

REVIEW

Role of early post-settlement mortality in recruitment of benthic marine invertebrates

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ABSTRACT: Newly settled invertebrates usually are subject to high rates of mortality (Type III survivorship). Therefore, knowledge of early post-settlement events is critical in determining if and when patterns of abundance and distribution of juveniles reflect settlement patterns. Causes of mortality of early juvenile invertebrates include delay of metamorphosis, biological disturbance, physical disturbance and hydrodynamics, physiological stress, predation, and competition. Predation is the best documented cause of early mortality, particularly for mobile species. Other possible causes which have not yet been investigated are developmental abnormalities, insufficient energy reserves, disease and parasitism. In most studies of sessile invertebrates, early post-settlement mortality did not obscure the relationship between recruit and settler abundance. This relationship appears to be more variable among mobile species for which migration also can modify the distribution of settlers. There is still insufficient data to support general conclusions about the conditions under which recruitment rate can be predicted from settlement rate. Studies have found evidence of the effects of both settlement and early post-settlement mortality on the distribution of some sessile species at small spatial scales, but mortality appears to have less influence at larger scales. Much of the present knowledge of the early post-settlement period has come from studies of barnacles and ascidians and more information is needed for other groups of benthic marine invertebrates, particularly mobile species. The relative importance of mortality during the early post-settlement period compared to other life history stages can only be determined in studies which examine several stages.

KEY WORDS: Early post-settlement mortality · Settlement · Recruitment · Marine invertebrates · Density dependence · Spatial scale · Disturbance · Predation · Physiological stress · Competition

INTRODUCTION

Over the last 15 years, our understanding of recruitment variability of benthic marine invertebrates, and its role in population and community dynamics, has increased considerably. Variation in recruitment rate has been shown to affect competitive interactions (Sutherland & Ortega 1986), predation (Fairweather 1988, Menge et al. 1994, Robles et al. 1995) and other community level processes on rocky shores (for review see Booth & Brosnan 1995), and there is increasing evidence that adult population size is limited by recruitment for species on hard substrata in both intertidal (e.g. Connell 1985, Sutherland 1987, 1990, Menge &

Farrell 1989, Raimondi 1990, Menge 1991) and subtidal habitats (e.g. Hughes 1990, Karlson & Levitan 1990). Consequently, recent models of population dynamics (Roughgarden et al. 1985, Roughgarden & Iwasa 1986, Alexander & Roughgarden 1996) and community organization on rocky bottoms (Menge & Sutherland 1987) incorporate recruitment variability as a limiting factor. Recruitment limitation has received less attention from researchers studying soft bottom communities (but see Peterson & Summerson 1992, Peterson et al. 1996, Butler & Herrnkind 1997). A recent review by Ólafsson et al. (1994) concluded that larval supply is generally not limiting, and therefore is probably not a major determinant of patterns of species distribution and abundance in sedimentary habitats. However, interactions between adults and

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settlers/recruits have been shown to affect recruitment rate (Peterson 1982, Peterson & Black 1993, Ólafsson et al. 1994, Thrush et al. 1996) and may limit the density of infauna (Thorson 1966, Woodin 1976, Peterson 1979).

Many factors can influence the intensity and variability of recruitment of benthic marine invertebrates. The abundance of larvae in the water column is influenced by adult reproductive cycles, larval mortality (Roughgarden et al. 1988), and settlement rate itself (Gaines et al. 1985). Physical factors which affect dispersal of larvae include wind (Bertness et al. 1996, Morgan et al. 1996), linear oceanographic features (for review see Kingsford 1990), upwelling (Farrell et al. 1991, Roughgarden et al. 1991, Wing et al. 1995), cold water plumes (Ebert & Russell 1988), water residence time in estuaries (Gaines & Bertness 1992), and vertical distribution of larvae in the water column (Grosberg 1982, Le Fèvre & Bourget 1991, Miron et al. 1995). Settlement onto the substratum occurs once the larvae reach a suitable habitat. Settlement is a process that may include reversible or irreversible contact with the substratum, exploratory behaviour, orientation, and metamorphosis (which may occur before, during, or after contact with the substratum) (Pawlik 1992). At this time, the pattern of larval supply may be modified by larval response to various abiotic and biotic cues on the substratum, including surface texture or chemistry, conspecifics, and the presence or absence of other macrobenthic species or microbial films (reviewed by Pawlik 1992). Hydrodynamic conditions may determine the scale at which active selection of a substratum occurs (Butman 1987).

In this review, we will focus on the period between settlement and recruitment. Monitoring newly settled individuals is difficult due to their small size and because sampling must be frequent enough to avoid confounding patterns of settlement with patterns modified by early post-settlement mortality. For convenience, most researchers measure recruitment days to months after settlement (e.g. Shanks & Wright 1987, Ebert & Russell 1988, Gaines & Bertness 1992, Ebert et al. 1994, Wing et al. 1995). Knowledge of early post-settlement events is critical in determining if and when recruitment patterns reflect settlement patterns. In situations where early post-settlement events substantially alter the abundance of recruits, they may regulate population size and adult distribution, and reduce the importance of interactions between adults. Goselin & Qian (1997) recently reviewed 30 studies of rates of mortality of juvenile benthic invertebrates. They discussed causes of early post-settlement mortality, methods of quantifying mortality rates, and the influence of juvenile mortality on age at maturity. In our review, we strive for a more comprehensive exam-

ination of the major functional groups of benthic marine invertebrates, including sessile species on hard substrates, mobile epifauna, and infauna in sedimentary habitats. We begin by discussing problems with the definition of recruitment and the early post-settlement period. We then review the rates and patterns of early post-settlement mortality reported in the literature and discuss factors which affect the survival of newly settled and early juvenile individuals. Finally, we address the influence of mortality of recent settlers on patterns of abundance and distribution of recruits.

EARLY POST-SETTLEMENT PERIOD

Recruitment is an operational term rather than a biological event, and consequently, has been defined in many different ways. Definitions of recruitment of benthic marine invertebrates include (Booth & Brosnan 1995) (1) presence of juveniles after a specified time interval, (2) attainment of a specified size, (3) survival through a period of high early mortality, (4) survival to a size when the settlers become vulnerable to predators, and (5) retention on a particular sieve mesh size (in soft bottom studies, Butman 1987). Differences in the time interval to recruitment are inevitable due to differences in the life histories and lifespans of organisms. For example, it might not be reasonable to consider a barnacle which reaches maturity in 6 wk and a slow-growing coral which may live more than 20 yr to be recruits after the same time interval. Also, the time interval before a settler can be censused by an observer (recruitment *sensu* Keough & Downes 1982) will differ among species because of variability in initial size and growth rate (Rumrill 1989) and also because of differences in our ability to sample different habitats.

Booth & Brosnan (1995) have suggested that survival through high (usually Type III, *sensu* Deevey 1947) mortality in the first few days to weeks after settlement may be a biologically meaningful definition of recruitment. This suggestion is reasonable, considering that early mortality often follows this pattern (see Table 1 and the following section). However, survival curves of early juveniles of some species exhibit other patterns, and this type of information is not available for many species. A combination of criteria may be necessary to define the early post-settlement stage for a particular species. For mobile epibenthic species, differences in behaviour and habitat between early juveniles and older juveniles and adults may help define the time at which recruitment occurs. Because recruitment is not a distinct biological event like settlement, definitions will continue to differ from species to species. However, efforts should be made to harmonize definitions

of recruitment (or to redefine the term, see 'Conclusions and directions for future research') and to use biologically meaningful criteria when defining the early post-settlement period.

Comparisons of studies are complicated by differences in sampling interval. Variation in sampling interval has been shown to affect estimates of recruitment and (or) early post-settlement mortality of oysters (Michener & Kenny 1991) and barnacles (Minchinton & Scheibling 1993b, Gosselin & Qian 1996). Minchinton & Scheibling (1993b) found that estimates of recruitment and early post-settlement mortality of the barnacle *Semibalanus balanoides* decreased significantly when the sampling interval was changed from 1.3 to 2.1 d, and continued to decrease exponentially with increasing sampling interval. Sampling interval also altered comparisons of early post-settlement mortality rate between intertidal zones. These results suggest that comparisons of studies with different sampling regimes should be made cautiously.

RATES AND PATTERNS OF EARLY MORTALITY

In the field, monitoring mortality immediately after settlement is difficult, if not impossible, for many species. However, without knowledge of events shortly after settlement, post-settlement mortality can be underestimated and settlement patterns can be confounded by patterns produced by or modified by mortality. Mortality rate in the field during the first few hours or days after settlement is known for only 2 groups of benthic marine invertebrates: barnacles and ascidians. Survival rates of barnacle cyprids during the first 24 to 48 h range from 22 to 87% (*Balanus glandula*, Gosselin & Qian 1996; *Semibalanus balanoides*, Connell 1961, Kendall et al. 1985, Bergeron & Bourget 1986; *Chthamalus fragilis*, Young 1991), and mortality risk does not necessarily decline after metamorphosis (*S. balanoides*, Wetthey 1986). In studies of colonial ascidians, 50 to >70% of settlers survive the first 24 h (*Diplosoma similis*, Stoner 1990; *Podoclavella moluccensis*, Davis 1987). Mobile species probably also experience elevated mortality immediately after settlement, but survival rates have not been measured. Indirect evidence of high early mortality is provided by Eggleston & Armstrong's (1995) study of Dungeness crabs (*Cancer magister*): settlement patterns and density of first benthic instar crabs were decoupled in less than 48 h. The first day after settlement may be a critical period for many benthic invertebrates. Gosselin & Qian (1996) found that mortality of the barnacle *Balanus glandula* was 1.5 to 6 times higher during the first day after settlement than during the second day. Indeed, for 2 of the 3 cohorts monitored, mortality dur-

ing the first day after settlement was almost as high as total mortality during the subsequent 44 d.

Mortality in the days to weeks after settlement is generally high (Table 1; Gosselin & Qian 1997). In 2 studies of tropical colonial ascidians (*Trididemnum solidum*, van Duyl et al. 1981; *Diplosoma similis*, Stoner 1990), all visible settlers disappeared during the 1 to 4 mo monitoring period. However, neither study was able to follow the fate of individuals which settled in crevices or other protected microhabitats. Small individuals of some species have high survival rates. For example, 63% of settlers of the colonial ascidian *Podoclavella moluccensis* survived 1 mo (Davis 1988a), and 65 to 80% of settlers of the barnacle *Chthamalus anisopoma* survived to reach maturity at 6 wk of age (Raimondi 1990).

Survival curves of new settlers (Table 1) are often Type III: survival rate decreases rapidly and then levels off (Deevey 1947). Gosselin & Qian (1997) pooled data from 30 studies of juvenile benthic invertebrates to produce a general survivorship curve and found an interspecific trend of exponentially decreasing survivorship during the first days to weeks after settlement. Decreases in mortality rate of early juveniles with time also have been noted in studies which do not present survival curves (Keough 1986, Keough & Chernoff 1987, Günther 1992). A Type III pattern of mortality can even occur in the benign conditions of the laboratory (e.g. Roegner 1991). However, newly settled invertebrates also exhibit other patterns of survivorship. Hurlbut (1991a) found that mortality rate of a number of sessile species on subtidal panels was higher in the second week after settlement than in the first week, and suggested that the increase in mortality was due to density dependent predation. Early mortality may also follow a Type II survivorship curve in which mortality is independent of age (Table 1). In some cases, however, the reported survival curve may represent only a portion of the overall curve. High mortality may have occurred in the first hours to days after settlement before survival was monitored, or mortality rate may level off over a longer time interval than the period of study. However, Gaines & Roughgarden (1985) found that weekly survivorship of the barnacle *Balanus glandula* was independent of age for the entire first year of life, and that survival rate of settlers monitored from the first low tide after settlement did not differ from that of older barnacles.

VARIABILITY IN EARLY POST-SETTLEMENT MORTALITY

Studies examining variability in early post-settlement mortality have found variation at several spatial

Table 1. Summary of studies examining patterns of survival of recently settled benthic marine invertebrates. Location indicates if the settlers were monitored in their original location or if they were transplanted (trans) (nat: settled in field; lab: settled in laboratory); na: not applicable

	Location	Sampling interval	Sampling period	Survival rate (%)	Standardized survival rate (% wk ⁻¹)	Survival curve type	Sources of variability in survival rate	Source
(a) Sessile species								
Cirripedia								
<i>Chthamalus fissus</i>	Original	1 mo	18 mo	0–20	89–93 (1st 2 mo)	II, III	Cohort, site	Sutherland (1990)
<i>Chthamalus anisopoma</i>	Original	3 / 7 d	60 d	65–80	91–92	II	Cohort	Raimondi (1990)
	Trans (nat)	1 wk	90 d	0–90	92–99	III, II, I	Tidal height	Raimondi (1991)
	Trans (nat)	5–15 d	40 d	10–90	84–98	III, II	Rock type, tidal height, site	Raimondi (1988b)
<i>Balanus eburneus</i>	Trans (nat)	2–3 d	12 d	65–95	80–97	II, I	Site	Bingham (1992)
<i>Semibalanus balanoides</i>	Original	1 d	2 mo	6–70	90–97	III	Cohort	Connell (1961)
	Original	1 d	6 wk	5–90	85–98	Mostly III	Cohort	Welsh (1986)
<i>Balanus amphitrite</i>	Original	1 d	1–2 wk	0–90	50–95	III, II, I	Cohort, panel, substrate	De Wolf (1973)
<i>Balanus crenatus</i>	Original	1 d	2 wk	0–100	50–100	III, II, I	Cohort	De Wolf (1973)
<i>Balanus glandula</i>	Original	1 d	42 d	22	87	III	Tidal height, exposure, cohort	Gosselin & Qian (1996)
Ascidacea								
<i>Ascidia nigra</i>	Original, trans (lab)	1 d–1 wk	45 d	2 to 18	85–87	III, II, I	Date, depth	Goodbody (1963)
<i>Diplosoma similis</i>	Original	1 d	28 d	0	10 (1st wk)	III	Settlers in crevices (10%) not monitored	Stoner (1990)
<i>Potoclavella cylindrica</i>	Original	1 d	30 d	11–78	79–95	III, II	Substratum	Davis (1987)
<i>Didemnum candidum</i>	Original	3 d	18 d	20–40	69–77	III	Depth, transplants between depths	Hurlbut (1991c)
<i>Diplosoma</i> sp.	Original	3 d	18 d	10–25	65–70	III	Depth, transplants between depths	Hurlbut (1991c)
<i>Phallusia nigra</i>	Original	1 d	14 d	–15	57	I	na	Hurlbut (1991a)
<i>Didemnum candidum</i>	Original	1 d	14 d	–60	80	I	na	Hurlbut (1991a)
<i>Diplosoma listerium</i>	Original	1 d	14 d	–65	82	I	na	Hurlbut (1991a)
<i>Diplosoma</i> sp.	Original	1 d	14 d	–40	70	I	na	Hurlbut (1991a)
<i>Botryllus schlosseri</i>	Original, trans (nat)	3–10 d	22 d	0–100	68–100	III, II	Site, density	Osman et al. (1992)
<i>Botrylloides</i> sp.	Original	2–30 d	45–57 d	5–10	85–90	III	Year, includes substrate loss	Worcester (1994)
Bryozoa								
<i>Acyonidium hirsutum</i>	Original	2–4 wk	1 yr	0–1	94–99 (1st 3 mo)	III	Year	Seed & Wood (1994)
Octocorallia								
<i>Acyonium siderium</i>	Original, trans (nat)	1 wk–1 mo	1 yr	5–25	89–94 (1st 2 mo)	III	Year, distance from adult	Sebens (1983)
Gastropoda								
<i>Serpulorbis squamigerus</i>	Original	6–10 wk	400 d	20–90	95–99 (1st 3 mo)	III, II	Site	Osman (1987)
Bivalvia								
<i>Cassostrea virginica</i>	Trans (lab)	1 wk	30 d	<15	<80	III	Season	Roegner & Mann (1995)
(b) Mobile species								
Gastropoda								
<i>Lacuna vincta</i>	Original	1 mo	8 mo	4–5	97–98	III	Site, year	Fretter & Manly (1977)
<i>Halotis rubra</i>	Original	4–5 mo	4–5 mo	<5	<95	na	Site	McShane (1991)
<i>Aphysia juliana</i>	Original	1 wk	30 d	0	77	III	na	Sarver (1979)
Bivalvia								
<i>Cerastoderma edule</i>	Original	14 d–1 mo	1 yr	1–10	80–85 (1st mo)	III	Year	Guillou & Tartu (1994)
<i>Tapes japonica</i>	Original	1–2 mo	9 mo	1	95–96 (1st 4 mo)	III	Adult clam density	Williams (1980a)
Polychaeta								
<i>Capitella</i> sp. 1	Trans (lab)	3–4 wk	90–90 d	25–50	91–96	III	Sibling group	Qian & Chia (1994)
Decapoda								
<i>Penaeus merguensis</i>	Original	2 wk	3 mo	<5	<93	III	Cohort-study lasted 3 yr	Haywood & Staples (1993)
Echinoidea								
<i>Strongylocentrotus purpuratus</i>	Original	10–15 d	45 d	5–15	85–87	II/III	Habitat	Rowley (1990)

and temporal scales. Spatial variability in mortality of barnacle settlers has been detected at scales of metres to kilometres (Meadows 1969, De Wolf 1973, Caffey 1982, 1985, Wethey 1986, Bingham 1992). However, in some of these studies, estimates of post-settlement mortality were based on counts of 1 to 2 mo old juveniles (Meadows 1969, Caffey 1982, 1985), and consequently excluded mortality occurring shortly after settlement. Spatial variability in early post-settlement mortality at scales of kilometres also has been reported for the sea hare *Aplysia juliana* (Sarver 1979). In contrast, Keesing et al. (1996) found that early post-settlement mortality of the sea star *Acanthaster planci* did not vary significantly among habitats (front reef slope, reef flat, back reef lagoon) or sites within habitats.

A number of studies which have monitored barnacle cohorts have detected differences in mortality rate between cohorts settling within 1 or 2 d of one another (Connell 1961, De Wolf 1973, Wethey 1986, Kendall & Bedford 1987, Raimondi 1990, Sutherland 1990). Wethey (1986) suggested that temporal dispersion of settlement (i.e. an extended settlement season) is advantageous when there is no temporal trend in mortality, as was the case in his study of *Semibalanus balanoides*. In contrast, Raimondi (1990) and Connell (1961) found that earlier cohorts of barnacles (*Chthamalus anisopoma* and *S. balanoides* respectively) had higher survivorship. They suggested that early settlers fill up the most suitable settlement sites (pits or other concavities), leaving later settlers vulnerable to high temperatures and desiccation or gales. On a rocky shore in England, Bowman (1986) found that limpets (*Patella vulgata*) which settled earlier in the fall had a lower mortality rate than those which settled later. She hypothesized that limpets suffer high mortality if they are not large enough to emigrate from their settlement microhabitat before winter. Variation in mortality among cohorts (determined from size frequency analysis) also has been detected for 2 species of prawns in Australia, *Penaeus merguensis* (Haywood & Staples 1993) and *Penaeus esculentus* (O'Brien 1994a). For both species, cohorts which entered estuaries in summer (the wet season) suffered higher mortality than prawns settling in other seasons.

Intensity and variability of early post-settlement mortality can differ among species which are monitored simultaneously. Bingham (1992) transplanted recruits of mangrove epifaunal species to different channels in a mangrove island and found that mortality of barnacle (*Balanus eburneus*) recruits was greater and more variable than that of ascidians (*Sympyga viride*, *Diplosoma glandulosum*, and *Botryllus planus*) or polychaetes (*Hydroides* sp.). Keesing et al. (1996) transplanted 1 mo old sea stars from the laboratory to the field, and found that the mortality rate of *Acan-*

thaster planci was 5 times higher than that of the larger *Nardoa novaecaledoniae*. Hurlbut (1991a) found that the intensity, age dependence, and density dependence of early post-settlement mortality differed among species in a sessile community on subtidal panels. Such variability in early mortality among species suggests that recruitment patterns measured for one species will not predict patterns for other members of the community, an assumption of some models which strive to predict the effect of recruitment strength on community organization (e.g. Menge & Sutherland 1987).

CAUSES OF EARLY POST-SETTLEMENT MORTALITY

Delay of metamorphosis

For many invertebrate species, delay of metamorphosis eventually results in a decrease in larval condition, substratum selectivity, or ability to metamorphose (for review see Pechenik 1990). Extended larval life also has the potential to affect juvenile survival and condition in some species (Table 2). In the laboratory, delayed metamorphosis reduced survival of juveniles of the polychaete *Capitella* sp. I (Pechenik & Cerulli 1991) and appeared to reduce stress tolerance of the sand dollars *Dendraster excentricus* and *Echinarachinus parma* (Highsmith & Emler 1986). Prolonged larval life decreased survival of juveniles of the nudibranch *Phetilla sibogae* that were raised as lecithotrophic larvae but not of those raised as facultatively planktotrophic larvae (Miller 1993). Unlike planktotrophic larvae, lecithotrophic larvae experience depletion of stored nutrients during delay of metamorphosis, resulting in decreased size at metamorphosis (Miller 1993). An extended competency period had little effect on survival of juveniles of the barnacle *Balanus amphitrite* (Pechenik et al. 1993) and no effect on survivorship of the gastropod *Crepidula fornicata* (Pechenik & Eyster 1989). To date, there is only indirect evidence of delay of metamorphosis in the field (for review see Pechenik 1990). The consequences of prolonged larval life for early post-settlement mortality will depend on how frequently delayed metamorphosis occurs and on how it affects juvenile survival in nature.

Biological disturbance

Accidental ingestion or 'bulldozing' by grazers such as limpets, littorinids and sea urchins has been well documented as a cause of early post-settlement mortality and reduced recruitment of barnacles, limpets,

ascidians, and corals (Table 2). Vulnerability to disturbance by grazers may decrease with size (age) (Miller & Carefoot 1989, Safriel et al. 1994) and substratum heterogeneity (Sammarco 1980, Miller & Carefoot 1989, but see Denley & Underwood 1979). Grazers can also influence the abundance of sessile invertebrates indirectly through their effects on algal abundance. For example, Petraitis (1990) attributed the negative effect of *Littorina littorea* on mussel recruitment to the gastropod's reduction of the algae on which mussels settle. Low densities of grazers may positively affect the abundance (Petraitis 1983), survival (Creese 1982), or condition (Sammarco 1980) of recruits, presumably due to reduction of the abundance of algae and other competitors which either prevent settlement or overgrow recently settled individuals.

On hard substrata, biological disturbance by organisms other than grazers has received less attention. Davis (1988b) found that crabs kill recruits of the colonial ascidian *Podoclavella moluccensis* by trampling them with their sharp dactyls. In the intertidal zone, fucoid algae have both positive and negative effects on barnacle recruitment (Dayton 1971, Hawkins 1983 and references therein). Fucoids have been hypothesized to decrease settlement of barnacles by a whiplash effect or by altering water flow, and to increase (by whiplash) or decrease (by reduced desiccation) early post-settlement mortality (for discussion see Grant 1977, Hawkins 1983). In the only study to directly measure canopy effects on barnacle mortality, Grant (1977) found that an artificial algal canopy (strips of inner tube rubber) decreased post-settlement survival of *Semibalanus balanoides*. Heavy cover of *Fucus* is also associated with decreased limpet (*Patella vulgata*) recruitment (Lewis & Bowman 1975).

Adult infauna in soft-bottom communities can cause mortality of newly settled macrofauna by bioturbation of the sediments (but see McCann & Levin 1989). Peterson (1977) found that removal of the ghost shrimp *Callinassa californiensis*, a deposit feeder, increased recruitment of the clam *Sanguinolaria nuttallii*. He suggested that burial and direct consumption of juvenile clams by *C. californiensis* were the most likely mechanisms for the negative effect of the shrimp on clam recruitment. Brenchley (1981) demonstrated that densities of spionid polychaetes (*Rhynchospio arenicola*) and tanaid crustaceans (*Leptochelia dubia*), particularly small individuals, were decreased by addition of macroinfaunal (the lug worm *Abarenicola pacifica* and the mud shrimps *Ugopebia pugettensis* and *C. californiensis*) or macroepifaunal (the sand dollar *Dendraster excentricus*) burrowers. Addition of sediment also reduced densities, suggesting that physical events were important in the interaction between bioturbators and recruits (Brenchley 1981). In the laboratory, Ahn et

al. (1993) found that the clam *Gemma gemma* reduced survival of recent settlers of another clam (*Mercenaria mercenaria*) in muddy sand but not in sand, and suggested that the increased mortality in muddy sand was due to burial and exposure to pore water metabolites from sediment reworking by *G. gemma*. Interference with feeding can also cause early post-settlement mortality. Cummings et al. (1996) found that the tube building spionid polychaete *Boccardia syrtis* decreased survival of early juvenile clams (*Macoma liliana*) in the laboratory. The polychaetes did not ingest the clams but caused them to retract their siphons, and thus interrupted feeding. Meiofaunal burrowers also can cause mortality of newly settled macrofauna. In the field, Watzin (1986) showed that meiofauna other than turbellarians (primarily nematodes and copepods) decreased the survivorship of recently settled bivalves, most likely by sediment destabilization. However, Zobrist & Coull (1994) found that meiofaunal bioturbators (copepods, nematodes, foraminifera) did not affect the survival of newly settled bivalves (*M. mercenaria*) and polychaetes (*Streblospio benedicti*) in the laboratory. They suggested that meiofauna (with the possible exception of predaceous turbellarians) do not play a large role in early post-settlement mortality of macrofaunal species.

Physical disturbance and hydrodynamics

Physical disturbance has received relatively little attention as a cause of mortality for newly settled invertebrates. Connell (1961) found that mortality of both cyprids and newly metamorphosed barnacles (*Semibalanus balanoides*) increased during gales, when mortality was greater at convexities on the substratum than in more protected microhabitats such as crevices or depressions. Eckman (1987) determined that current speed affected post-settlement survival of one species of bivalve (*Argopecten irradians*) but not another (*Anomia simplex*) in eelgrass meadows. Survival of *A. irradians* was lower in regions with faster currents, possibly because recruits were dislodged (Eckman 1987). Survival of abalone (*Haliotis iris*) settlers transplanted to the field was greater in deep than shallow habitats, possibly due to reduced dislodgment by wave action (McShane & Naylor 1995).

Physiological stress

Newly settled invertebrates are generally more susceptible than older juveniles and adults to physiological stress (Hatton 1938, Foster 1971, Branch 1975, Olson 1983, Dungan 1985, Baker & Mann 1992, Gos-

Table 2. Summary of studies examining effects of various factors on non-predatory early post-settlement mortality in benthic marine invertebrates. Recr: recruitment rather than mortality was measured in determining effect on survival; obs: observations

Factor	Species	Method	Effect	Source
Delayed metamorphosis				
	Echinoidea			
	<i>Dendraster excentricus</i>	Lab expt	Yes	Highsmith & Emlet (1986)
	<i>Echinarachinus parma</i>	Lab expt	Yes	Highsmith & Emlet (1986)
	Gastropoda			
	<i>Crepidula fornicata</i>	Lab expt	No	Pechenik & Evster (1989)
	<i>Phestilla sibogae</i>	Lab expt	Dependent on larval life history	Miller (1993)
	Polychaeta			
	<i>Capitella</i> sp. I	Lab expt	Yes	Pechenik & Cerulli (1991)
	Barnacle			
	<i>Balanus amphitrite</i>	Lab expt	Mixed	Pechenik et al. (1993)
Biological disturbance				
Grazers				
Gastropods				
	Cirripedia			
	<i>Tesseropora rosea</i>	Field expt	Yes	Denley & Underwood (1979)
	<i>Semibalanus balanoides</i>	Lab expt	Yes	Miller & Carefoot (1989)
		Field expt (recr)	Yes	Hawkins (1983)
		Field expt (recr)	Yes	Connell (1961)
		Field expt (recr)	Yes	Menge (1976)
		Field obs	Yes	Hatton (1938)
		Field expt (recr)	Yes	Petratis (1983)
	<i>Balanus amphitrite</i>	Field expt	Yes	Satriel et al. (1994)
	<i>Chthamalus fissus</i>	Field obs	No	Sutherland & Ortega (1986)
	<i>Balanus glandula</i>	Field obs	Yes	Stimson (1970)
		Field expt (recr)	Yes	Dayton (1971)
	Not identified to sp.	Field expt (recr)	Yes	Turner & Todd (1991)
	Monoplacophora			
	<i>Patella latistrigata</i>	Field expt	Density dependent	Creese (1982)
	Ascidacea			
	<i>Corella inflata</i>	Lab expt	Yes	Young & Chia (1984)
	<i>Boltenia villosa</i>	Lab expt	Yes	Young & Chia (1984)
	<i>Styela gibbsii</i>	Lab expt	Yes	Young & Chia (1984)
	Not identified to sp.	Field expt (recr)	Yes	Turner & Todd (1991)
	Bryozoa			
	Ctenostome	Field expt (recr)	Yes	Turner & Todd (1991)
	Cheilostome	Field expt (recr)	Yes	Turner & Todd (1991)
	Hydroida	Field expt (recr)	Yes	Turner & Todd (1991)
	Polychaeta	Field expt (recr)	Yes	Turner & Todd (1991)
Urchins				
	Anthozoa			
	<i>Favia fragum</i>	Field expt	Yes	Sammarco (1980)
	<i>Agaricia</i> spp.	Field expt	Yes	Sammarco (1980)
	<i>Porites</i> spp.	Field expt	Yes	Sammarco (1980)
	Echinoidea			
	<i>Echinometra mathaei</i>	Field expt (recr)	No	Prince (1995)
	Gastropoda			
	<i>Turbo intercostalis</i>	Field expt (recr)	No	Prince (1995)
	<i>Cypraea caputserpentis</i>	Field expt (recr)	No	Prince (1995)
	<i>Thais orbita</i>	Field expt (recr)	No	Prince (1995)
	<i>Siphonaria zelandica</i>	Field expt (recr)	Yes	Prince (1995)
Crab				
	Ascidacea			
	<i>Podoclavella moluccensis</i>	Field expt	Yes	Davis (1988b)
Algae				
	Cirripedia			
	<i>Semibalanus balanoides</i>	Field expt	Yes	Grant (1977)
Adult infauna				
Macrofauna				
	Polychaeta			
	<i>Streblospio benedicti</i>	Field expt	No	McCann & Levin (1989)
	<i>Rhynchospio arenicola</i>	Field and lab expts	Yes	Brenchley (1981)

Table 2 (continued)

Factor	Species	Methods	Effect	Source
Meiofauna	Crustacea			
	<i>Leptochelia dubia</i>	Lab expt	Yes	Brenchley (1981)
	Bivalvia			
	<i>Sanguinolaria nuttallii</i>	Field expt	Yes	Peterson (1977)
	<i>Mercenaria mercenaria</i>	Lab expt	Dependent on sediment type	Ahn et al. (1993)
	<i>Macoma liliana</i>	Lab expt	Yes	Cummings et al. (1996)
	Bivalvia			
	mostly Veneridae	Field expt	Yes	Watzin (1986)
	<i>Mercenaria mercenaria</i>	Lab expt	No	Zobrist & Coull (1994)
Polychaeta				
<i>Streblospio benedicti</i>	Lab expt	No	Zobrist & Coull (1994)	
Physical disturbance				
Storms				
	Cirripedia			
	<i>Semibalanus balanoides</i>	Field obs	Yes	Connell (1961)
Hydrodynamics				
	Bivalvia			
	<i>Argopecten irradians</i>	Field expt	Yes	Eckman (1987)
	<i>Anomia simplex</i>	Field expt	No	Eckman (1987)
Physiological stress				
Aerial exposure				
	Neogastropoda			
	<i>Nucella emarginata</i>	Field and lab expt	Yes	Gosselin & Chia (1995a, b)
	Monoplacophora			
	<i>Patella granularis</i>	Lab expt	Yes	Branch (1975)
	<i>Patella oculus</i>	Lab expt	Yes	Branch (1975)
	<i>Patella granatina</i>	Lab expt	Yes	Branch (1975)
	<i>Patella longicosta</i>	Lab expt	Yes	Branch (1975)
	<i>Patella cochlear</i>	Lab expt	Yes	Branch (1975)
	<i>Patella argenvillei</i>	Lab expt	Yes	Branch (1975)
	<i>Patella barbara</i>	Lab expt	Yes	Branch (1975)
	Cirripedia			
	<i>Chthamalus anisopoma</i>	Field expt	Yes	Dungan (1985)
Tidal height				
	Cirripedia			
	<i>Tesseropora rosea</i>	Field expt	Yes	Denley & Underwood (1979)
	<i>Tetracitella purpurascens</i>	Field expt	Yes	Denley & Underwood (1979)
	<i>Semibalanus balanoides</i>	Field expt/obs	Yes	Foster (1971)
		Field expt	Yes	Hatton (1938)
		Field obs	Yes	Minchinton & Scheibling (1991)
		Field expt	Yes, effect of algae	Minchinton & Scheibling (1993a)
	<i>Balanus cariosus</i>	Field expt/obs	Yes	Strathmann & Branscombe (1979)
	<i>Chthamalus anisopoma</i>	Field expts	Yes, effect of rock type	Raimondi (1988a, b, 1990, 1991)
	<i>Chthamalus montagui</i>	Field obs	No	Kendall & Bedford (1987)
	<i>Pollicipes polymerus</i>	Field obs	Yes	Hoffman (1989)
	Bivalvia			
	<i>Mytilus viridis</i>	Field expt	Yes	Tan (1975)
	<i>Crassostrea virginica</i>	Field expt	Yes	Roegner & Mann (1995)
Warm weather				
	Cirripedia			
	<i>Semibalanus balanoides</i>	Field obs	Yes	Connell (1961)
		Field obs	Yes	Foster (1971)
	Bivalvia			
	<i>Crassostrea virginica</i>	Field expt	Yes	Roegner & Mann (1995)
Light				
	Ascidacea (colonial)			
	<i>Diplosoma listerianum</i>	Field expt	No	Hurlbut (1993)
	<i>Diplosoma</i> sp.	Field expt	No	Hurlbut (1993)
	<i>Didemnum candidum</i>	Field expt	Yes	Hurlbut (1993)
	<i>Didemnum molle</i>	Field expt	Yes	Olson (1983)

Table 2 (continued)

Factor	Species	Methods	Effect	Source
Hypoxia/anoxia				
	Bivalvia			
	<i>Crassostrea virginica</i>	Lab expt	Yes	Baker & Mann (1992)
Siltation				
	Ascidacea			
	<i>Corella inflata</i>	Field expt	Yes	Young & Chia (1984)
	<i>Ascidia callosa</i>	Field expt	Yes	Young & Chia (1984)
	<i>Ascidia paratropa</i>	Field expt	Yes	Young & Chia (1984)
	<i>Pyura haustor</i>	Field expt	Yes	Young & Chia (1984)
	<i>Boltenia villosa</i>	Field expt	Yes	Young & Chia (1984)
	<i>Styela gibbsii</i>	Field expt	Yes	Young & Chia (1984)
	<i>Diplosoma listerianum</i>	Field expt	Yes	Hurlbut (1993)
	<i>Diplosoma</i> sp.	Field expt	Yes	Hurlbut (1993)
Salinity and temperature				
	Decapoda			
	<i>Menippe adina</i>	Lab expt	Yes	Brown & Bert (1993)
	<i>Menippe mercenaria</i>	Lab expt	Yes	Brown & Bert (1993)
		Lab expt	Yes	Brown et al. (1992)
	<i>Penaeus esculentus</i>	Lab expt	Yes	O'Brien (1994a)
		Field obs	No (temperature)	O'Brien (1994b)
	<i>Penaeus merguensis</i>	Lab expt	Yes	Staples & Heales (1991)
		Field obs	Yes (temperature)	Haywood & Staples (1993)
	Amphipoda			
	<i>Corophium volutator</i>	Lab expt	Yes	Mills & Fish (1980)
	<i>Corophium arenarium</i>	Lab expt	Yes	Mills & Fish (1980)
	Asteroidea			
	<i>Patiriella pseudoexigua</i>	Lab expt	Yes	Chen & Chen (1993)
	Demospongiae			
	<i>Haliclona tubifera</i> ,	Lab expt	Yes (only temperature	Maldonado & Young (1996)
	<i>Halichondria magniconulosa</i>		tested)	
Dinoflagellate bloom				
	Bivalvia			
	<i>Argopecten irradians</i>	Field obs	Yes	Summerson & Peterson (1990)
Competition/overgrowth				
	Cirripedia			
	<i>Tetraclitella purpurascens</i>	Field expt	Yes	Denley & Underwood (1979)
	<i>Tesseropora rosea</i>	Field expt	Yes	Denley & Underwood (1979)
	Anthozoa			
	<i>Pocillopora damicornis</i>	Field and lab expts	Yes	Harriott (1983)
	<i>Capnella gaboensis</i>	Lab expt	Yes	Farrant (1987)
	Octocorallia			
	<i>Alcyonium siderium</i>	Field obs	Yes	Sebens (1983)
	Ascidacea			
	<i>Corella inflata</i>	Field expt	Depth dependent	Young & Chia (1984)
	<i>Ascidia callosa</i>	Field expt	Depth dependent	Young & Chia (1984)
	<i>Ascidia paratropa</i>	Field expt	Yes	Young & Chia (1984)
	<i>Pyura haustor</i>	Field expt	Depth dependent	Young & Chia (1984)
	<i>Boltenia villosa</i>	Field expt	Depth dependent	Young & Chia (1984)
	<i>Styela gibbsii</i>	Field expt	Yes	Young & Chia (1984)
	<i>Podoclavella cylindrica</i>	Field obs	Yes	Davis (1987)
	Bryozoa			
	<i>Bugula pacifica</i>	Field obs	Yes	Young & Chia (1981)
	Fouling community	Field expt	Yes	Osman & Whitlatch (1995b)
	Bivalvia			
	<i>Crassostrea virginica</i>	Field and lab expts	Yes	Osman et al. (1989)
		Field and lab expts	Yes	Zajac et al. (1989)
	<i>Tapes japonica</i>	Field expt	No	Williams (1980a)
	Monoplacophora			
	<i>Patelloida latistrigata</i>	Field expt	Yes	Creese (1982)
	<i>Cellana tramoserica</i>	Field expt	Yes	Underwood et al. (1983)

selin & Chia 1995a, but see Mills & Fish 1980). This has been attributed to a greater surface area to volume ratio (Vermeij 1972), an inferior ability to reduce energy consumption under conditions of stress (Baker & Mann 1992), and incompletely developed protective adaptations (e.g. pigment and calcareous spicules in the ascidian *Didemnum molle*, Olson 1983). For mobile species, the age dependence of tolerance to physiological stress may depend on the habitats of juveniles and adults. Branch (1975) showed, in the laboratory, that tolerance to desiccation remained fairly constant in non-migratory species of patellid limpets but increased rapidly with size in species which settled low on the shore and migrated upwards as juveniles. Survival of early juvenile invertebrates may also be reduced by stressful physiological conditions which interfere with larval development. Developmental abnormalities associated with extreme physical conditions have been documented (e.g. Watts et al. 1983), but their effects on juvenile survival have not yet been investigated.

In the intertidal zone, newly settled invertebrates are highly vulnerable to mortality from desiccation (Table 2). Hatchling whelks (*Nucella emarginata*) are unable to survive 4 to 6 h emersion in the field or the laboratory unless they are in a protective microhabitat (Gosselin & Chia 1995a, b). Survival of settlers often decreases with increasing height on the shore. Small barnacles which settle or are transplanted above the limit of the adult distribution generally die (*Semibalanus balanoides*, Hatton 1938, Foster 1971; *Balanus cariosus*, Strathmann & Branscomb 1979; *Tetraclitella purpurascens*, Denley & Underwood 1979; *Chthamalus anisopoma*, Raimondi 1988a, 1991). Hatton (1938) demonstrated that a small amount of dripping water could keep barnacle cyprids alive above the adult zone. Within the vertical range of distribution of adult barnacles, early post-settlement mortality may increase with tidal height (*S. balanoides*, Minchinton & Scheibling 1991, Bertness et al. 1992; *Pollicipes polymerus*, Hoffman 1989; *C. anisopoma*, Raimondi 1988b, 1990) or remain constant (*Chthamalus montagui*, Kendall & Bedford 1987). Early post-settlement mortality also has been shown to increase with tidal height for mussels (*Mytilus viridis*, Tan 1975) and oysters (*Crassostrea virginica*, Roegner & Mann 1995). Lewis & Bowman (1975) and Bowman & Lewis (1977) suggested that desiccation was responsible for the restriction of limpet (*Patella vulgata*) spat on the upper shore to crevices and pits. However, this distribution could also be due to preferential settlement or migration.

Weather and other conditions that influence desiccation rates can account for temporal variability in survival rates of young juveniles. Increased mortality of attached cyprids (Connell 1961) and early post-meta-

morphic juveniles (Foster 1971) of the barnacle *Semibalanus balanoides* has been observed during periods of warm weather and prolonged aerial exposure due to neap tides (Foster 1971) or diminished wave action (Connell 1961). Roegner & Mann (1995) showed that recently settled oysters (*Crassostrea virginica*) survived transplantation to 25 cm above mean low water in September, but not in June or July when aerial temperatures were $>30^{\circ}\text{C}$. Substratum type also can affect the risk of mortality from desiccation. Schubart et al. (1995) demonstrated that settlement inside empty barnacle tests increased the survival of recently settled barnacles (*Balanus glandula*) in the high intertidal zone. Minchinton & Scheibling (1993a) found that early post-settlement mortality of the barnacle *S. balanoides* increased with tidal height in the absence but not in the presence of ephemeral algae. Raimondi (1988b) showed that survival of juvenile barnacles (*Chthamalus anisopoma*) was reduced at higher tide levels on basaltic rocks compared to granitic rocks, most likely because higher temperatures were attained by basalt. However, rock type did not affect the survival of early juveniles of the barnacle *Tesseropora rosea* in Australia (Caffey 1982).

Exposure to bright light is a cause of early post-settlement mortality for some species of ascidians (*Didemnum candidum*, Hurlbut 1993; *Didemnum molle*, Olson 1983), but not others (*Diplosoma listerianum* and *Diplosoma* sp., Hurlbut 1993). Siltation also causes mortality of recently settled ascidians, resulting in greater survival of new settlers on the undersides of panels (Young & Chia 1984, Hurlbut 1993).

In the laboratory, combinations of extreme temperature and salinity have been shown to cause mortality of recent settlers of several species of invertebrates (Table 2). However, most species tested survived virtually all conditions they are likely to experience in the field (Mills & Fish 1980, Brown et al. 1992, Chen & Chen 1993, O'Brien 1994b). Field estimates of mortality of early juveniles were significantly related to temperature for 1 species of Australian prawn (*Penaeus merguensis*, Haywood & Staples 1993), but not another (*Penaeus esculentus*, O'Brien 1994a). Laboratory experiments indicated that environmental temperatures were suboptimal for survival of *P. merguensis* (Staples & Heales 1991), but less detrimental to survival of *P. esculentus* (O'Brien 1994b). Also, the field study (O'Brien 1994a) was carried out near the southern limit of the range of *P. esculentus* in Australia, where water temperatures were lower. For estuarine species, periods of anoxia or hypoxia may also be a source of early post-settlement mortality. Baker & Mann (1992) demonstrated that low levels of oxygen decreased survival of recently settled oysters (*Crassostrea virginica*) in the laboratory. The absence of

adult barnacles from tidepools in New England, USA, has been attributed to early post-settlement mortality from decreased dissolved oxygen levels (Singletary & Shadlou 1983) or accumulation of toxins (e.g. substances secreted by the alga *Ulva lactuca*, Magre 1974) during tidal isolation. Blooms of toxic dinoflagellates also may result in mortality of early juveniles of benthic invertebrates. Summerson & Peterson (1990) found that recruitment of the bay scallop *Argopecten irradians concentricus* was extremely low (2% of previous years) during a red tide (*Ptychodiscus brevis*) outbreak in North Carolina, USA. The increased abundance of empty shells of juvenile scallops after the red tide suggests that the recruitment failure resulted at least partly from elevated early post-settlement mortality.

Despite the vulnerability of recently settled invertebrates to physiological stress, environmental conditions may not commonly cause mortality of early juveniles in the field. Most studies examining survivorship under conditions of physiological stress have transplanted settlers or modified the conditions to which they were exposed. Many individuals may avoid these sources of mortality by settling in (Connell 1961, Denley & Underwood 1979, Olson 1983, Young & Chia 1984, Hurlbut 1993, Schubart et al. 1995) or migrating to (Gosselin & Chia 1995b) locations where environmental conditions are not lethal.

Predation

Mobile epifauna

Predation on early juveniles has been documented most often for mobile epifaunal species (Table 3). Fish and crabs are the most commonly reported predators of early juveniles of many species, including lobsters, crabs, shrimp, queen conch, scallops, and sea urchins (Table 3). These were the only types of predators, out of the 45 species of intertidal invertebrates tested in the laboratory by Gosselin & Chia (1995a), that preyed on recently hatched intertidal whelks (*Nucella emarginata*). Other predators of early juveniles include shrimp (preying on blue crabs), sea stars (on scallops and urchins), whelks (on scallops), octopus (on spiny lobster), lobster (on urchins), and urchins (on sea cucumbers) (Table 3). Some species of recently settled echinoderms are preyed upon primarily by small predators. In the laboratory, small individuals (<1.5 mm) of the sand dollar *Dendraster excentricus* were heavily preyed upon by tanaid crustaceans but not eaten by gammarid amphipods or holothurians (Highsmith 1982). Survival of 1 mo old sea stars (*Acanthaster planci* and *Nardoa novaecaledoniae*) in rubble on the Great Barrier Reef, Australia, was decreased by

epifauna consisting primarily of polychaetes, amphipods and gastropods (Keesing & Halford 1992, Keesing et al. 1996), but predators had little effect on survival of another species of *Nardoa* on the Okinawan Reef, Japan (Keesing et al. 1996). Rumrill (1989) was unable to find any significant predators of juveniles of *Asterina miniata* when he exposed them to crabs, other sea stars, and fish in the laboratory. Most of the studies of predation on early juveniles of mobile species have involved individuals several weeks to months after settlement (Table 3) and the vulnerability of recently settled individuals to predators may differ from that of slightly older juveniles. However, several studies have found high predation rates on settling or recently settled decapods in the laboratory (Lavalli & Barshaw 1986, Johns & Mann 1987, Barshaw & Lavalli 1988, Olmi & Lipcius 1991, Dittel et al. 1996) and in the field (Eggleston & Armstrong 1995).

Tethering is the most common technique used to evaluate predation rates on early juveniles of mobile epifaunal species (Table 3). Recent papers have pointed out potential artifacts of tethering (Barbeau & Scheibling 1994c, Peterson & Black 1994, Zimmer-Faust et al. 1994, Aronson & Heck 1995, Micheli 1996). For example, tethering may increase predation rates by limiting the escape response of prey, particularly for highly mobile species (Peterson & Black 1994, Zimmer-Faust et al. 1994, Aronson & Heck 1995), or by decreasing the ability of prey to burrow in certain substrates (Barshaw & Able 1990). Also, tethering may differentially affect predation by different predators, potentially complicating comparisons of predation rate among predator species (Barbeau & Scheibling 1994c) and habitats (if predator species composition or behaviour differs among habitats) (Peterson & Black 1994, Micheli 1996). Despite these artifacts, tethering with thoughtful controls remains an effective way to assess predation on small, mobile invertebrates.

Predator inclusion or exclusion cages also have been widely used to measure predation rates of juveniles of mobile (and sessile) species (Table 3). There are various artifacts of caging (reviewed by Dayton & Oliver 1980, Hall et al. 1990) which are particularly relevant to studies of juvenile survival and recruitment. By altering the micro-environment (e.g. reducing water flow, shading, creating structure), cages may increase settlement rate and/or early post-settlement survival, which may confound an assessment of predator effects. Also, mesh size will determine the size of predators that are manipulated, including those which may not be part of the original experimental design. Thus, effects of excluding a particular predator may be confounded by other smaller and perhaps unknown predators (including juveniles of species that are being manipulated as adults) which can pass through the

mesh and may even be attracted to cages. As with tethering, the use of adequate procedural controls to evaluate artifactual effects is crucial to the design of any caging experiment. However, only 2 (Denley & Underwood 1979, Reise 1979) of the 14 studies we reviewed that employed exclusion cages or fences also used inclusion or partial cages/fences to assess cage artifacts (although in Reise's study treatments were not replicated). Two other studies (Keough 1984, Eggleston & Armstrong 1995) measured settlement or short-term recruitment rates in caged and uncaged plots to determine if the presence of a cage altered settlement rates. Studies employing predator inclusion cages were less problematic, as most (7 out of 8) compared mortality or recruitment rates between cages with and without predators, which would share the same artifacts.

The risk of predation for early juveniles may vary with recruit size. In tethering experiments, the mortality rate of small juvenile lobsters (*Panulirus argus*, Smith & Herrnkind 1992; *Homarus americanus*, Wahle & Steneck 1992) was greater than that of larger individuals, but the effect of body size on predation rate on juvenile blue crabs varied among studies (Wilson et al. 1987, 1990, Pile et al. 1996). The effect of juvenile sea scallop size on predation rate depended on predator type, site, and season (Barbeau & Scheibling 1994a, Barbeau et al. 1994). For some species, predation risk may be greater for intermediate sized individuals than for early juveniles or adults. Gut contents of mobile benthic predators from the Gulf of Maine examined by Ojeda & Dearborn (1991) contained mostly juveniles or small species of invertebrates, but most predators did not seem to exploit the smallest size range of prey available. The bimodal size distribution commonly observed in sea urchin populations may be the result of increased predation on intermediate sized urchins in transition between the spatial refuge of the cryptic early juvenile stage and the size refuge of adults (for review see Scheibling 1996). Similarly, Wiedermeyer (1994) found that the importance of predation as a source of mortality for juvenile sea cucumbers (*Actinopyga echinites*) increased over time, and suggested that this increase in mortality resulted from a decrease in cryptic behaviour.

Predation risk for early juveniles varies among habitats and microhabitats for many invertebrate species including scallops, lobsters, crabs (but see Olmi & Lipcius 1991), shrimp, urchins, and gastropods (but see Scheibling & Hatcher 1997) (Table 3). Predation intensity is lower in vegetation and other structurally complex substrata (Table 3). Attachment above the bottom on vegetation (*Argopecten irradians*, Pohle et al. 1991, Ambrose & Irlandi 1992) or occurrence near (*Den- draster excentricus*, Highsmith 1982) or under

(*Strongylocentrotus franciscanus*, Tegner & Dayton 1977) adults can also offer protection from predation. Early juveniles of many species occur primarily in these protective habitats (e.g. Tegner & Dayton 1977, Highsmith 1982, Breen et al. 1985, Wahle & Steneck 1991, Garcia-Esquivel & Bricelj 1993, Gosselin & Chia 1995b). Older juveniles may outgrow their spatial refuges or shift habitats as their vulnerability to predation decreases (Tegner & Dayton 1977, Scheibling & Hamm 1991, Smith & Herrnkind 1992, Garcia-Esquivel & Bricelj 1993).

Predation risk for early juveniles also can be influenced by physical factors which affect predator-prey interactions. In laboratory and field experiments with juvenile sea scallops (*Placopecten magellanicus*), predation rate by crabs and sea stars increased with temperature due to increased predator activity and decreased effectiveness of the scallops' escape response (to sea stars) (Barbeau & Scheibling 1994b, Barbeau et al. 1994). In a tethering experiment with juvenile blue crabs (*Callinectes sapidus*), Pile et al. (1996) found that mortality was lower during and immediately after a storm than before the storm. They attributed the reduction in mortality to decreased predator activity resulting from altered physical conditions associated with the storm, such as a drop in water temperature, increased turbidity and turbulent flow, and increased salinity. Similarly, Scheibling & Hatcher (1997) observed that mortality of juvenile snails (*Trochus histrio*) tethered outside of a spatial refuge (live branching coral) was lowest during a gale which temporarily reduced the abundance of predatory fish.

Infauna

Early juveniles of macrofauna in soft-bottom communities are vulnerable to predation by a variety of predators. Jensen & Jensen (1985) suggested that juvenile crabs (*Carcinus maenus*) were responsible for the rapid decline in the number of juvenile cockles (*Cerastoderma edule*) after the settlement peak in the Danish Wadden Sea. In the laboratory, *C. maenus* can consume large numbers of cockles and selectively preys on small individuals (Jensen & Jensen 1985, Sanchez-Salazar et al. 1987). Reise (1979) found that densities of early juveniles of *C. edule* in cages in the Wadden Sea were reduced in predator inclusion cages with a nereid polychaete or a nemertine, and increased in predator exclusion cages. However, his failure to replicate treatments may have confounded differences between treatments with differences between locations. In Sweden, Möller (1986) found that exclusion of epibenthic predators using cages also increased densities of spat of several species of bivalve, primarily *Mya arenaria* and *C. edule*. In Ches-

peake Bay, USA, Holland et al. (1987) showed that exclusion of fish and crabs increased the peak abundance of macrofaunal recruits in trays of azoic sediment. Beal (1983) found that 2 species of snapping shrimp (*Alpheus heterochaelis* and *Alpheus normanni*) selectively prey on small juveniles of the clam *Mercenaria mercenaria* in the laboratory, suggesting they may be important predators of juvenile macrofauna. Meiofaunal predators (organisms <0.5 mm) also feed on recently settled macrofauna (Thorson 1966, Bell & Coull 1980). Watzin (1983, 1986) showed that increased densities of turbellarians reduced the survival of spionid and terebellid polychaetes, oligochaetes, and amphipods.

Deposit feeders, particularly surface-feeding species, ingest early juvenile macrofauna, as well as causing mortality by sediment reworking. Thorson (1966) calculated that deposit feeders could ingest large numbers of macrofaunal settlers, but suggested that some settlers may survive passage through the digestive tract. However, Mileikovsky (1974) reviewed reports of the presence of larvae and small juvenile invertebrates in the digestive tracts of deposit feeders and concluded that passage alive through the digestive system is probably rare and does not play an important role in recruitment. In the laboratory, adult polychaetes and crustaceans decrease the survival of recently settled individuals of several species of bivalves (*Gemma gemma*, *Mulinia lateralis*, *Macoma balthica*) and polychaetes (*Abarenicola pacifica*, *Nerinides* spp., *Nerinopsis* sp., *Armandia brevis*) (Table 3). Elmgren et al. (1986) tested the mechanism for the increased mortality of settlers of the bivalve *M. balthica* in the presence of adult amphipods (*Pontoporeia affinis*) and found crushed shells of *M. balthica* only in the aquaria in which *P. affinis* were present. Increased sediment depth, which would decrease the probability of physical contact between amphipods and early juvenile clams, increased the survival of *M. balthica* in the presence but not in the absence of *P. affinis*. Weinberg (1984) showed that the deposit-feeding polychaete *Polydora ligni* ingested recently settled clams (*G. gemma*) thereby reducing recruitment in the laboratory, but he did not find these clams in the gut contents of polychaetes collected in the field. However, Qian & Chia (1994) found that recently settled polychaetes (*Capitella* sp. I), which were marked with red dye and transplanted to the field, had high mortality in trays containing large numbers of deposit-feeding polychaetes and other predators.

Sessile species

Exclusion of macrofaunal predators often results in increased recruitment of sessile subtidal invertebrates,

which can ultimately affect community structure (Table 3). In California (USA), Keough & Downes (1982, 1986) examined the effects of predators on patterns of recruitment of sessile invertebrates on subtidal rock walls off Santa Catalina Island. Exclusion of predators (fish and urchins) with cages altered the abundance (the bryozoan *Tubilopora* spp.), spatial distribution (*Tubilopora* spp., the ascidian *Trididemnum opacum*), and size distribution (the bryozoan *Scrupocellaria bertholletti*) of recruits of several species, but had little effect on other species (the bryozoan *Celleporaria brunnea*, the polychaete *Spirorbis eximus*). In South Africa, Barkai & Branch (1988) demonstrated that high densities of rock lobsters prevented recruitment on uncaged plates in the subtidal zone of Malgas Island, while caged plates developed a community of barnacles and mussels. Caging also increased recruitment, although less dramatically, on plates at nearby Marcus Island where rock lobsters were nearly absent and whelks (*Burnupena* spp.) were the most abundant predators. Caging studies also have shown that predation on recent settlers has a major effect on the structure of fouling communities in New England. The small gastropods *Anachis lafresnayi* and *Mitrella lunata* prey on newly settled ascidians, resulting in a shift of community dominance from ascidians to bryozoans (Osman et al. 1992, Osman & Whitlatch 1995a).

Predation by whelks is well known to be an important source of post-recruitment mortality for sessile invertebrates in the intertidal zone (e.g. Connell 1961, 1970, Dayton 1971, Menge 1976). However, studies of the effect of whelks on recently settled invertebrates have yielded conflicting results. Exclusion of the whelk *Morula marginalba* had no effect on survival of the barnacle *Tessieropora rosea* in the first few months after settlement in Australia (Denley & Underwood 1979). In contrast, Menge (1991) found that recruitment of the barnacle *Balanus inexpectatus* in Panama was lower in the presence of predatory gastropods (including whelks), and that recruitment of the bivalves *Chama echinata* and *Ostrea palmula* was lower in the presence of various predators (gastropods, crabs, fish). However, gastropod removal treatments and controls were pseudoreplicated in his study, confounding differences between locations with differences between treatments. Carroll (1996) found that exclusion of whelks and sea stars increased recruitment of barnacles (*Semibalanus balanoides*, *S. cariosus*, *B. glandula*) in Alaska, USA, in a year with low settler densities, but had no effect in 2 years with higher settlement. In Maine, USA, the whelk *Nucella lapillus* had little (Petratis 1991) or no (Petratis 1990) effect on recruitment of the mussel *Mytilus edulis*. In southern Chile, Moreno (1995) found that recently settled mussels (*Choromytilus chorus*) only survived on

Table 3. Summary of studies examining predation on recently settled or early juvenile benthic marine invertebrates. For experiments examining the effects of predator inclusion or exclusion on recruitment, the age given is the duration of the experiment. For laboratory experiments and field tethering experiments, the size of the prey is indicated

Species	Size/age	Predator	Methods	Patterns/conclusions	Source
Echinodermata					
<i>Acanthaster planci</i>	1–16 mo old	Rubble epifauna	Transplant	High mortality rate due to predation	Keessing & Halford (1992)
<i>Nardoa novaecaledoniae</i> , <i>A. planci</i>	1 mo old	Rubble epifauna	Transplant	Predation rate varied among sites within habitats and was higher for <i>A. planci</i> than for <i>N. novaecaledoniae</i>	Keessing et al. (1996)
<i>Nardoa</i> sp.	5 d old	Rubble epifauna and nektonic predators	Transplant	Mortality rate was very low	Keessing et al. (1996)
<i>Asterina miniata</i>	8–27 mm	Crabs, sea stars, fish	Lab observation	Almost no predation occurred	Rumrill (1989)
<i>Dendroaster excentricus</i>	<2.5 mm	Crustaceans	Lab observation	Tanaids only ate sand dollars <1.5 mm	Highsmith (1982)
<i>Cucumaria frondosa</i>	<23 mm	Urchins	Field/lab observation	Direct observations of predation	Hauai & Mercier (1996)
<i>Actinopyga echinites</i>	>3 g	Gastropods, fish	Predator exclusion cages	Exclusion of predators reduced mortality	Widdemeyer (1984)
<i>Strongylocentrotus droebachiensis</i>	3–6 mm	Fish, whelks, crabs, lobsters	Predator inclusion cages	No effect of whelks or green crabs. Cobbles (spatial refuge) decreased predation by rock crabs and lobsters	Scheibling & Hamm (1991)
	0–30 mm	Fish	Lab experiment (gut contents)	Urchins were not preferred prey in lab (0–15 mm urchins eaten most often), but were primary prey in field	Ojeda & Dearborn (1991)
	<20 mm	Fish	Artificial reef	Construction of artificial reefs increased predator densities and decreased densities of juvenile urchins	Ojeda & Dearborn (1991)
<i>Strongylocentrotus franciscanus</i>	<10 mm <10 mm	Sea stars, fish, lobsters Sea stars, fish, lobsters	Lab/field observations Manual removal of adult urchins	Direct observations of predation Juveniles protected from predation under spine canopy of adults. Removal of adults decreased juvenile abundance	Tegner & Dayton (1977) Tegner & Dayton (1977)
Gastropoda					
<i>Nucella emarginata</i>	2–8 d old	45 spp. tested Crabs	Lab observation Lab experiment	Only crabs and fish were significant predators Predation was reduced for whelks in algae or in clumps of mussels and barnacles	Gosselin & Chia (1995a) Gosselin & Chia (1995b)
<i>Strombus gigas</i>	<54 mm 9–13 mm	Decapods, fish Decapods, fish	Field observation Tethering	Early juveniles occurred under sand Predation was reduced in medium density eelgrass compared to sand	Sandt & Stoner (1993) Ray & Stoner (1995)
<i>Trochus histrio</i>	7–25 mm	Fish	Tethering	Predation rate was lower in branching coral than in open areas, and decreased with increasing snail size	Scheibling & Hatcher (1997)
<i>Tectus pyramis</i>	12–34 mm	Fish	Tethering	Predation rate negligible, even on small <i>T. pyramis</i> in open areas	Scheibling & Hatcher (1997)
Bivalvia					
<i>Argopecten irradians</i>	6–20 mm	Crabs, sea stars	Tethering	Predation decreased with increasing height of attachment on seagrass	Pohle et al. (1991)
	12 mm	Crabs, whelks	Tethering	Predation decreased with increasing height of attachment on eelgrass	Ambrose & Irlund (1992)
<i>Placopecten magellanicus</i>	7–30 mm	Sea stars, crabs	Tethering	Predation rate was affected by predator species, scallop size and density, site and season	Barbeau et al. (1994)
	7–30 mm 5–25 mm	Sea stars, crabs Sea stars, crabs	Tethering Lab experiment	Predation rate varied among seasons Crabs actively preferred large scallops, while the preference of sea stars for small scallops occurred passively	Hatcher et al. (1996) Barbeau & Scheibling (1994a)
	5–25 mm	Sea stars, crabs	Lab experiment	Predation rate increased with increasing temperature	Barbeau & Scheibling (1994b)

Table 3 (continued)

Species	Size/age	Predator	Methods	Patterns/conclusions	Source
<i>Crassostrea virginica</i>	1–30 mm	Blue and mud crabs	Lab experiment	Predation rate increased by decreased prey size or increased predator size, and affected by the species of predator	Bisler & Castagna (1987)
<i>Mytilus californianus</i> , <i>Mytilus trossulus</i>	5–45 mm	Blue crabs	Lab experiment	Predation rate increased with decreasing prey size and increasing prey density	Eggleston (1990)
<i>M. trossulus</i> , <i>Mytilus edulis</i>	1–5 mm	Whelks	Lab experiment	Early juvenile whelks strongly preferred mussels over other species of prey and consumed 1 and 2 mm SL mussels more often than larger individuals	Gosselin & Chia (1996)
	0.5–8 mm	Whelks	Lab experiment	Size of mussels consumed increased with increasing size of juvenile whelks	Hunt & Scheibling (in press)
	<2 mm	Whelks	Field observations	The majority of mussel shells drilled by juvenile whelks were <2 mm SL	Hunt & Scheibling (in press)
	<2 mm	Whelks	Manual removal	No effect of removal of juvenile whelks on mussel cover or size distribution	Hunt & Scheibling (in press)
<i>M. edulis</i>	Recruitment after 2.5 mo	Whelks	Inclusion and exclusion cages	No effect of whelks on mussel recruitment	Petratilis (1990)
	Recruitment after 3–10 wk	Whelks	Exclusion cages	Barnacles were provided as alternative prey	Petratilis (1991)
<i>Choromytilus chorus</i>	7 mo (sampled monthly)	Whelks	Settlement collectors	Predator exclusion cages had a small but significant effect on mussel recruitment	Moreno (1995)
<i>Chama echinata</i>	Unspecified	Gastropods, crabs, fish	Manual removal and cages	Mussel mortality greater on collectors attached to the substratum at several points than on those with a single attachment point	Jensen & Jensen (1985)
<i>Ostrea palmula</i>	Unspecified	Gastropods, crabs, fish	Manual removal and cages	Recruitment lower in presence of gastropods	Jensen & Jensen (1985)
<i>Cerastoderma edule</i>	2–35 mm	Green crabs	Lab experiment	Recruitment lower in presence of predators	Menge (1991)
	2–6 mm	Green crabs	Field enclosure	Predation decreased with increasing prey size and increased with increasing temperature	Menge (1991)
	<5 mm	Polychaetes, nemertines	Inclusion and exclusion cages	Juvenile crabs prey on <i>C. edule</i>	Sanchez-Salazar et al. (1987)
<i>Mercenaria mercenaria</i>	4.5–20 mm	Shrimps	Lab experiment	Crabs preferred <i>C. edule</i> to <i>M. balthica</i> or annelids	Jensen & Jensen (1985)
<i>Gemma gemma</i> <i>Macoma balthica</i>	1 mo survival <0.3 mm	Polychaetes Amphipods	Lab experiment	Cage treatments were unreplicated. Juvenile cockles were found only in enclosures, and not in predator inclusion cages	Reise (1979)
	0.25–0.3 mm 0.5–1.5 mm	Nereid polychaetes Nereid polychaetes	Lab experiment Lab experiment	Predation rate decreased with increasing prey size	Bval (1983)
<i>Mytilus lateralis</i> Soft-bottom bivalves	0.2–0.25 mm Recruitment after 49 d	Polychaetes Decapods, fish	Lab experiment Exclusion cages	Polychaetes prey on juvenile <i>G. gemma</i>	Weinberg (1984)
Decapoda <i>Panulirus argus</i>	5–35 mm	Fish, crabs, octopus	Tethering	Increased sediment depth decreased predation rate	Elmgren et al. (1986)
	7–11 mm	Fish, crabs, octopus	Tethering	Polychaetes decreased survival of <i>M. balthica</i>	Ölafsson (1989)
				Predation rate decreased with increasing prey size	Rönn et al. (1988)
				Polychaetes decreased survival of <i>M. lateralis</i>	Luckenbach (1987)
				Densities of bivalve spat were greater inside than outside predator exclusion cages	Möller (1986)
				Predation rate on lobsters decreased with increasing prey size, and was greater for lobsters without shelter	Smith & Herrnkind (1992)
				Predation rate on lobsters greater in open than in algae	Herrnkind & Butler (1986)

Table 3 (continued)

Species	Size/age	Predator	Methods	Patterns/conclusions	Source
<i>Panulirus cygnus</i> <i>Homarus americanus</i>	<26 mm	Fish	Stomach contents	Small juveniles detected in stomach contents	Howard (1988)
	2–40 mm	Fish, crabs	Tethering	Predation rate decreased with increasing prey size, and was greater on bare or PVC substrate than on cobble	Wahle & Stepien (1992)
<i>Cancer magister</i>	Post-larval/1st benthic instar	Fish, crabs	Lab experiment	Fish predation occurred in eelgrass, sand and mud substrata but not in rock, while crab predation occurred on all substrata	Lavalli & Barshaw (1986), Barshaw & Lavalli (1988)
	1st benthic instar	Fish	Lab experiment	Predation rate was decreased by algae	Johns & Mann (1987)
	Recruitment after 48 h	Conspecifics, fish	Predator exclusion cages	Predation affected survival at 1 site but not at another	Eggleston & Armstrong (1995)
	10–34 mm	Fish, conspecifics	Tethering	Total predation rate was less in shell than in mud substrate, but cannibalism was higher in shell	Fernandez et al. (1993a)
<i>Callinectes sapidus</i>	<8 mm	Conspecifics	Lab/field experiment (recruitment)	Abundance of early juveniles was greater in unoccupied shell plots than in plots occupied by an earlier cohort	Fernandez et al. (1993b)
	11–100 mm	Fish, conspecifics	Tethering	Predation rate was lower in medium density than in low or high density sea grass. Prey size did not affect predation rate	Wilson et al. (1987)
	11–70 mm	Fish, conspecifics	Tethering	Predation rate was lower in macroalgae than in eelgrass or at an unvegetated site. Prey size affected predation rate only at the unvegetated site	Wilson et al. (1990)
	1st, 3rd, 7th, 9th instar	Fish, conspecifics	Lab (tethering)	Predation rate was lower in vegetation and when prey were untethered and decreased with increasing prey size	Pile et al. (1996)
<i>Panopeus herbstii</i>	1st, 3rd, 7th, 9th instar	Fish, conspecifics	Field (tethering)	Predation rate was decreased by vegetation increasing prey size, and storm and post-storm conditions, but not affected by prey density or location	Pile et al. (1996)
	Megalopae	Shrimp	Lab experiment	Predation rate affected by predator species but not by substratum type or prey density	Olmi & Lipcius (1993)
<i>Penaeus esculentus</i>	Megalopae	Fish, shrimp, crabs	Lab experiment	Predation rate was lower on shell substratum than on sand, marsh grass or <i>Ulva</i> spp. Predation rate by crabs was lower than that of the other predator species	Dittel et al. (1996)
	4–5 mm	Fish	Lab experiment	Predation rate was greater on bare substratum than in seagrass	Kenyon et al. (1995)
<i>Penaeus aztecus</i>	8–12 mm	Fish	Lab experiment	Predation rate was decreased by artificial seagrass or thick sand (in day but not night)	Laprise & Blaber (1992)
	8–32 mm	Fish	Lab experiment	Vegetation decreased the predation rate of most of the fish species	Minello et al. (1989)
	30–35 mm	Fish	Field-predator exclusion	Mortality rate of shrimp in predator exclusion cages was much lower than mortality rate of cohorts outside of cages	Minello et al. (1989)

Table 3 (continued)

Species	Size/age	Predator	Methods	Patterns/conclusions	Source
Cirripedia					
<i>Tesseropora rosea</i>	1 mo survival	Whelks	Exclusion fences	Exclusion of whelks had no effect on barnacle survival	Denley & Underwood (1979)
<i>Semibalanus balanoides</i> , <i>Balanus glandula</i> , <i>Semibalanus cariosus</i>	Recruitment after 7–5 d	Gastropods, sea stars	Exclusion fences	Exclusion of predators increased recruitment rate in a year with low settler densities but not during 2 years with high settler densities	Carroll (1996)
<i>Balanus inexpectatus</i>	Recruitment after 1–4 mo	Gastropods, fish, crabs	Manual removal and cages	Predation by gastropods but not by fish or crabs decreased barnacle recruitment	Menge (1991)
Ascidacea					
<i>Botryllus schlosseri</i>	1–3 d old	Gastropods	Transplantation	Very few newly recruited <i>B. schlosseri</i> survived when transplanted to a site where gastropods were present	Osman et al. (1992)
<i>Botryllus schlosseri</i> , <i>Botrylloides diegensis</i> , <i>Diplosoma</i> sp.	Recruitment after 8–18 d	Gastropods	Inclusion cages	Predators affected recruitment of <i>B. schlosseri</i> and <i>Diplosoma</i> sp. throughout the settlement season, but had no effect on <i>B. diegensis</i>	Osman et al. (1992), Osman & Whitlatch (1995a)
<i>Trididemnum opacum</i>	Recruitment after 1 mo	Fish, urchins	Exclusion cages	Substratum heterogeneity decreased predation rate	Keough & Downes (1986)
<i>Podoclavella moluccensis</i>	Recruitment after 3 wk	Fish, crabs	Exclusion cages	Fish predation had no effect on recruitment	Davis (1988b)
Didemnid ascidians	Recruitment (sampled every 2 mo)	Fish	Exclusion cages	The effect of crabs was due to physical disturbance rather than predation	Keough (1984)
Bryozoa					
<i>Tubulopora</i> spp., <i>Celleporella brunnea</i> , <i>Scrupocellaria bertholletti</i>	Recruitment after 3–4 wk	Fish	Exclusion cages	Spatial distribution and abundance affected. Little effect on distribution or abundance.	Keough & Downes (1982)
<i>Cryptosula pallasiana</i> , <i>Bugula turrita</i>	Recruitment after 8–18 d	Gastropods	Inclusion cages	Size distribution affected by predation	Osman et al. (1992), Osman & Whitlatch (1995a)
Polychaeta					
<i>Spirorbis eximus</i>	Recruitment after 3–4 wk	Fish	Exclusion cages	Gastropods had only small effects on bryozoan recruitment	Keough & Downes (1982)
<i>Phragmatopoma virgini</i>	Recruitment after 1 mo	Snails, crabs, seastars	Exclusion cages	Predator exclusion cages had little effect on recruitment rate	Zamorano et al. (1995)
<i>Abarenicola pacifica</i>	2 mo survival	Polychaetes, cumaceans	Lab experiment	Recruitment greater on rough substratum	Wilson (1981)
<i>Capitella</i> sp. 1	2–3 wk survival	Polychaetes	Transplant	Predators reduced survival of juveniles	Qian & Chia (1994)
<i>Nerineopsis</i> spp., <i>Armandia brevis</i>	7–10 d survival	Amphipods, tanaid crustaceans	Lab experiment	Predators reduced survival of juveniles	Oliver et al. (1982), Oliver & Slattery (1985)
Communities					
Sessile species on subtidal panels	Recruitment after 2 mo	Rock lobsters	Exclusion cages	Some species of crustaceans had no effect on mortality rate of <i>Nerineopsis</i> spp. or <i>Nerineopsis</i> sp. Increased sediment depth did not decrease the predation rate	Barkai & Branch (1988)
Soft bottom	<2 mm	Meiofauna, deposit feeders, omnivores	Observations and gut contents	Recruitment was increased by substratum complexity. Effects of predation differed between islands	Thorson (1966)
Soft-bottom estuary, polychaetes and crustaceans	Recruitment after 2.5 mo	Not specified	Exclusion cages	Literature review suggests high post-settlement mortality	Holland et al. (1987)
Soft-bottom macrofauna	Recruitment after 1–2 wk	Meiofauna	cores with/without predators	Predators decreased amplitude of recruitment pulse but did not change shape of abundance curve	Watzin (1983, 1986)

filamentous algae or artificial collectors which were inaccessible to the whelk *Nucella crassilabrum*. However, much of the whelk predation probably occurred several weeks to months after the mussels settled. Also in southern Chile, exclusion of all consumers (whelks and other carnivorous gastropods, crabs, and sea stars) increased recruitment of the reef-building polychaete *Phragmatopoma virgini* (Zamorano et al. 1995).

Researchers investigating predation on older individuals have commented that adult whelks were not observed feeding on newly settled barnacles (*Semibalanus balanoides*, Connell 1961; *Tesseropora rosea*, Fairweather 1988), although Connell (1970) noted that *Balanus glandula* was attacked by predators (primarily 3 species of *Nucella*) soon after settlement. Whelk recruits are probably more important predators of recently settled barnacles and mussels than adult whelks. In the laboratory, Gosselin & Chia (1996) found that 15 to 18 d old *Nucella emarginata* strongly preferred *Mytilus californianus* and *Mytilus trossulus* over 4 other species presented (the barnacles *B. glandula*, *Chthamalus dalli* and *Pollicipes polymerus* and the bivalve *Lasaea* sp.). The whelks preferentially consumed the smallest (1 and 2 mm shell length) size classes of mussels offered. Hunt & Scheibling (in press) found that recruits (<5 mm SL) of *Nucella lapillus* prey on a range of sizes of mussels (*M. trossulus* and *Mytilus edulis*) in the field and the laboratory, including individuals <1 mm shell length. Reduction of the density of recently recruited whelks had no effect on either cover or size distribution of *Mytilus* spp. However, manual removal of whelk recruits was not very effective because the high densities of recruits necessitated a small spatial scale of manipulation that was difficult to maintain.

A number of factors can modify the intensity of predation on recent settlers of sessile species. In the laboratory, predation on juvenile oysters (*Crassostrea virginica*) by blue crabs (*Callinectes sapidus*) decreases with increasing oyster size (Bisker & Castagna 1987, Eggleston 1990). For colonial species, the consequences of predation may also be greater for early juveniles than for adults. Davis (1988b) demonstrated that removal of all zooids (to simulate predation) of the ascidian *Podoclavella moluccensis* killed all juvenile (2 to 3 mo old) colonies in <24 d but did not cause mortality of adults which quickly regenerated. Certain substrata can offer protection from predation, as described above for mussels (Moreno 1995). Settlement beside adults decreased mortality of recently settled octocorals (*Alcyonium siderium*), most likely because adults prevented urchin grazing (Sebens 1983). Protection from predation is probably also the reason for the increased survival of early juvenile vermetid gastropods which settle on bryozoans (Osman 1987).

Competition for space and food

For recently settled invertebrates, particularly sessile ones, overgrowth is an important cause of mortality. Overgrowth by algae is associated with decreased survival of recently settled corals (*Pocillopora damicornis*, Harriott 1983), ascidians (Young & Chia 1984), barnacles (*Tetraclitella purpurascens*, *Tesseropora rosea*, Denley & Underwood 1979), and limpets (*Patelloida latistrigata*, Creese 1982). Survival of early juveniles is increased by factors which decrease algal abundance, such as shade for ascidians (Young & Chia 1984) and the presence of adult limpets for the limpet *P. latistrigata* (Creese 1982).

Overgrowth by other invertebrates is a common cause of mortality for encrusting species (e.g. Buss 1979, 1981, Grosberg 1981), and new settlers may be particularly vulnerable. Overgrowth by ascidians has been suggested as a cause of mortality for early juveniles of the octocoral *Alcyonium siderium* (Sebens 1983) and the bryozoan *Bugula pacifica* (Young & Chia 1981), and for several members of the fouling community in Long Island Sound, USA (Osman & Whitlatch 1995b). Overgrowth also was the likely cause of decreased survival of settlers of the coral *Capnella gaboensis* on biofilmed substrata compared to bare substrata in the laboratory (Farrant 1987). In New South Wales, Australia, Denley & Underwood (1979) showed that survival of newly settled barnacles (*Tetraclitella purpurascens*) in the low intertidal zone was increased by removal of settling polychaetes (*Galeolaria caespitosa*). Also in Australia, mortality of the subtidal colonial ascidian *Podoclavella moluccensis* in the first month after settlement varied among sponge and bare wood substrata due to differences in the risks of overgrowth and dislodgment of substrata: ascidians preferentially settled on substrata on which their survival was increased (Davis 1987). Crowding and overgrowth in dense aggregations of settlers can result in density-dependent early post-settlement mortality (Weiss 1948), although crowding is more likely to cause post-recruitment mortality as the recruits grow and begin to contact one another. Flexibility of body form can lessen the effects of crowding. Young & Braithwaite (1980) reported that gregarious settlers of the ascidian *Chelyosoma productum* produce an epidermal ampulla to access the overlying water column for space to grow.

Limitation of food intake also can cause early post-settlement mortality. In laboratory and field experiments, mortality of newly settled oysters (*Crassostrea virginica*) increased with the density of fouling species, possibly due to food depletion (Osman et al. 1989, Zajac et al. 1989), although some overgrowth occurred (Osman et al. 1989). Increased food supply in the labo-

ratory experiments had mixed effects on oyster spat survival, initially ameliorating density effects and later exacerbating them (Zajac et al. 1989). Underwood et al. (1983) showed that barnacles reduced survivorship of recruits of the limpet *Cellana tramoserica*, probably by decreasing the space available for grazing. In sedimentary habitats, competition for food may be less important as a source of early post-settlement mortality. Although recruitment rates of several species of bivalves in soft-bottom habitats are inversely related to the density of adult conspecifics (e.g. Peterson 1979, Möller 1986, Thrush et al. 1996), this is attributed primarily to a reduction in settling larvae by filter feeding adults rather than early juvenile mortality (Ólafsson et al. 1994). For example, Williams (1980b) found that settlement of clams (*Tapes japonica*) on a beach in Washington was greater in areas with low or moderate densities of adult clams, but adult density had no effect on survival of early juvenile clams (Williams 1980a).

RECRUIT-SETTLER RELATIONSHIP

Relationship between recruit and settler density

A positive relationship between the abundances of recruits and settlers (measured at 1 to 4 d intervals) has been found in most studies of sessile species (mainly barnacles). Recruitment of the barnacle *Chthamalus fissus* in Costa Rica reflected settlement for the first 120 d (Sutherland 1990). Similarly, settlement explained >70% of the variance in the number of *Chthamalus anisopoma* reaching maturity (6 wk of age) in the Gulf of California, Mexico (Raimondi 1990), and in the abundance of *Semibalanus balanoides* recruits at the end of the main settlement season in Nova Scotia, Canada (Minchinton & Scheibling 1991). Connell's (1985) analysis of unpublished data from several studies of barnacles revealed a positive relationship between recruit and settler density for *Tesseropora rosea* at 2 of 3 shore levels in Australia, and for *S. balanoides* in England but not in Scotland or in Massachusetts, USA. In Rhode Island, USA, Bertness et al. (1996) found that interannual differences in abundance and distribution of recruits of *S. balanoides* reflected settlement patterns associated with wind-induced changes in larval concentrations. Davis (1988a) monitored settlement of the colonial ascidian *Podoclavella moluccensis* on wooden pilings in South Australia and found that settlement explained 86% of the variation in recruitment 1 mo later. In California, zooid density of 2 to 4 wk old bryozoans (*Membranipora membranacea*) was primarily related (68% of variance) to recruitment, which was monitored bi-weekly (Yoshioka 1986).

Studies of the relationship between recruit and settler abundance for mobile species have produced variable results. In North Carolina, density of settlers of the bay scallop *Argopecten irradians concentricus* on spat collectors explained 71% of the variance in the number of recruits 2 mo later in 1988, but only 4% in 1989 when settlement was very high at 2 sites (Peterson & Summerson 1992). Herrnkind & Butler (1994) were unable to make consistent, accurate predictions of recruitment of the spiny lobster (*Panulirus argus*) over 3 yr in Florida Bay, USA, based on samples of lobster larvae in the plankton, settlers on floating and benthic collectors, and information on geography and substratum type. More accurate models were generated based on data from a single year, but the most influential variables varied from year to year. Butler & Herrnkind (1997) experimentally tested the importance of settler abundance and availability of shelters for recruitment of *P. argus*. They found that the number of small juvenile lobsters increased at sites where artificial shelters were added, apparently as a result of reduced predation on small juveniles, but did not measurably increase from the addition of new settlers. In New Zealand, Morgan et al. (1982) found no clear relationship between density of juveniles of the rock lobster *Panulirus cygnus* and density of settlers on collectors 1 to 1.3 yr earlier, although Chittleborough & Phillips (1975) had reported a significant relationship based on a smaller portion of the same data set. However, Phillips (1990) suggested that the estimates of densities of juvenile rock lobsters, based on mark-recapture methods, are inaccurate due to migration of lobsters among reefs. There appears to be a stronger relationship between abundances of the early life history stages of the American lobster *Homarus americanus* in the Gulf of Maine, USA. Incze & Wahle (1991) found that the number of 1 yr old lobsters (10 to 16 mm) was significantly correlated with the density of recent benthic recruits (7 to 8 mm carapace length) sampled the previous year. In Australia, the density of juvenile (>3 mm carapace length) tiger prawns (*Penaeus semisulcatus*) was related to the density of recently settled benthic postlarvae (<3 mm) 2 wk earlier (Vance et al. 1996).

For soft-bottom communities, studies examining temporal variability in early juvenile densities provide some information about the recruit-settler relationship. Muus (1973) monitored densities of 11 species of infaunal bivalves (<2 mm shell length) in Denmark. Abundances of most species decreased rapidly after settlement peaked and leveled off at a density unrelated to the peak settler abundance. In South Carolina, USA, Feller et al. (1992) examined the correspondence between peaks of abundance of meiofaunal (<0.5 mm) and macrofaunal-sized (>0.5 mm) polychaetes and

bivalves in sediment samples and larvae in plankton tows. There was better correspondence between peaks of abundance of meiofaunal-sized individuals and planktonic larvae than between macrofauna and larvae, or between macrofauna and meiofauna, suggesting that mortality of new settlers was variable.

McGuinness & Davis (1989) have suggested that using correlation or regression to analyze the relationship between recruit and settler abundance (as was done in most studies described above) is not appropriate because recruit density is constrained to be equal to or less than settler density. However, the relationship between recruitment and settlement in these studies is generally clear even without the use of statistics. McGuinness & Davis (1989) suggested that statistical analyses should be confined to the relationship between mortality and initial settler density. Analysis of the relationship between mortality and settler density is useful, but may not reveal whether spatial or temporal patterns of recruitment reflect differences in settlement (see next section).

Under what conditions are recruit and settler densities positively related?

Connell (1985) suggested that recruitment will reflect settlement only when early post-settlement mortality is density independent. However, Holm (1990) pointed out that settlement and recruitment may still be positively related when mortality is weakly density dependent. When mortality is positively density dependent, predictions of recruitment will be most accurate when settler densities are low, whereas when mortality is inversely density dependent, predictions will be most accurate at high settler densities (Holm 1990).

Positive density dependence of early post-settlement mortality may result from density-dependent predation (Gaines & Roughgarden 1985, Hurlbut 1991a, c), lack of suitable settlement sites (McShane 1991) or crowding (Weiss 1948). Crowding may be a less important cause of density-dependent mortality for recent settlers than it is for recruits which have grown large enough to contact one another (e.g. barnacles, Grant 1977, Denley & Underwood 1979, Bertness 1989, Stephens & Bertness 1991). Inversely density-dependent mortality of recent settlers may arise when conspecific settlers provide protection to one another from harsh physical conditions, as is the case for post-recruitment mortality of the barnacle *Semibalanus balanoides* in the high intertidal zone (Bertness 1989, Stephens & Bertness 1991).

Studies have reported a positive relationship between recruitment and settlement when mortality

was density independent (most studies analyzed by Connell 1985, Davis 1988a, Raimondi 1990, Minchinton & Scheibling 1991) or inversely density dependent (Minchinton & Scheibling 1991). McGuinness & Davis (1989) reanalyzed the data of Davis (1988a) by weighted least-squares regression (to meet the assumption of homogeneity of variances), and those of Caffey (from Connell 1985) by pooling observations, and found significant inversely density-dependent mortality. These studies, all but 1 of which involved barnacles, are the only ones to have simultaneously examined the relationship between recruit and settler abundance and the density dependence of early post-settlement mortality. No consistent trend in the density dependence of early mortality has emerged from other studies of sessile invertebrates. Early post-settlement mortality was positively density dependent for the ascidian *Didemnum candidum* on floating docks (Hurlbut 1991c) and for barnacles (predominantly *Balanus improvisus*) on settlement panels (Weiss 1948). Hurlbut (1991a) found that mortality of 1 d old juveniles was density dependent for the 3 most abundant settlers on subtidal plates (the serpulid polychaete *Hydroides elegans*, the bivalve *Anomia nobilis*, and the bryozoan *Schizoporella unicornis*) but not for the less abundant ascidians (*Phallusia nigra*, *D. candidum*, *Diplosoma listerianum*, and *Diplosoma* sp.). In laboratory studies, survivors of the coral *Porities porities* were clumped (Goreau et al. 1981), suggesting inversely density-dependent mortality, while early post-settlement mortality of the oyster *Crassostrea virginica* was density independent (Roegner 1991). Mortality of bryozoans (*Bugula neritina*) transplanted to the field on artificial seagrass blades was either inversely density dependent or had no trend with density (Keough 1986, Keough & Chernoff 1987).

The density dependence of early post-settlement mortality of mobile species has been examined in fewer studies. McShane (1991) found that the decrease in recruit density (after 5 mo) of the abalone *Haliotis rubra* in southeastern Australia depended on initial recruit density. In contrast, Haywood & Staples (1993) reported that mortality rate of cohorts of the prawn *Penaeus merguensis* was not significantly related to prawn density, although densities decreased dramatically within 2 wk of settlement regardless of initial density. Guillou & Tartu (1994) found that the decline in density of the bivalve *Cerastoderma edule* during the early post-settlement period was not clearly related to initial recruit density. Early post-settlement mortality of sea stars (*Acanthaster planci*) transplanted to the field was density independent (Keesing et al. 1996). Pile et al. (1996) found a hyperbolic relationship between densities of small instars of the blue crab *Callinectes sapidus*, indicating density-dependent proc-

esses. They suggested that this relationship was more likely due to emigration from the nursery habitat than to mortality.

Temporal or spatial variability in mortality may obscure any relationship between recruitment and settlement, even if early post-settlement mortality is density independent (Holm 1990). In the laboratory, Roegner (1991) found that temporal variability of mortality of the oyster *Crassostrea virginica* precluded estimation of recruit density from settler density, despite density-independent mortality.

EFFECTS OF SETTLEMENT AND EARLY POST-SETTLEMENT MORTALITY ON RECRUIT DISTRIBUTION

Sessile species

Association with substrata

Both selective settlement and early post-settlement mortality determine the distribution of recruits at small spatial scales, such as among microhabitats on the substratum. In California, USA, recruits of the ascidian *Trididemnum opacum* occurred primarily in pits and crevices because of both selective settlement and predation of more exposed settlers by fish and urchins (Keough & Downes 1986). Fish predation also determined the spatial distribution of recruits of the bryozoan *Tubulipora* spp., such that recruit abundance was related to the proportional surface area of microhabitat refuges, but it did not affect the distributions of 2 other bryozoans (*Scrupocellaria bertholetti* and *Celleporaria brunnea*) or a polychaete (*Spirorbis eximus*) (Keough & Downes 1982). In North Carolina, early post-settlement mortality did not modify the distribution of recently settled barnacles (*Balanus amphitrite*) and bryozoans (*Bugula neritina*) on an artificial substrata (Lego) with uniformly spaced roughness elements (Walters 1992). Walters & Wetthey (1996) found that both species selectively settled between the 'bumps', which acted as refuges from predation during the first week after settlement. Larvae of 2 species (the bryozoan *Schizoporella errata* and the hydrozoan *Tubularia crocea*) with unlimited growth along the substrata (clonal encrusting and stolon-mat forms respectively) were less specific in their settlement locations and grew out of refuge locations within days (Walters & Wetthey 1996).

Recruits of sessile species are also non-randomly distributed at small spatial scales on biotic substrata. In South Carolina, Young (1991) found that preferential settlement resulted in greater recruitment of the barnacle *Chthamalus fragilis* in the axils of cordgrass

(*Spartina alterniflora*), despite higher early post-settlement mortality in this location. In contrast, the distribution of the bryozoan *Bugula neritina* on seagrass (*Thalassia testudium*) blades in Florida (USA) resulted more from early mortality than from differential settlement (Keough 1986). Mortality of newly settled bryozoans on artificial seagrass blades transplanted to the field was lowest on the distal (oldest) parts of the blades where most adult colonies occurred; settlement accounted for <20% of the deviation from a uniform distribution (Keough 1986). Early post-settlement mortality also appeared to be important in determining the distribution of the colonial hydroid *Hydractinia echinata* on hermit crab shells (Yund et al. 1987). The entire surface of the shells was covered by settlement-inducing bacteria, but extensive differential mortality of juveniles resulted in the concentration of recruits on the undersurface of the shell, particularly at the aperture and siphon where polyps were bathed in the crab's feeding currents (Yund et al. 1987).

Early post-settlement mortality can also alter the association of settlers with particular substrata. Gotelli (1987) found that the association of the compound ascidian *Aplidium stellatum* with vertical surfaces in the field was stronger than the preference of larvae for vertical substrata in the laboratory, suggesting that juvenile mortality also contributed to the distributional pattern. Hurlbut (1991b) compared the distribution of settlers, juveniles, and adults of 2 species of bryozoans (*Flustrellidra hispida* and *Alcyonidium polyoum*) on various substrata in the rocky intertidal zone in New Hampshire, USA. For both species, survival of new settlers appeared to differ among substrata. The distribution of *F. hispida* seemed to result mainly from selective settlement on the most abundant alga, *Ascophyllum nodosum*. However, *A. polyoum* occurred mainly on rock, although it selectively settled on the relatively rare algae *Fucus distichus* and *Chondrus crispus*. Osman (1987) found that the vermetid gastropod *Serpulorbis squamigerus* recruited primarily on encrusting bryozoans. Based on observations of newly settled individuals and measures of post-recruitment mortality, he suggested that although the general association of *Serpulorbis* with bryozoans resulted from both settlement and early post-settlement mortality, differences in recruitment among different bryozoan substrata were caused primarily by mortality.

Vertical distribution

The relative importance of settlement and early post-settlement mortality in determining the vertical distribution of barnacles differs among species. Numerous studies have noted that barnacles settle above the dis-

tributional limit of adults, usually in very small numbers, and that many of these settlers die shortly after settlement (for review see Connell 1985). The vertical distributions of some species of barnacles (*Tesseropora rosea* and *Tetraclitella purpurascens*, Denley & Underwood 1979; *Chthamalus anisopoma*, Raimondi 1988a, 1991) have been attributed to settlement patterns. The vertical range of settlement can be limited by the vertical distribution of larvae in the water column (*Balanus crenatus* and *Balanus glandula*, Grosberg 1982), induction of settlement by conspecifics (*C. anisopoma*, Raimondi 1988a, 1991), or larval avoidance of cues present on the upper shore (*Balanus cariosus*, Strathmann & Branscomb 1979). The frequency of settlement above the upper limit of adults can vary among geographic locations (WetHEY 1984).

The abundance of recruits of subtidal sessile species often varies with depth. On floating docks in Hawaii, USA, non-random settlement resulted in greater abundance of the colonial ascidian *Didemnum candidum* at 0.25 m than 6 m depth, despite high density-dependent mortality of settlers (Hurlbut 1991c). Stoner (1990, 1992) demonstrated that vertical zonation of recruits of the ascidian *Diplosoma similis* in Hawaii was determined by directional larval swimming and active site selection. In contrast, post-settlement mortality appeared to determine the upper depth limit of subtidal ascidians in Florida (Dalby & Young 1992). The lack of recruits in the intertidal oyster zone did not result from larval zonation, as ascidians recruited to floating plates in this zone. Adults transplanted to the oyster zone died, primarily from physiological stress during emersion (e.g. desiccation, insolation, osmotic shock, or freezing), suggesting that new settlers, which are likely more vulnerable to these stresses, experience high mortality in this zone (Dalby & Young 1992).

Horizontal distribution

At horizontal scales of hundreds of metres to kilometres, early post-settlement mortality appears to be less important than settlement in determining the distribution of recruits of sessile species. Gaines & Roughgarden (1985) attributed differences in the abundance of the barnacle *Balanus glandula* between 2 sites on a rocky shore in California to settlement rate since survivorship was similar or greater at the site with lower barnacle abundance. In the San Juan Archipelago, USA, Shanks & Wright (1987) found that barnacle cyprids were abundant in the convergence zone of internal waves, suggesting that cyprids (and other larvae) can be transported shoreward by these waves. Recruitment of barnacles (*B. glandula*, *Semi-*

balanus cariosus) was greater in areas of a bay where surface drifters were frequently transported by internal waves than in areas where drifters were seldom transported. In the intertidal zone of Galveston Bay, Texas, USA, differential settlement results in domination by oysters (*Crassostrea virginica*) within 10 m of shore and by barnacles (*Balanus eburneus*) further from shore (Bushek 1988). Greater settlement of barnacles on the farther pilings was attributed to both preferential settlement and a higher rate of larval supply due to greater water motion (Bushek 1988). Hunt & Scheibling (1996) found that the pattern of distribution of mussel (*Mytilus trossulus*, *M. edulis*) recruits among intertidal habitats (ice-scoured and non-scoured tidepools and emergent rock) corresponded to the pattern of settlement. Bingham (1992) showed that the distribution of epifaunal species among channels in a mangrove island in Florida was best explained by larval supply; early post-settlement mortality of settlers transplanted on panels was low, and varied among channels for only 1 of 5 species tested. A short larval lifespan appeared to explain the absence of the bryozoan *Bugula neritina* from some suitable sites in seagrass beds in Florida. Keough & Chernoff (1987) found that early post-settlement mortality of transplanted bryozoans was lower at sites where adults were absent, suggesting that the patchy adult distribution results from limited dispersal of the short-lived larvae rather than from post-settlement mortality. In a lagoon in the Great Barrier Reef, Olson (1985) showed that the distribution of recruits and adults of the colonial ascidian *Didemnum molle* matched the dispersal pattern of the short-lived larval stage, indicating that early post-settlement mortality (which was not measured) did not modify the distribution of settlers. Also on the Great Barrier Reef, Sammarco & Andrews (1989) found that coral recruitment on plates decreased with distance from the reef, even though early post-settlement mortality due to overgrowth was higher on and directly adjacent to the reef. Coral spat were concentrated at stations with high water residence times.

Early post-settlement mortality appears to be responsible for the dominance of bryozoans in some New England fouling communities, although the contributions of larval supply and settlement to this pattern have not been examined. Osman et al. (1992) and Osman & Whitlatch (1995a) found that micropredators (the gastropods *Anachis lafresnayi* and *Mitrella lunata*) dramatically reduced the recruitment of ascidians, resulting in dominance by bryozoans. The gastropods were fairly specific in their prey preference and were capable of affecting the recruitment of ascidians throughout the settlement season (Osman & Whitlatch 1995a).

Mobile species

The distributional pattern of settlers of mobile species can be modified by migration (e.g. the sea cucumber *Psolus chitonoides*, Young & Chia 1982; the gastropod *Lacuna vincta*, Martel & Chia 1991) as well as early post-settlement mortality. Movement frequency of early juveniles of some species can be high. For example, Armonies (1994) estimated that juvenile bivalves (*Macoma balthica* and *Cerastoderma edule*) in a soft-bottom community in the German Wadden Sea moved at least once a week during summer. For species with high rates of movement, patterns of settlement and early post-settlement mortality are likely to influence the distribution of recruits only at scales larger than that of the movement of early juveniles.

Several studies have found evidence that early post-settlement mortality influences the distribution of recruits of mobile epifauna. Eggleston & Armstrong (1995) found that differences between sites in settlement rate of Dungeness crab (*Cancer magister*) attributed to postlarval supply disappeared in less than 48 h outside predator exclusion cages. The high densities of juveniles of the red and purple sea urchins *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus* beneath or near adults also have been attributed to early post-settlement mortality rather than preferential settlement or migration (Cameron & Schroeter 1980). However, Breen et al. (1985) found that juveniles of *S. franciscanus* in laboratory experiments actively associated with adults, particularly in the presence of predators, and suggested that the association in nature was due to migration rather than mortality. Early post-settlement mortality also has been implicated as a cause of between-habitat differences in the distributions of *S. franciscanus* and *S. purpuratus*. After a large settlement pulse, Rowley (1989) observed high densities of recently settled urchins in both a kelp bed and an adjacent barrens area. The density of these juveniles declined more rapidly in the kelp forest than in the barrens, suggesting that the lower numbers of adult urchins in kelp forests than barren grounds results from greater mortality in the kelp habitat (Rowley 1990). However, the generality of Rowley's conclusions is limited by the lack of replicate sites and the observation of a single settlement event.

Despite the influence of both mortality and movement, settlement can in some cases determine the distribution of recruits of mobile epifauna. O'Connor (1993) found that the distributions of the fiddler crabs *Uca pugnax* and *Uca pugilator* in a salt marsh in North Carolina were determined at settlement: the distributions of the 2 species differed within the marsh but the distribution of individuals of each species did not vary with age.

Early post-settlement mortality can influence the distribution of infauna in soft-bottom communities. In an intertidal community in South Carolina, Luckenbach (1984) compared sites with different densities of the polychaete *Diopatra cuprea* and showed that, although *D. cuprea* tubes did not influence settlement of the bivalve *Mulinia lateralis*, they resulted in reduced numbers of bivalves in the smallest size class 1 mo later. This reduction could have been due to emigration, but more likely resulted from interactions with other infauna (Luckenbach 1984). This conclusion was supported by a laboratory experiment (Luckenbach 1987) indicating reduced survival of recently metamorphosed *M. lateralis* in the presence of 2 polychaetes (*Nereis succinea* and *Streblospio benedicti*) which are common around *D. cuprea* tubes. Both settlement and post-settlement mortality appear to influence the distribution of male isopods (*Paragnatha formica*) in an English salt marsh (Upton 1987). Settlement is probably not indiscriminate as isopods were found only within a restricted vertical range and larval males were most abundant in core samples which contained adult males. However, juvenile males were disproportionately more abundant lower in the zone compared to adult males. Upton (1987) suggested that mortality of juveniles was greater lower in the zone where their molting chambers became waterlogged and anoxic. Settling larvae may be able to avoid some agents of early juvenile mortality. For example, larvae of the spionid polychaete *Pseudopolydophora kemp* appear to avoid the polychaete *Abarenicola pacifica*, whose defecation may have negative impacts on small infauna (Woodin 1985). After sediment cores were outplanted in the field for 1 wk, densities of small spionids were greater in blank cores than in cores which contained an undamaged polychaete, a regenerating polychaete, or worm smell (worm removed before transplant to the field).

The vertical distribution in the deep sea of benthic invertebrates with planktonic larvae can be influenced by patterns of both settlement and early post-settlement mortality. In the Rockall Trough (2800 to 2900 m) off the Hebrides Islands, UK, Gage & Tyler (1981) found large numbers of juvenile ophiuroids (*Ophiocten gracilis*), many of them corpses, in benthic samples collected in summer, but few in fall. The adult population of *O. gracilis* occurs from ca 600 to 1200 m depth on the slope surrounding the Trough and is most likely the source of this non-viable settlement in deep water (Gage & Tyler 1981). In some cases, individuals which settle below the lower depth limit of the reproductive population survive. Mileikovsky (1961) argued, based on the horizontal distribution of larval stages in a series of plankton samples, that the deep-water population of the polychaete *Euprosyne borealis* in the Norwegian

Sea was a 'pseudopopulation', existing only because of the influx of larvae from depths above 400 m.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Although our knowledge of the early post-settlement period is still limited, the number of studies addressing this topic is expanding rapidly. While the literature is currently biased towards a few groups of organisms (mainly barnacles and ascidians), the evidence to date suggests that early post-settlement mortality influences recruitment patterns of many different types of benthic marine invertebrates. The importance of events during this period arises from the very high rates of mortality of recent settlers (usually Type III survivorship, although mortality in the first few hours to days after settlement has only been observed for a few species) and the spatial and temporal variability of this mortality. Mortality patterns of early juveniles cannot necessarily be predicted from those of adults because vulnerability to different sources of mortality often varies with size (age). In many studies, spatial patterns of settlement or early post-settlement mortality were found to influence the distribution and abundance of adults, underscoring the importance of studying events which occur in the early benthic stage. Reviews of recruitment in other groups of marine organisms (e.g. benthic algae, Vadas et al. 1992; coral reef fish, Booth & Brosnan) also have suggested the importance of high rates of early post-settlement mortality, but have not as yet established a clear link between early juvenile mortality and the distribution and abundance of recruits.

Factors which are known to cause mortality of recent settlers of benthic marine invertebrates include biological and physical disturbance, delay of metamorphosis, physiological stress, predation, and competition for food and space (Gosselin & Qian 1997, this review). Predation has been the best-documented cause of early post-settlement mortality, particularly for mobile invertebrates, but most studies have focused on individuals several weeks to months after settlement. Similarly, mortality of juvenile fish on coral reefs is most often attributed to predation (Hixon 1991, Booth & Brosnan 1995). Physical disturbance has received relatively little attention as a source of early post-settlement mortality of invertebrates, although wave action and water flow have been shown to cause mortality of macroalgal zygotes and germlings (for review see Vadas et al. 1992) and probably have the same effect on invertebrate settlers in the intertidal zone of rocky shores. Many causes of mortality of recently settled algae are similar to those reported for sessile inverte-

brates, including grazing, canopy effects, presence of algal turf, and desiccation (reviewed by Vadas et al. 1992). Disease and parasitism are potential causes of early post-settlement mortality which have not yet been addressed, although the importance of these agents of mortality among older life history stages of marine invertebrates is well known (Kinne 1980). Problems arising at or before metamorphosis, such as developmental abnormalities (Rumrill 1990), complications during metamorphosis (Roegner 1991), or insufficient energy reserves (Gosselin & Qian 1996), are other possible causes of early post-settlement mortality which should be investigated. Observations of recently settled individuals under benign conditions in laboratory aquaria may give some indication of the frequency of such problems and their influence on survivorship. Even at sublethal levels, disease, parasitism, developmental abnormalities, or poor physiological condition may increase mortality by increasing the susceptibility of recent settlers to predation or physical disturbance. Future studies of early post-settlement mortality should evaluate the influence of the various causes of mortality on patterns of abundance and distribution of recruits. Because of the lack of data on many of the causes of early post-settlement mortality, it is not presently possible to rank the various factors as selective pressures (Gosselin & Qian 1997).

Early post-settlement mortality did not obscure the relationship between recruit and settler abundance in most studies of sessile invertebrates (almost all of barnacles), but this relationship appears to be more variable among mobile species. When recruit and settler density were related, mortality was either density independent or inversely density dependent. However, there is still insufficient data to support general conclusions about the conditions under which recruitment rate can be predicted from settlement rate. Studies examining the relationship between recruit and settler density under conditions of both density dependent and density independent mortality, and over a range of settler densities, are needed before conclusions can be drawn. Both early post-settlement mortality and settlement patterns have been shown to affect the distribution of recruits of sessile species at small spatial scales, but there is less evidence of the influence of mortality at larger scales. In addition to migration, early post-settlement mortality modifies the distribution of recruits of some mobile species. Differences among spatial scales in the importance of early post-settlement mortality may result from variation in the relative importance of different causes of mortality. Variation in the processes operating at different spatial scales has been documented for settlement. For example, active habitat selection becomes important at scales of centimetres to metres, but larvae tend to be

passively deposited at large spatial scales (reviewed by Butman 1987). However, the scale dependence of differing processes influencing early post-settlement mortality has not yet been addressed.

Early post-settlement mortality probably exerts strong selective pressure on settlement patterns of both sessile and mobile invertebrates. A number of invertebrate species selectively settle in locations where early post-settlement mortality is low (Highsmith 1982, Young & Chia 1984, Davis 1987, Hurlbut 1993). However, species with widely dispersing larvae may encounter different agents of mortality in different areas, resulting in 'fatal errors of set' (Strathmann et al. 1981). There may be tradeoffs between early post-settlement survivorship and adult or juvenile mortality (Keough 1986, Schubart et al. 1995). These tradeoffs can only be assessed in studies which examine the spatial and temporal variability of mortality of both settlers and older individuals. Genotype-specific post-settlement selection has been documented for mussel populations (for review see Gosling 1992), but most studies have not isolated the stage at which selection occurs. Pedersen (1991) examined temporal variation in isozyme frequencies within *Mytilus trossulus* and found no evidence of early post-settlement selection. Further genetic studies contrasting settlers and recruits are necessary to determine whether post-settlement selection varies among different microhabitats or under different environmental conditions.

Studies of barnacles and ascidians have contributed much of our knowledge of early post-settlement mortality of benthic invertebrates. More information is now needed for other groups of benthic marine invertebrates, particularly mobile ones. Obtaining information about the fate of settlers of mobile species, which may undertake frequent and extensive movements or remain cryptic or buried in sediment, is much more difficult than mapping sessile organisms on exposed substrata. A combination of methods will probably prove most useful. Field experiments involving tethering and predator enclosures or exclosures can be used to identify causes of mortality (e.g. Table 3). Settlement rate on collectors or in passive settlement traps can provide an index of larval supply for comparison with subsequent censuses of recruits (e.g. collectors, Morgan et al. 1982, Peterson & Summerson 1992, Forcucci et al. 1994, Herrnkind & Butler 1994, Eggleston & Armstrong 1995, Balch & Scheibling in press; tube traps: Wilson 1990), although patterns and rates of settlement on artificial substrata may differ from those on natural substrata (e.g. Hunt & Scheibling 1996). Laboratory-reared settlers can be transplanted to the field to examine mortality shortly after settlement when individuals from naturally settled cohorts are rare or difficult to detect (e.g. Keesing & Halford 1992, Ray &

Stoner 1995, Keesing et al. 1996). Tagging and marking methods using dye (Qian & Chia 1994), microwire tags (Forcucci et al. 1994), nailpolish (Gosselin 1993), and plastic 'bee' tags (Barbeau et al. 1996) which enable researchers to follow the fate of individuals or cohorts of very small invertebrates have been developed. Time-lapse video photography may reveal early mortality events such as predation or dislodgment, particularly at times (e.g. at night or during storms) when direct observations in the field are difficult or impossible.

The relative importance of the early post-settlement period compared to other life history stages can only be determined in studies which examine several stages. Studies examining larval supply, settlement, and early post-settlement mortality (or recruitment) are necessary to provide information about the contribution of the various components of recruitment (e.g. Davis 1988a, Bertness et al. 1992, Eggleston & Armstrong 1995). The importance of settlement and recruitment rates in regulating the dynamics of adult populations are best addressed in studies which follow individuals from settlement to adulthood (e.g. Davis 1988a, Raimondi 1990, Minchinton & Scheibling 1991) or compare patterns of abundance and distribution of various age classes over a time series (e.g. Feller et al. 1992, Peterson & Summerson 1992, Pile et al. 1996). Comparison of the distributions of different cohorts (settlers, recruits, and adults) at a single time also can provide valuable information (e.g. Grosberg 1982, Raimondi 1988a, Hurlbut 1991b, c, O'Connor 1993), but may confound temporal variation in abundance of cohorts with patterns of mortality. Matrix models can be used to explore the sensitivity of adult population size to changes in settlement rate and survivorship of various stages (e.g. Hughes 1990), although such models have seldom been applied to studies of marine invertebrates.

Finally, one of the major impediments to any synthesis of studies of recruitment in benthic marine invertebrates is the ambiguity in the operational definition of recruitment. While an operational definition of recruitment is appropriate to fisheries research (i.e. the size at which new individuals join the harvestable stock), there is no clear analogue in ecological studies of the marine benthos. The body size at which new individuals are recorded in invertebrate populations will be determined by the growth rate of early juveniles and (or) their behavioural and morphological adaptations for crypsis (perhaps by the persistence and eyesight of the observer as well!). Thus, the utility of the term recruitment according to its current usage in ecological studies of benthic marine invertebrates is questionable. The input of new individuals to a population can be quantified by censusing juveniles (= recruits) at a

particular size or time after settlement without invoking a term which may do more to obfuscate than clarify an ecological process. Recruitment may be more meaningful if it is used to quantify the addition of new individuals to the adult (breeding) population. This would require knowing the size (age) at sexual maturity for a given species, which can vary among populations and habitats but is easily measured in most cases. Recruitment as the number of individuals undergoing the transition to adulthood, a discrete biological event, would provide a more readily quantifiable and standardized measure of a demographic process than that given by current definitions of the term.

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