hypothesis is supported by data linking variation in juvenile mortality to tidal height (Roegner & Mann 1995), habitat (Davis 1987, Osman et al. 1989, Rowley 1990, Young 1991), and season (Grosberg 1988, Roegner & Mann 1995). In addition, the occurrence of either dominant or very small year classes in benthic populations has been attributed to unusually benign or harsh conditions at the time of early juvenile development (Connell 1961a, MacKenzie et al. 1985, Sebens & Lewis 1985).

Data for 3 species did not conform to the general trend (Table 1, Fig. 1). Mortality of the gastropod *Nerita atramentosa* was reported to be insignificant during the first 2 yr after settlement (Underwood 1975), whereas in the antarctic opisthobranch *Philine gibba* ~45% would survive to the age of 3 mo (Seager 1983). In a third species, the bivalve *Albra tenuis*, 50% and 24% of individuals were reported to survive the first 2 and 4 mo, respectively (Bachelet 1989), values that are somewhat above the general trend. These 3 reports, however, were based on cohort studies with long sampling intervals (Table 1), a methodology that does not reliably quantify mortality during the first weeks of juvenile life (see 'Cohort monitoring'). It is therefore possible that even these species conform to the pattern of high early mortality. Nevertheless, the prospect that a few species may achieve high survivorship during the early juvenile period is intriguing, as this suggests outcomes other than high early mortality are possible.

METHODS FOR QUANTIFYING EARLY JUVENILE MORTALITY

The accurate determination of the timing (relative to age) and magnitude of mortality are necessary to correctly assess when selective pressures are most intense and to accurately quantify their effect. The pattern of mortality plotted in Fig. 1 therefore has 2 methodological implications for studies of juvenile mortality. First, studies that do not quantify mortality from the onset of juvenile life may significantly underestimate juvenile mortality, miss critical events that impact population parameters, and incorrectly estimate the relative importance of larval and postlarval processes. Of the 30 studies listed in Table 1 only 6 (21%) quantified mortality from the onset (~first 24 h) of juvenile life; most juvenile mortality data may therefore be underestimates.

Secondly, since the early period of high mortality may last from a few days to up to 4 mo, a detailed survivorship curve is necessary to determine when the most intense selective pressures are in effect. The degree to which this second goal is reached is directly linked to sampling frequency. By increasing sampling frequency during the early juvenile period (e.g. to daily, tidally or hourly sampling), the resolution of the survivorship curve is improved, up to the point where observations become frequent enough to significantly interfere with natural events. Assessments of juvenile mortality, however, have often been based on sampling intervals ranging from weeks (Table 1; see also Muus 1973, Keough & Downes 1982, Grosberg 1988, Qian & Chia 1994) to months (Table 1; see also Denley & Underwood 1979, Osman 1987, Keough 1989) or even up to a year (Table 1). Low sampling frequencies have the additional disadvantage of providing a greater window for other processes to alter juvenile densities and thereby confound mortality estimates: net immigration or the establishment of new juveniles cause an underestimation of mortality, whereas net emigration leads to an overestimation of juvenile mortality. Longer intervals also provide more time for early juveniles to become established, die, and disappear before being recorded (Minchinton & Scheibling 1993, Gosselin & Qian 1996). For example, the thin shells of early juvenile *Macoma balthica*, a soft-sediment bivalve, can completely dissolve within only 5 d after the individual's death (Elmgren et al. 1986). As a rule of thumb, the most reliable way of quantifying juvenile mortality is to monitor the fate of individuals from the onset of independent benthic life, using sampling intervals ≤ 1 d.

The various methods used to quantify juvenile mortality in the field differ considerably in the level of resolution they can achieve. The 4 methods most com-

monly used to quantify natural rates of juvenile mortality are examined below. Tethering techniques, which have serious drawbacks for quantifying natural mortality (Barshaw & Able 1990, Barbeau & Scheibling 1994, Peterson & Black 1994, Zimmer-Faust et al. 1994), are not reviewed herein.

Mapping

The mapping technique consists of manually recording the positions, usually on flexible transparent plastic sheets, of all sessile individuals within a given area, noting whether they are dead or alive, and repeating the procedure at regular intervals. The major advantage of the method is that it allows the observer to monitor all individuals, including those hidden by surface irregularities or by other organisms, and to directly verify the identity and status of each individual, which is not always possible with imaging techniques. Although searching and mapping are time consuming, this is nevertheless the most reliable way of quantifying juvenile mortality of sessile organisms attached to flat or slightly irregular surfaces.

Imaging

Photography is the most commonly used imaging technique, although video recording has also been suggested for monitoring juveniles (Wright et al. 1991). Close-up images of benthic substrata provide a permanent record of sessile organisms that can subsequently be analyzed with digital or image analyzers. Images constitute a record of size, shape, and distribution of the juveniles, as well as characteristics of their immediate environment, that may help establish the causes of mortality. The images are 2-dimensional, however, and therefore individuals hidden by surface irregularities will not be detected. Larger individuals are recorded more clearly, and consequently there is potential for underestimating the arrival and mortality of small, new juveniles. Imaging techniques are most appropriate when the juveniles are well-spaced and easily identified, when weather and substratum conditions do not interfere with the clarity of the images, and when the resolution of the images is sufficient to detect even (and especially) the smallest recruits.

Mark and recapture

When mapping or imaging techniques cannot be used, as is the case with motile individuals, mark and recapture may be the only way to monitor animals over

time and associate their fate with elements of their history (e.g. initial location, age, body size, lineage). The simplest approach to mark and recapture is to simultaneously label many early juveniles, for instance by staining (Levin 1990, Qian & Chia 1994) or by painting external hard structures such as gastropod shells (Boulding & Van Alstyne 1993). The fate of individuals, however, cannot be determined if all receive the same label. Individualized marks have been applied to small juveniles with hard external structures (Gosselin 1993) but have yet to be used to determine natural mortality rates in the field. A comparable method used in 2 studies of sessile animals (Table 1) consists of marking the substratum near each individual to enable relocation on subsequent inspections. In motile species, recapture is complicated by the small size, dispersal, cryptic distribution, and short persistence time of dead bodies of most early juveniles. Consequently, the fate of missing individuals can be uncertain. Since handling and marking can have deleterious or beneficial effects on survival, a preliminary study should be done to quantify the effects of the method. Mark and recapture promises to be useful for short-term studies of motile juveniles with limited dispersal if marking can be accomplished without excessive disturbance to the organisms.

Cohort monitoring

It is not always possible to repeatedly monitor a given set of individuals over time. An alternative is to sample the population at intervals without attempting to relocate the same individuals. In such cases, the unit being monitored is the cohort rather than the individual, and decreases in density over time are interpreted as mortality. Cohort monitoring has been the most commonly used method of studying juvenile mortality (17 of 30 studies). In its simplest form, cohort monitoring consists of 2 samplings, once before and once after a given interval (Spight 1975, Osman et al. 1989, McShane 1991). Such 'snap-shot' evaluations are simple and demand relatively little time, but are sensitive to atypical events and provide no information on the variability of mortality over time. A more commonly used approach is based on histogram analysis and consists of the establishment of size- or age-frequency distributions for a time series of samples. When cohorts overlap, size measurements are necessary to distinguish cohorts by graphical or mathematical procedures (modal analysis: Macdonald & Pitcher 1979, Fournier & Breen 1983, Grant et al. 1987).

Since individual organisms are not monitored over time, searching and handling are reduced and habitats are not disturbed prior to sampling. There are impor-

tant limitations, however, to cohort monitoring techniques. The arrival of new juveniles is not always in sufficiently discrete pulses to monitor distinct cohorts, or sample sizes required for cohort analysis can be unfeasibly large (Grant et al. 1987). In addition, migration, settlement, or hatching of new juveniles during the study will interfere with mortality determinations unless these processes are also quantified. Migration can be substantial even among early juveniles generally thought to have limited motility (e.g. Emerson & Grant 1991, Martel & Chia 1991a, b). Cohort studies are generally not effective for measuring mortality during the potentially critical first days of early juvenile life because it is rarely possible to distinguish between cohorts on a very short time scale (e.g. daily cohorts). Nevertheless, cohort monitoring may be the only way of obtaining mortality estimates for highly motile juveniles or where sampling excessively disturbs the organism and its environment, as can be the case for infaunal juveniles.

In conclusion, mapping is the most reliable way of quantifying mortality through the early juvenile period, although estimates from photographic records can be satisfactory under appropriate conditions. Both methods, however, are only applicable to sessile organisms. No study has yet monitored the fate of individual early juveniles of motile species in the field. This situation might be partly resolved by improving marking techniques to mark and recapture juveniles with limited dispersal. Data obtained by monitoring cohorts rather than individuals can be used as rough estimates of early juvenile mortality but generally do not reveal the precise timing or intensity of mortality and cannot be used to accurately describe changes in mortality rate over periods of a few days or less. Since the biological significance of mortality data is highly dependent on the method, sampling frequency, and age of study organisms, reports should include detailed information on the methodology as well as the age of the juveniles when they first appear in the samples. Future reports should also provide untransformed mortality data to facilitate comparisons with other published results.

CAUSES OF EARLY JUVENILE MORTALITY

The data compiled herein (Fig. 1) show that juvenile mortality is highest early in juvenile life. In addition, the processes operating early in the juvenile period, including those regulating mortality, differ from those operating at any other time of life (Gosselin 1994). This suggests that mortality factors specific to the early juvenile phase may be important determinants of population parameters as well as driving forces in the evo-

lutionary development of the species. This section aims to identify all factors reported as causes or potential causes of early juvenile mortality as a first step towards characterizing the selective pressures operating during this period of life. To date, 5 biotic factors (predation, competition, energy depletion, disease, developmental complication) and 5 abiotic factors (desiccation, temperature, salinity, water motion, solar radiation) have been suggested as causes of early juvenile mortality.

Biotic factors

Predation, including cannibalism (Hines et al. 1990, Fernandez et al. 1993a) and ingestion or crushing by grazers ('bulldozing'; Connell 1961a, Dayton 1971), is often assumed to be the single most important cause of early juvenile mortality (Thorson 1966, Spight 1976, Keough & Downes 1982, Stoner 1990, Hurlbut 1991a, b, Fernandez et al. 1993b). Early juveniles are indeed vulnerable to predation and may be killed in great numbers if exposed to predators, as shown in bivalves (Thorson 1966, Elmgren et al. 1986, Pohle et al. 1991), gastropods (Gosselin & Chia 1995a, b, Ray & Stoner 1995), decapod crustaceans (Smith & Herrnkind 1992, Barshaw et al. 1994), echinoderms (Highsmith 1982), and ascidians (Young & Chia 1984, Osman et al. 1990, 1992, Osman & Whitlatch 1995). Decapod crustacean predators are often identified as a major source of predation on early juveniles (Thorson 1966, Möller & Rosenberg 1983, MacKenzie et al. 1985, Ojeda & Dearborn 1991, Guillou & Tartu 1994, Gosselin & Chia 1995a). The potentially large impact of decapods results from their generally high abundances, broad distribution in both intertidal and subtidal habitats, high motility, their ability to crush protective structures, and their need to process large amounts of food. Juvenile invertebrates may nevertheless be consumed by predators from a broad spectrum of taxa. The impact of pelagic predators, particularly fish, is rarely examined but could be substantial (e.g. Ojeda & Dearborn 1991, Wahle & Steneck 1992, Fernandez et al. 1993b).

Competition for space by undercutting, overgrowth, or aggressive contacts among sessile organisms can be a direct cause of early juvenile mortality, and can involve inter- or intraspecific interactions (ascidians, Young & Chia 1984, Davis 1987; barnacles, Hatton 1938, Connell 1961a, b, Denley & Underwood 1979). Competition for space can also be an indirect cause of mortality: at high densities, many juveniles of the limpet *Patella cochlear* were located on the shells of adults, and high mortality occurred when they attempted to make the transition from shell to rock surface (Branch 1974, 1975a). These interactions are most

frequent when recruitment is intense and growth rates are high, therefore leading to density-dependent mortality (Connell 1961a, 1985). Competition for space should be a minor cause of death among juveniles in many populations that do not experience density-dependent mortality.

Competition for food can lead to reduced early juvenile growth (oysters, Zajac et al. 1989; oysters and ascidians, Osman et al. 1990; amphipods, Hill 1992) but there is only equivocal evidence that it causes early juvenile mortality in the field (oysters, Osman et al. 1989, Zajac et al. 1989; snails, Branch & Branch 1980; amphipods, Hill 1992). Laboratory studies have shown that food availability to early juveniles can affect their growth and survival (oysters, Zajac et al. 1989; abalone, McBride 1990; snails, Gosselin & Chia 1994), but there is no evidence yet that food is limiting for early juveniles in the field.

Survival through the first days of juvenile life can also depend on the amount of energy reserves remaining after metamorphosis, since feeding in some species is initially insufficient to meet the needs of the early juvenile (oysters, Whyte et al. 1992). Feeding by early juveniles may be delayed or assimilation of food may be incomplete due to a transition in metabolism (clams, Guillou & Tartu 1994). Early juvenile survival might therefore be dependent on the amount of energy accumulated during the larval phase or remaining from the initial content of the egg. There is in fact considerable variation in duration of survival without food during the early juvenile period. Newly hatched *Nucella emarginata*, a muricid snail, can survive 50 to 120 d of starvation (Gosselin & Chia 1994), while hatchling *Ocenebra* sp. (Luckens 1970) and *Urosalpinx cinerea* (Rittschof et al. 1983), also muricids, survive a week or less without food. The importance of energy depletion as a cause of early mortality may therefore vary substantially among species.

Diseases have caused high mortality in late juvenile seastars *Acanthaster planci* (Zann et al. 1987) and in juvenile oysters ≤ 25 mm (Davis & Barber 1994). Blooms of toxic dinoflagellates also kill juvenile oysters (Luckenbach et al. 1993). Generally, however, little is known of the prevalence of diseases and parasites or of the impact of toxic phytoplankton on juveniles. The ephemeral nature of remains of dead early juveniles, largely due to their rapid invasion by protozoans and bacteria, render positive identification of these factors difficult. These factors may nevertheless be important, and a better understanding of their contribution to early juvenile mortality is needed.

In many species, a considerable reorganization of the body occurs at metamorphosis (e.g. see Chia & Burke 1978). During this process, developmental complications that are genetically determined or induced

by environmental conditions such as temperature extremes, salinity extremes, or ultraviolet radiation might produce dysfunctional juveniles. Physiological defects have been proposed as possible causes of mortality in cases where traditional biotic and abiotic mortality factors could not account for early juvenile mortality (MacKenzie 1981, Gosselin & Chia 1995a, Roegner & Mann 1995, Gosselin & Qian 1996).

Abiotic factors

While predation is the most documented cause of mortality, abiotic factors might be locally more important, as in intertidal habitats where conditions fluctuate to extremes over just a few hours, or in bays and estuaries where seasonal changes in physical conditions are amplified by freshwater runoff and greater thermal fluctuations relative to the open ocean.

Early juveniles inhabiting the intertidal zone, when emersed, can lose water much faster than adults because of the greater surface-to-volume ratio of small individuals (Foster 1971, Wolcott 1973). Early juveniles are consequently much more vulnerable to desiccation stress than adults (barnacles, Foster 1971; limpets, Davies 1969, Wolcott 1973, Branch 1975b; snails, Gosselin & Chia 1995a). Early juvenile mortality in the field has been attributed to desiccation in barnacles (Denley & Underwood 1979), limpets (Wolcott 1973, Branch 1975b, Lewis & Bowman 1975) and snails (Behrens 1972).

Thermal tolerance is also lower in early juveniles than in adults (Kinne 1970, Gosselin & Chia 1995a), but field temperatures are reported to be within early juvenile tolerance limits (crabs, Brown et al. 1992; limpets, Wolcott 1973; snails, Gosselin & Chia 1995a; seastars, Chen & Chen 1993). For instance, the occurrence of temperature extremes over a 3 yr period did not correspond to increased levels of mortality in the bivalve *Cerastoderma edule* (Guillou & Tartu 1994). It is not clear, however, whether thermal tolerance limits of early juveniles are exceeded in tropical and polar climates, since most studies to date have examined organisms from temperate habitats. In addition, suboptimal temperatures may be indirectly responsible for early juvenile mortality by aggravating the effects of other factors such as reduced salinity and desiccation (Wolcott 1973, Gosselin & Chia 1995a).

Persistent low salinity levels cause early juvenile mortality in crabs (Brown et al. 1992, Brown & Bert 1993), snails (Berry & Hunt 1980), urchins (Himmelman et al. 1984), and seastars (Chen & Chen 1993). Nevertheless, short-term reductions in salinity (e.g. during a low tide) were not lethal to early juvenile limpets (Wolcott 1973) or snails (Berry & Hunt 1980),

and tolerance limits of early juveniles have in some cases been found to exceed the range of conditions occurring in the natural habitat (crabs, Brown et al. 1992; seastars, Chen & Chen 1993). Low salinity becomes a greater threat to early juveniles when combined with suboptimal temperatures (Berry & Hunt 1980, Brown et al. 1992, Brown & Bert 1993, Chen & Chen 1993).

Water motion can cause early juvenile mortality in a variety of ways. For instance, mortality can be caused by the transport and deposition of sand (abalones, Schiel 1993) or silt (ascidians, Young & Chia 1984) on early juveniles. Recently settled barnacles can also be killed as a result of scouring by waterborne material (Connell 1961a) or dislodgement by algal fronds moving with the waves ('algal whiplash', Lewis 1964, Hawkins 1983). However, dislodgement of non-sessile animals by wave action (Behrens 1972, Sarver 1979, Gosselin & Chia 1995a) should not simply be equated with death. Indeed, most early juveniles sink very slowly due to their large surface-to-volume ratio and, in several bivalve and gastropod species, to the release of a thin mucous thread which allows them to reattach or drift until they encounter a favorable habitat (Sigurdsson et al. 1976, Vahl 1983, Martel & Chia 1991a, b, Armonies 1992, 1994).

Solar radiation, particularly the ultraviolet component, can cause mortality in encapsulated gastropod larvae developing in intertidal (Rawlings 1996) and shallow subtidal habitats (Biermann et al. 1992) and in planktonic larvae in coral reef-waters (Gleason & Wellington 1995). Exposure to natural UV radiation can also cause rapid mortality in postlarval phases of a variety of 'shade-loving' species, including bryozoans and ascidians (age and size not specified, Jokiel 1980). Among animals with protective shells, tubes or pigmentation, the less-protected early juveniles may be highly vulnerable (Jokiel 1980). The actual effects of solar radiation on early juveniles have yet to be determined.

In conclusion, the available information suggests that desiccation (intertidal habitats) and predation are widespread and may often be the most important causes of early juvenile mortality. Their importance as selective pressures is supported by studies indicating a close association of early juveniles with structurally complex microhabitats (Bayne 1964, Sarver 1979, Wahle & Steneck 1991, Smith & Herrnkind 1992, Sandt & Stoner 1993, Gosselin & Chia 1995b) which constitute refuges from these factors (Gosselin & Chia 1995b). However, some early juveniles remain exposed to predators and desiccation throughout juvenile life, particularly juveniles of sessile species. This suggests either that predation and desiccation have not been important selective pressures on early juve-

niles of these species or that other solutions have been found (e.g. physiological or chemical defenses): in both cases, other factors may presently be responsible for more mortality than are predation or desiccation. At present, however, there is insufficient information on the occurrence of most other factors or on the frequency of exposure of early juveniles to determine their relative importance as causes of death. Factors such as solar radiation, diseases, and 'internal' causes (energy depletion, physiological defects appearing during metamorphosis) may have a significant effect on survival in some populations.

IMPLICATIONS OF JUVENILE MORTALITY

Population parameters

The high levels of early juvenile mortality reported in Table 1 are clearly sufficient to cause profound transformations of cohorts. Small variations in early juvenile mortality should therefore have significant repercussions on population size. Field studies have shown that early juvenile mortality does indeed have a determining effect on benthic population parameters (Connell 1985, Osman et al. 1990, 1992, Osman & Whitlatch 1995, Roegner & Mann 1995). Mortality during the early juvenile period has been shown to regulate population size (lobsters, Smith & Herrnkind 1992; polychaetes, Qian & Chia 1994; crabs, Eggleston & Armstrong 1995; oysters, Roegner & Mann 1995) and distribution (hydroids, Yund et al. 1987; nudibranchs, Sarver 1979; barnacles, Connell 1985; urchins, Rowley 1989; abalones, McShane 1991; oysters, Roegner & Mann 1995). Even among benthic macroalgae, colonization of free space can largely depend on the survival of a few individuals through an early postsettlement period (cf. review by Vadas et al. 1992). In addition, early juvenile mortality can have a determining effect on community composition (Osman et al. 1992, Ólafsson et al. 1994, Osman & Whitlatch 1995).

Although cohorts generally sustain heavy losses during the larval period, mortality during the early juvenile phase can exceed larval mortality. In the ascidian *Diplosoma similis*, for instance, mortality during the brief planktonic larval period, lasting ≤ 15 min, was 29% whereas mortality during the first day following settlement was 50% (Stoner 1990). The processes involved in early juvenile mortality can also be at least as important as larval processes (dispersal, mortality, settlement) in determining the distribution and abundance of adults (urchins, Rowley 1989; abalone, McShane 1991; ascidians, Osman et al. 1992; polychaetes, Qian & Chia 1994).

Any event that would influence the number of individuals surviving to the end of this early period would thus have a greater effect on survival to first reproduction than comparable events in later periods of life, a conclusion also reached by Osman (1987) for the vermetid *Serpulorbis squamigerus*. A trait that would enhance early juvenile survivorship even slightly should therefore be more strongly favoured than a trait producing a similar enhancement of survival at later stages of life. In evolutionary terms, early juvenile traits should be more dynamic and responsive to environmental change than traits occurring later in life.

Age at maturity

One postulate of life history theory is that demographic pressures, including juvenile mortality, are a major evolutionary determinant of age at maturity (Bell 1980, Stearns & Koella 1986, Stearns 1992). If age at maturity is reduced, fewer individuals may die before reaching maturity. When increased survivorship to maturity due to earlier maturation outweighs the physiological and developmental costs (cf. Stearns 1992) of this change, then earlier maturation is favoured. Although age at maturity can be influenced by a variety of factors, such as growth rate, fecundity, and developmental, phylogenetic and environmental constraints (Roff 1984, Stearns & Koella 1986, Stearns 1992, Hutchings 1993), the timing and magnitude of juvenile mortality are nevertheless believed to be major determinants of age at maturity.

Some life history models regarding age at maturity assume that, after the larval period, a constant proportion of the population dies in each time unit (Roff 1984, Stearns 1992), and that mortality rates reach low, stable levels only at maturity (but see Stearns & Koella 1986). The data reviewed herein indicate these assumptions often do not hold among benthic marine invertebrates. Instead, survivorship decreases exponentially in most species during an initial period lasting up to ~4 mo (Fig. 1). The selective pressure exerted by juvenile mortality is therefore highly age dependent, being most intense during a brief initial period, rather than constant or linearly decreasing as a function of age.

Demographic pressure favouring a change in age at maturity will be greatest when a small change in age at maturity produces a large change in number of individuals surviving to maturity. Using a generalized survivorship curve (Fig. 2) patterned on Fig. 1, we observe that a reduction in age at maturity during a period of high mortality, from an age α to $\alpha-1$, could lead to a substantial increase in number of individuals reaching

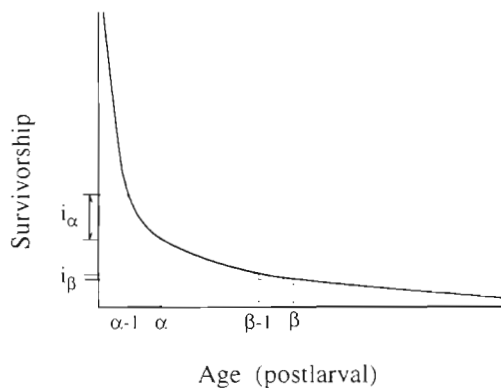


Fig. 2. Implications for age at maturity of a survivorship curve with an initial period of exponential decrease. This generalized model of age-specific survivorship is based on data shown in Fig. 1. A reduction in age at maturity in a species maturing during the exponential phase (e.g. from α to $\alpha-1$) is shown to result in a greater increase (i_α) in survival to maturity than an equal change (e.g. from β to $\beta-1$) in a species maturing after the exponential phase

maturity (i_α). A similar reduction in age at maturity from a later age β to $\beta-1$ would result in a much smaller increase (i_β) in survival to maturity. Given the pattern of mortality described in Fig. 1, juvenile mortality is likely to have little influence on age at maturity in species maturing beyond the age of 4 mo since mortality then remains low. However, species maturing earlier might experience much stronger selection in favour of an earlier age at maturity. Juvenile mortality would therefore have a more restricted influence on age at maturity than had been postulated. Juvenile mortality may be a major determinant of age at maturity only in species maturing within ~4 mo, whereas in late maturing species juvenile mortality may play a minor role, if at all. Age at maturity among early and late maturing species could thus be largely controlled by different factors.

The postulate that juvenile mortality is a determinant of age at maturity has not been verified with empirical data for benthic marine invertebrates. We therefore collated published data on age at first reproduction for 92 species of benthic marine invertebrates distributed among 6 phyla (Appendix 1). Significantly, benthic marine invertebrates were largely partitioned into 2 groups (Fig. 3A); 21.7% of these species matured within 45 d after beginning juvenile life, whereas 59.8% matured after at least 1 yr. With the exception of a modest peak at 6 mo, frequencies of age at first reproduction beyond the first 4 mo remained low up to the age of 12 mo (Fig 3A). The influence of juvenile mortality on age at maturity is expected to differ substantially among these 2 groups and, as a result, the timing of age at maturity in the 2 groups could be largely controlled by different selective pressures.

If the pattern of juvenile mortality is a major determinant of age at maturity among species maturing within ~4 mo of juvenile life, then the distribution of ages at maturity within this period should be skewed towards early ages. Frequencies of age at first reproduction among age classes ≤ 4 mo (Fig. 3B) were indeed skewed towards younger age classes. Twenty species began to reproduce before or at the age of 45 d, but only 6 did so during the following 75 d (i.e. to the age of 4 mo; Fig. 3B). Physiological and developmental constraints would ultimately set the minimum limit for age at maturity, resulting in the observed clustering of species within the first weeks of postlarval life, with frequencies peaking at 15 to 30 d (Fig. 3B). Unfortunately, the direct relationship of survivorship as a function of age at first reproduction could not be determined because there were few species for which both parameters had been fully documented. Nevertheless, these age at first reproduction results are consistent with the hypothesis that juvenile mortality has influenced age at maturity in species maturing within ~4 mo.

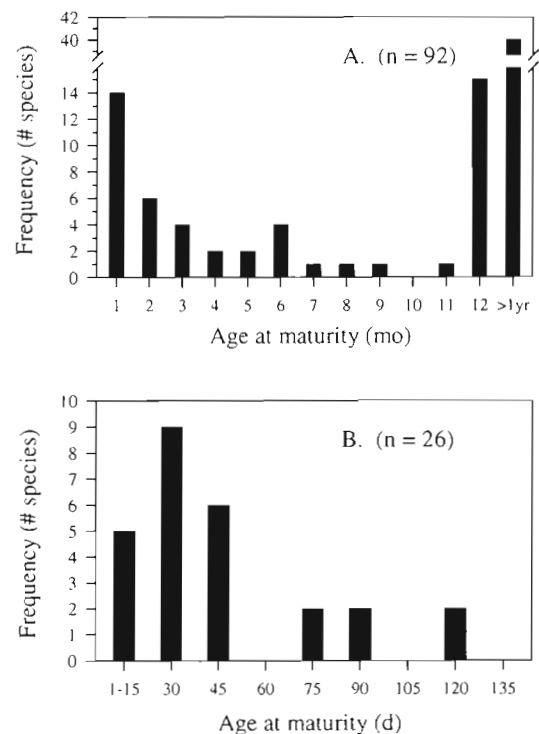


Fig. 3. Frequency distribution of age at first reproduction among benthic marine invertebrates, as obtained from published reports (data and sources listed in Appendix 1). Age represents the time elapsed since the onset of juvenile life, and thus does not include the egg-to-juvenile period. (A) All species pooled with 30 d intervals. (B) Species with age at maturity ≤ 135 d pooled with 15 d intervals

CONCLUSION

Heavy mortality during the larval phase has often been used as an argument to justify or encourage larval biology studies because the processes at work during the larval phase should play an important role in the evolution of the species. The same argument can also be made for the early juvenile phase. High early juvenile mortality is widespread among benthic marine invertebrates. We suggest that extreme vulnerability at the onset of juvenile life to a range of mortality factors is a shared trait that is largely responsible for the common pattern of exponential decrease in survivorship during juvenile life. Natural variation within this pattern, however, would be largely a consequence of variation in intensity of mortality factors. A better understanding of the sources of variation of early juvenile mortality will undoubtedly help resolve the problematic link (cf. Ólafsson et al. 1994) between larval abundance and recruitment to the adult segment of the population.

Although selective pressures specifically operating early in juvenile life may influence the evolutionary development of age at maturity, the effect of juvenile mortality is likely to be limited to species maturing within ~4 mo and will therefore not be equal or directly comparable among all species. Our limited knowledge of juvenile mortality factors, which precludes a ranking of factors as causes of mortality, may be the most important obstacle to progress in understanding the adaptive and evolutionary significance of juvenile and life history traits.

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Appendix 1. Age at first reproduction of 92 species of benthic marine invertebrates. Age is defined here as starting at the onset of juvenile life

Taxa	Age at first reproduction	Source
ANNELIDA, POLYCHAETA		
<i>Dinophilus gyrotiliatus</i>	<11 d ^a	Åkesson & Costlow (1991)
<i>Ophryotrocha diadema</i>	~13 d ^a	Åkesson (1976)
<i>Pseudopolydora kempj japonica</i>	2 wk	Miyohara (1979)
<i>Ophryotrocha maculata</i>	~24–29 d ^a	Åkesson (1973)
<i>Ophryotrocha puerilis</i>	~28 d ^a	Åkesson (1967)
<i>Romanchella pustulata</i>	40–50 d	Canete & Ambler (1990)
<i>Armandia brevis</i>	6 wk	Hermans (1966)
<i>Capitella</i> sp. 1	67.1 d ^a	Bridges et al. (1994)
<i>Streblospio benedicti</i>	78.9 d ^a	Bridges et al. (1994)
<i>Kinbergonuphis simoni</i>	5–10 mo ^a	Hsieh & Simon (1991)
<i>Typosyllis pulchra</i>	6–9 mo ^a	Heacox (1980)
<i>Eteone longa</i>	1 yr	Rasmussen (1973)
<i>Nereis vexillosa</i>	In 2nd yr	Roe (1975)
<i>Melinna palmata</i>	2 yr	Grehan (1991)
MOLLUSCA, POLYPLACOPHORA		
<i>Lepidochitona fernaldi</i>	~6 mo ^a	Eernisse (1984)
<i>Mopalia mucosa</i>	In 2nd yr	Heath (1907)
<i>Onithochiton quercinus</i>	2 yr	Otway (1994)
<i>Plaxiphora albida</i>	2 yr	Otway (1994)
MOLLUSCA, BIVALVIA		
<i>Mytilus trossulus</i> (published as <i>M. edulis</i>)	1–2 mo	Suchanek (1981)
<i>Spisula solidissima</i>	3 mo ^b	Chintala & Grassle (1995)
<i>Bankia setacea</i>	4 mo	Quayle (1955, 1959)
<i>Mytilus californianus</i>	4–8 mo	Suchanek (1981)
<i>Lasaea subviridis</i>	6–8 mo ^a	Strathmann (1987)
<i>Tapes philippinarum</i>	~1 yr	Holland & Chew (1974)
<i>Albra tenuis</i>	1 yr	Bachelet (1989)
<i>Idas argenteus</i>	1 yr	Dean (1993)
<i>Crassostrea virginica</i>	1–2 yr	Galtsoff (1964)
<i>Calyptogena magnifica</i>	1–4 yr	Kennish & Lutz (1992)

(Appendix continued on next page)

Appendix 1 (continued)

Taxa	Age at first reproduction	Source
MOLLUSCA, BIVALVIA (continued)		
<i>Cerastoderma edule</i>	1.5 yr	Seed & Brown (1977)
<i>Lithophaga lithophaga</i>	2+ yr	Galinou–Mitsoudi & Sinis (1994)
<i>Nitidotellina nitidula</i>	2 yr	Kawai et al. (1993)
<i>Phacosoma japonicum</i>	2–5 yr ^c	Sato (1994)
<i>Tresus nuttallii</i>	3 yr	Campbell et al. (1990)
<i>Tresus capax</i>	3–4 yr	Bourne & Smith (1972)
<i>Panope abrupta</i>	3/4 yr ^d	Andersen (1971)
<i>Modiolus modiolus</i>	4–6 yr	Seed & Brown (1977)
<i>Chlamys islandica</i>	4–9 yr	Pedersen (1994)
<i>Arctica islandica</i>	7 yr	Rowell et al. (1990)
MOLLUSCA, GASTROPODA		
<i>Alderia modesta</i>	10 d	Seeleman (1967)
<i>Olea hansineensis</i>	2–3 wk	Chia & Skeel (1973)
<i>Phestilla sibogae</i>	20 d	Miller & Hadfield (1990)
<i>Doridella steinbergae</i>	3–4 wk	Strathmann (1987)
<i>Eubranchus rustyus</i>	3–5 wk	Robilliard (1971)
<i>Stylocheilus longicauda</i>	27 d ^a	Switzer–Dunlap & Hadfield (1979)
<i>Aplysia juliana</i>	35–45 d ^a	Hadfield & Switzer–Dunlap (1990)
<i>Aplysia dactylomeda</i>	66 d ^a	Switzer–Dunlap & Hadfield (1979)
<i>Littorina</i> sp.	~140 d ^a	Boulding & Van Alstyne (1993)
<i>Dolabella auricularia</i>	180–294 d ^a	Switzer–Dunlap & Hadfield (1979)
<i>Lacuna vincta</i>	~7 mo	Smith (1973)
<i>Lacuna pallidula</i>	~8 mo	Smith (1973)
<i>Littorina littorea</i>	8.5 mo ^e	Hughes & Roberts (1980)
<i>Tritonia diomedea</i>	277 d ^a	Kempf & Willows (1977)
<i>Lottia digitalis</i>	~1 yr	Choat & Black (1979)
<i>Retusa obtusa</i>	~1 yr	Berry (1989)
<i>Umbonium costatum</i>	1 yr	Noda et al. (1995)
<i>Umbonium vestiarium</i>	~1 yr	Berry (1989)
<i>Bembicium vittatum</i>	1 yr	Black et al. (1994)
<i>Trichotropsis cancellata</i>	1 yr	Yonge (1962)
<i>Nucella emarginata</i>	1 yr	Spight (1982)
<i>Littorina nigrolineata</i>	18 mo ^e	Hughes & Roberts (1980)
<i>Littorina rudis</i>	18 mo ^e	Hughes & Roberts (1980)
<i>Nerita atramentosa</i>	20 mo	Underwood (1975)
<i>Nucella canaliculata</i>	2–3 yr	Spight (1975)
<i>Nucella lapillus</i>	2–3 yr	Crothers (1985)
<i>Drupella cornus</i>	2.5–3.5 yr	Black & Johnson (1994)
<i>Littorina neritoides</i>	3 yr ^e	Hughes & Roberts (1980)
<i>Haliotis discus hannai</i>	3 yr	Sakai (1962)
<i>Haliotis laevigata</i>	~3 yr	Shepherd & Laws (1974)
<i>Haliotis ruber</i>	~3–4 yr	Shepherd & Laws (1974)
<i>Haliotis iris</i>	~3–4 yr	Poore (1973)
<i>Strombus gigas</i>	3.2–3.3 yr	Appeldoorn (1990)
<i>Philine gibba</i>	3.75 yr	Seager (1983)
<i>Haliotis tuberculata</i>	~4 yr	Poore (1973)
<i>Nucella lamellosa</i>	4 yr	Spight (1975)
<i>Buccinum undatum</i>	4–7 yr	Gendron (1992)
<i>Busycon carica</i>	9 yr ^d	Castagna & Kraeuter (1994)
ARTHROPODA, CRUSTACEA		
<i>Chthamalus fissus</i>	3 wk	Page (1984)
<i>Chthamalus anisopoma</i>	42 d	Lively (1986)
<i>Semibalanus balanoides</i>	11 mo	Connell (1985)
<i>Pollicipes polymerus</i>	100–175 d	Page (1986)
<i>Dorhynchus thomsoni</i>	1–2 yr	Hartnoll & Rice (1985)
<i>Tetraclita squamosa</i>	~2 yr	Hines (1978)
UROCHORDATA, ASCIDIACEA		
<i>Botryllus schlosseri</i>	25–70 d	Grosberg (1988)
<i>Didemnum candidum</i>	6–8 wk	Hurlbut (1991a)

Appendix 1 (continued)

Taxa	Age at first reproduction	Source
BRYOZOA		
<i>Bugula neritina</i>	~35 d	Keough (1986)
ECHINODERMATA		
<i>Strongylocentrotus purpuratus</i>	2 yr	Gonor (1972)
<i>Strongylocentrotus droebachiensis</i>	2–3 yr	Munk (1992)
<i>Centrostephanus rodgersii</i>	~3 yr	King et al. (1994)
<i>Cucumaria pseudocurata</i>	~3 yr	Rutherford (1973)
<i>Amphiura filiformis</i>	3 yr	Muus (1981)
<i>Amphiura chiajei</i>	~4 yr	Munday & Keegan (1992)
<i>Pisaster ochraceus</i>	5 yr	Menge (1974)
^a Data obtained from laboratory reared individuals		
^b <i>Spisula solidissima</i> was previously reported to mature after 1–4 yr (Ropes 1979, Sephton & Bryan 1990)		
^c Range of ages at maturity corresponds to site-specific differences		
^d Data for male / female		
^e Mean age at maturity		

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