Are planktonic larvae of marine benthic invertebrates too scarce to compete within species ?

Richard R. STRATHMANN

Friday Harbor Laboratories and Department of Zoology, University of Washington, 620 University Road, Friday Harbor, WA 98250, USA.

ABSTRACT

Several models for the evolution of complex life histories have assumed a carrying capacity for both larval and postlarval stages. In addition, the densities of larvae in laboratory experiments are often so high that there is competition for food. Published values for maximal clearance rates and estimated abundances of larvae suggest that these assumptions and experimental conditions are unrealistic for most marine larvae. For most ciliated larvae, maximum clearance rates are at most a few ml of water daily, and their estimated larval concentrations are at most one to several larvae per liter. Therefore these larvae appear to be too scarce for their grazing to affect their food supply. Larvae of most species are also scarce relative to co-occurring planktonic animals that feed on particles in the same size range. Larvae of many species are scarce relative to co-occurring larvae with a similar feeding apparatus. These observations suggest that larvae of most species have a negligible effect on their food supply. Exceptions could occur when a single species of larva dominates the zooplankton; such circumstances appear to be rare, although extreme aggregations of larvae dominated by a single species could be missed by pump or net samples. Analogous but more conjectural arguments can be made for density-dependent attraction of predators to larval prey. These inferences apply to single species, not to meroplanktonic larvae as a whole: in some coastal waters, larvae of benthic invertebrates comprise a large portion of the multicellular planktonic animals. Also, a species' larval growth may be food-limited in many waters, even when the abundance of food is independent of the abundance of its larvae.

RÉSUMÉ

Les larves planctoniques des invertébrés benthiques sont-elles trop rares pour entrer en compétition avec les autres espèces ?

Plusieurs modèles traitant de l'évolution de complexes cycles de vie ont supposé qu'il existait une capacité de charge du milieu pour les larves et les post-larves. Les densités de larves dans les expériences de laboratoire sont souvent si fortes qu'il existe une compétition pour la nourriture. Les valeurs publiées concernant les taux de filtration maximum et les abondances estimées de larves suggèrent que ces hypothèses, de même que les conditions expérimentales, ne reflètent pas la réalité en ce qui concerne la plupart des larves marines. Pour la majorité des larves ciliées, les taux de filtration maximum sont de quelques millilitres d'eau de mer par jour et les concentrations larvaires correspondantes estimées à environ une larve par litre. Ces larves sont donc trop peu nombreuses pour que leur broutage affecte le potentiel trophique dont elles disposent. Les larves de la plupart des espèces sont également faiblement représentées par rapport à leurs com-

pétiteurs planctoniques se nourrissant des particules de même taille. Et beaucoup de ces larves sont rares par rapport aux larves concurrentes présentant le même système d'alimentation. Ces observations suggèrent que les larves de la plupart des espèces ont un effet négligeable sur la quantité de nourriture présente. Des exceptions pourraient cependant se présenter quand une seule espèce de larve domine le zooplancton, mais de telles circonstances sont rares, bien que les systèmes de prélèvements comme les pompes ou les filets, peuvent mal échantillonner ces types extrêmes d'agrégation où dominerait une seule espèce. Des arguments analogues mais plus conjecturaux indiqueraient que l'attraction des prédateurs dépend de la densité des proies. Ces considérations s'appliquent à une seule espèce, non à l'ensemble des larves méroplanctoniques: dans certaines eaux côtières, les larves des invertébrés benthiques comprennent une large proportion d'animaux planctoniques multicellulaires. La croissance larvaire d'une espèce peut alors être limitée par le potentiel trophique, même quand l'abondance de la nourriture est indépendante de l'abondance des larves.

INTRODUCTION

Does an increase in abundance of larvae of a species result in decreased growth or survival ? This question arises because some models for the evolution of complex life histories have assumed density-dependence in the form of a carrying capacity for larvae within a species (Istock, 1967; Ebenman, 1992). The assumption of density-dependent limits is convenient but is it plausible for larvae of most marine species?

The question also arises because of laboratory methods for the culture of marine invertebrates. Larvae are commonly reared at high densities, hundreds or thousands of larvae per liter. Even unusually low experimental concentrations have still exceeded densities common in the plankton (Scheltema, 1986). If such high concentrations are rare in nature, then the laboratory results could be misleading. For example, when larvae deplete the food in culture vessels, higher concentrations of food may be required for maximal growth, and as the larvae develop higher ingestion rates, the concentrations of food required for maximal growth rates may increase (Davis and Guillard, 1958; Rhodes and Landers, 1973). In contrast, when the densities of larvae are so low that food is not depleted, the actual satiating concentrations may be lower and more nearly constant during larval development (Strathmann, 1987).

A third source of interest in density dependent limitations on larvae is the relationship between stock and recruitment. This issue has been examined at length for fishes (Sinclair, 1988; Myers and Cadigan, 1993; Leggett and Deblois, 1994). When similar numbers of recruits are produced from low spawning stocks and from high spawning stocks (Myers *et al.*, 1994), then presumably some mechanism is preventing larger numbers of eggs from yielding larger numbers of recruits (Hilborn and Walters, 1992). To put it another way, the resilience of stocks under exploitation argues for density-dependent survival in the first year of life (Shepherd and Cushing, 1980). Variation in fecundity of spawning animals does not account for this density-dependent recruitment. The problem of density-dependent

recruitment has focused attention on potentially density-dependent sources of mortality for fish larvae.

A debated question is whether fish larvae are «too dilute» to deplete their food supply or attract predators in a density-dependent fashion (Cushing, 1983). The question is more complicated than it first seems. For example, Cushing (1983) argued that even abundant fish larvae are probably too dilute to affect their food supply at early stages but at later stages could affect the supply enough to generate density-dependent growth. Kiørboe *et al.* (1988) estimated that herring larvae did influence the density of their food in a productive frontal area. Fortier and Harris (1989) suggested that feeding stages of fish larvae risked predation by moving to depths with more abundant food but calculated that the larvae themselves had little impact on their food resources, whose abundance was affected by other planktonic predators. Bollens (1988) simulated the population dynamics of larvae of two species of fish and their prey and concluded that some fish larvae could affect populations of their prey but that the impact of the fish larvae was sensitive to fecundity, growth rates, mortality rates and initial numbers of the prey, as well as to abundance and feeding behavior of the fish larvae. Similarly, Munk and Nielsen (1994) concluded that abundance of fish larvae could affect the abundance of their copepod prey, but production of the copepods was also influenced by other predators, whose abundance could also fluctuate.

The larvae of many marine invertebrates differ from fish larvae because many are small ciliary suspension feeders that capture unicellular prey. A separate discussion of the abundance of several kinds of invertebrate larvae in relation to intraspecific density-dependent growth or mortality is therefore warranted. As in some studies of fish larvae, I shall ask whether invertebrate larvae are too scarce to affect their food supply. The rationale is similar to discussions of fish larvae. If larvae of a given species can deplete their food supply, then growth can be density-dependent. Density dependent growth could result in density-dependent mortality because a prolonged period of larval feeding could result in more deaths from predation or, when adults are benthic and sedentary, more transport away from favorable benthic

sites. Alternatively, slow growth could result in smaller juveniles at metamorphosis and as a consequence greater postlarval mortality. I shall ignore other sources of mortality that might be density-dependent, such as selective predation on larvae that are more abundant or transmission of pathogens. It is possible, however, that extreme scarcity of a larval form relative to alternative prey species could preclude density-dependent predation on that form.

This paper examines the potential for larval competition by considering (1) the abundance of meroplanktonic species relative to holoplanktonic suspension feeders, (2) concentrations of larvae relative to their clearance rates, and (3) concentrations of larvae relative to other larvae that are similar in form or feeding. Inferences from these data required several assumptions, which I shall state at the outset.

Of necessity, I have assumed that sampling methods have not obscured aggregations of larvae or differences in distribution among species. Sampling with a net or pump averages abundances within a large volume of water.

I have also assumed that different larvae eat the same prey in nature if they feed with similar structures or ingest particles of similar sizes. Different feeding mechanisms may capture different foods. Animals with opposed-band ciliary feeding are reported to capture small (1 to 3 μm) particles more efficiently than many of those with upstream capture and are often unable to capture particles as large as those available to those with upstream capture (Ayukai, 1994; Hansen, 1991; Hart and Strathmann, 1995). Surface properties affect retention during capture (Gallager et al., 1988) or subsequent selection (Appelmans, 1994), which adds a further possibility of specialization. Even among species of cirripede nauplii (Stone, 1989) or echinoderm larvae (Rivkin et al., 1991) there are differences in the sizes or kinds of particles suitable as food. Nevertheless, larvae of diverse phyla capture and ingest particles of the same or broadly overlapping sizes (Strathmann, 1987; McEdward and Strathmann, 1987; Hansen, 1991), and the same species of cultured algae (such as *Isochrysis galbana, Chaetoceros calcitrans*, or *Rhodomonas lens*) are adequate foods for a great variety of larvae. I know of no evidence for specialized diets among anatomically similar co-occurring larvae. I have ignored possible interference between larvae, beyond simple depletion of food.

ABUNDANCE OF MEROPLANKTON RELATIVE TO HOLOPLANKTON

Anyone who has collected zooplankton by towing nets in coastal waters has been struck by the abundance of copepods and their nauplii. Examination of samples for smaller suspension-feeders often reveals an abundance of ciliates. The obvious abundance of these holoplanktonic suspension feeders has influenced models of the population dynamics of unicellular planktonic organisms. These models commonly focus on suspension-feeding copepods or ciliates and ignore meroplanktonic larvae. Recent examples are the results and discussions of Kamiyama (1994), Nielsen and Kiørboe (1994), and White and

Roman (1992). The common opinion is that holoplanktonic suspension feeders control the abundance of unicellular planktonic organisms. If this view is correct, then the abundance of food for meroplanktonic larvae has little or no relation to their own abundance; it is controlled by other species. In that case, although growth of meroplanktonic larvae may be food-limited (Fenaux et al., 1994), the limitation does not depend on the density of the larvae.

Do samples from coastal waters indicate an overwhelming dominance of holoplanktonic suspension feeders ? For abundance of meroplanktonic larvae as a whole, I surveyed 111 abstracts retrieved from Aquatic Sciences and Fisheries Abstracts (1978 to March 1994) by the key word "meroplankton". I used a report if the abstract had mentioned abundances of holoplanktonic and meroplanktonic animals and if sufficient data were reported. Differences among locations were confounded with differences in sampling. Biases included differences in net mesh sizes, differences in volumes of water sampled or aggregation of data into means over time or locations, and differences in time of day or year. The data are nevertheless useful, as long as these limitations are kept in mind. Although many meroplanktonic larvae would pass through the larger meshes used, so would many copepod nauplii, rotifers, and ciliates. For example, Sprung (1994) obtained a high proportion of larvae when sampling with a 32 μm mesh: in summer 80 to 90 % of numbers and 40 to 80 % of biomass, but about three quarters of the larvae were nauplii, presumably of holoplanktonic copepods, and the remaining quarter meroplanktonic larvae.

The examples obtained indicate that the meroplanktonic larvae are a small part of the zooplankton under a wide variety of conditions but occasionally comprise a large portion of the zooplankton (Tab. 1).

At most of the open coastal waters and some of the bays, about 20 % or less of the zooplankton was meroplankton, even at the season of greatest abundance of meroplanktonic larvae. In these circumstances, it is difficult to imagine how meroplanktonic larvae could have a greater effect on their food than holoplanktonic animals.

In contrast, in some bays, estuaries, or lagoons, larvae of benthic species are more numerous or have a higher total organic content than the holoplankton. Grazing by larvae of benthic animals could sometimes exceed grazing by holoplanktonic animals. Holoplanktonic animals may not always control the abundance of unicellular planktonic organisms. To assess density-dependent competition for food, it is necessary to examine the abundance and grazing of larvae of particular species.

CONCENTRATIONS OF LARVAE RELATIVE TO THEIR CLEARANCE RATES

The volume of water cleared of food daily is one indication of the effect that larvae could have on their food supply. If larvae of a species are sufficiently abundant to "sweep" a large fraction of the water daily, then they may have an effect on their food supply. Hence the maximum

Limfjord, Denmark (Blanner, 1982), 110 μm mesh, vertical tows, % of individual in zooplankton, extremes for meroplankton selected from data for 1 year at two stations

	Station 3		Station 17	
	March	November	March	February
copepods including nauplii		56 %		46 %
meroplankton	95	15	90	5
larvae of *Balanus balanus*	81		68	

Estuary of Rio Paraíba do Norte, Brazil (Alves Pekala, 1980), 200 μm mesh, March, mean % of individuals in zooplankton

	Inner 6 stations	Outer 7 stations
copepods	6 %	34 %
meroplanktonic larvae	93	59
cirripede nauplii	78	33

Etang de Thau, France, North Mediterranean (Hai, 1985), 150 μm mesh, all months of year, 3 sites, % of individuals in zooplankton

copepods, all stages	41 %
meroplanktonic larvae	53
larvae of spionid polychaetes	22

Lagoons of Po delta, Italy (Ferrari *et al.*, 1982), 90 μm mesh, monthly samples, mean % of individuals in zooplankton

	Scardovari (4 sites)	Canarin (3 sites)
copepod nauplii	26 %	11 %
cirripede nauplii	34	49
meroplanktonic larvae	57	54

Arabian Sea at Nethravati-Gurupur Estuary, India (Bhat and Gupta, 1983), 200 μm mesh, water column, % of individuals in the zooplankton at station 6

	February	October
meroplanktonic larvae	62 %	2 %
copepods and copepodites	36	84

Bristol Channel, England (Williams and Collins, 1986), 280 μm mesh, one year, oblique tows, % of "omnivores" as organic carbon

	N. Outer Channel	Inner Channel
holoplanktonic crustaceans	39 %	71 %
meroplanktonic crustacean larvae	55	9

Tampa Bay, Florida (Hopkins, 1977), 74 μm mesh, surface tows, % of zooplankton at 42 stations

	Mean for year		Spring
	dry weight	individuals	individuals
copepods of 4 species	38 %	60 %	
copepod nauplii	6	29	31 %
meroplanktonic larvae	8	19	22

North Inlet, South Carolina (Lonsdale and Coull, 1977), 153 μm mesh, surface and oblique tows, % of zooplankton

	4 sites and 20 months		June
	dry weight	individuals	individuals
copepods	61 %	55 %	42 %
copepod nauplii	7	14	23 %
meroplanktonic larvae	22	25	21

Kalpeni and Agatti atolls, Indian Ocean (Achuthankutty *et al.*, 1989), Mesh not reported, surface tows, April and May, % of individuals in zooplankton

	Sea		Lagoon	
	Kalpeni	Agatti	Kalpeni	Agatti
copepods	76 %	75 %	13 %	25 %
decapod larvae	11	11	71	68

South coast of Puerto Rico, 0.5 to 1 km offshore (Youngbluth, 1979), 202 μm mesh, upper 3 m; mean % of individuals in zooplankton for sites with greatest and least means for meroplanktonic larvae

	Punta Verraco	Punta Higuero
copepods	73 %	84 %
meroplanktonic larvae	17	2

New Caledonia, lagoon of coral reef, surface waters (Champalbert, 1993), 200 μm mesh, upper 10 cm, March and April, % of individuals in zooplankton

holoplankton	80 - 90 %
meroplanktonic larvae	5 - 20

Galician coast, Spain (Valdes *et al.*, 1990), 202 μm mesh, oblique tows, 100 to 0 m, % of individuals in zooplankton at 22 sites

	June	September
holoplankton	95 %	95 %
copepods	51	91
larvaceans	18	1
meroplanktonic larvae	8	4

◀ Table 1

Abundance of meroplanktonic larvae and holoplankton. Adult copepods and copepodites are lumped as copepods.

clearance rate measures the maximum effect of an individual larva. The maximum clearance rate can be uncertain for several reasons. It sometimes can be estimated from the size of larvae (Strathmann, 1987) or the lengths of ciliary bands and cilia (Hansen and Ockelmann, 1991; Hart and Strathmann, 1994, 1995) if these are reported, but they rarely are reported. Of the literature searched, only Jørgensen (1981) included mean sizes of larvae in each sample and estimated clearance rates. The maximum clearance rates that I have assigned to larvae are estimates for advanced stages and possibly high. My discussion is limited to peak abundances of a few types of larvae. These larvae are ciliary suspension feeders that are abundant, easily recognized, and often counted. Examples of species whose larvae are very scarce were not included because they are not sampled and counted.

Cyphonautes of bryozoans

The cyphonautes is a distinctive larval form that occurs in a few species of bryozoans. A single form of cyphonautes often dominates at a site, indicating that a single species may account for the great majority of larvae in a sample. Therefore I used data on abundance of cyphonautes larvae as indications of abundance of a species (Tab. 2). The «bryozoan larvae» of Hopkin's samples from Tampa Bay are assumed to be the cyphonautes form. Sibert (pers. comm.) says that the larvae in his samples from the Nanaimo River delta were cyphonautes. To estimate maximum effects, I have selected the peak abundance reported by each author.

The estimated proportion of water cleared daily does not exceed 0.2 % in any of the cases examined (Tab. 2). This rate is low compared to the cell division rates of the unicellular organisms consumed by the cyphonautes. Phytoplankton cells commonly divide once or more per day (Banse, 1991). If cell division rates of prey were 1 d^{-1}, the grazing of the cyphonautes would reduce rates of increase by an estimated 0.006 to 0.2 % and thus have little impact on their food supply. By this estimate, intraspecific, density-dependent effects of grazing would be negligible relative to other factors.

There are biases in these estimates. The scarcity of the cyphonautes may be exaggerated by early stage larvae passing through the meshes. In my experience, cyphonautes sampled from a 125 μm mesh net are much larger than 125 μm. Perhaps the flat triangular forms pass through the square meshes diagonally. This bias is not severe for estimates of clearance rates because the underrepresented early stage larvae also have lower maximum clearance rates than the larger larvae. A second bias is that the cyphonautes have an unusually low maximum clearance rate for their size (McEdward and Strathmann, 1987), which reduces their expected impact to about 0.2 of that of other larvae of comparable size. Neither of these biases are great enough to alter the conclusion drawn from the data.

Table 2

Estimated proportion of water cleared daily by cyphonautes larvae at the peak abundances reported in each study. Some samples may lump several species. Sizes are for the net mesh except for Yoshioka's (1982) counts above the stated size. A maximum clearance rate of 1 ml d^{-1} is assumed for all cyphonautes. M. m. = probably Membranipora membranacea; E. p. = Electra pilosa.

Abundance number l^{-1}	Proportion of water cleared d^{-1}	Species, location, net mesh, author
0.3	3×10^{-4}	*M. m.*, S. California coast, >350 µm, Yoshioka (1982)
0.06	6×10^{-5}	*M. m.*, >125 µm, San Juan Channel, Pennington (1986)
0.34	3×10^{-4}	Nanaimo River delta, >100 µm, Sibert (1981)
1.84	2×10^{-3}	Tampa Bay, Florida, >75 µm, Hopkins (1977)
0.058	6×10^{-5}	Coast of Galicia, >200 µm, Valdes *et al.* (1990)
0.58	6×10^{-4}	*E. p.*, Chupa Inlet, White Sea, >75 µm, Oshurkov *et al.* (1982)

Echinoderm larvae

Echinoderm larvae are seldom distinguished to species, but even when lumped by class or phylum, they seldom are abundant (Tab. 3). A maximum clearance rate of 6 ml d^{-1} is typical for larvae well advanced in development (Strathmann, 1971; Hart, 1993) and was assumed for all samples. This value overestimates grazing for Pedrotti's (1993) data, because many of the larvae were at early stages of development. It probably overestimates grazing for instances where no information on stages is given, because echinoderm larvae are usually at early stages when at peak abundances. It underestimates clearance rates for asteroid larvae at advanced stages. Table 3 begins with samples identified to species and progresses to larger taxonomic categories.

The proportion of water cleared daily is small in all cases (Tab. 3), and greatest for an extreme value from Tampa Bay, where all echinoderm larvae were lumped. The echinoderm larvae are usually too scarce to deplete a large fraction of their food daily.

Bivalve veligers

Veligers of bivalves are commonly more abundant than the cyphonautes or echinoderm larvae, and one species of veliger may dominate a sample. Jørgensen (1981) described an instance, in which 90 % of the bivalve veligers were *Mytilus edulis*, and the cohort was sampled for several weeks (Tab. 4). In this case, veligers of a single species were so abundant that they may have reduced their food supply. This cohort grew rapidly but not maximally. Mean shell length increased from 170 to 270 µm in 13 days in contrast to 8.5 days for veligers of *M. edulis* fed satiating concentrations of *Isochrysis galbana* at 18 °C (Sprung, 1984 *a*). This instance appears to meet two necessary

Table 3

Estimated maximum proportion of water cleared daily by echinoderm larvae at peak abundances reported in each study.

Abundance, number l^{-1}	Proportion of water cleared d^{-1}	Location, net mesh, author species
		Bay of Villefranche and vicinity, 200 µm, Pedrotti (1993)
0.014	8×10^{-5}	Ophiopluteus bimaculatus
0.011	7×10^{-5}	Ophiopluteus compressus
0.04	2×10^{-4}	*Amphiura filiformis*
0.00044	3×10^{-6}	*Ophiothrix fragilis*
0.023	1×10^{-4}	*Paracentrotus lividus*
0.01	6×10^{-5}	*Arbacia lixula*
		Kiel Bay, Germany, 110 µm, Banse (1986)
1.34	8×10^{-3}	*Ophiura albida*
		Nakkolmen, Oslofjord, 125 µm, Schram (1970)
0.0057	3×10^{-5}	*Ophiura albida*
0.020	1×10^{-4}	*Ophiura robusta*
0.028	2×10^{-4}	*Psammechinus miliaris*
0.0041	2×10^{-5}	*Asterias rubens*
		Monterey Bay, 202 µm, Cameron and Rumrill (1982)
0.7	4×10^{-3}	*Dendraster excentricus*
		East Sound, Orcas Is., 125 µm mesh, Emlet (1986)
0.657	4×10^{-3}	*Dendraster excentricus*
		San Juan Channel, 125 µm, Pennington (1986)
0.115	7×10^{-4}	Echinoplutei
0.026	2×10^{-4}	Ophioplutei
0.050	3×10^{-4}	Auriculariae and Bipinnariae
		Coast of Galicia, 202 µm, Valdes *et al.* (1990)
0.069	4×10^{-4}	Echinoderm Larvae
		Tampa Bay, Florida, 74 µm, Hopkins (1977)
3.774	2×10^{-2}	Echinoderm Larvae

conditions for density-dependent growth rates: clearance of a large portion of the water daily and food-limited growth.

The larval concentrations decribed by Jørgensen are unusually high for bivalves (Tab. 5). Although larvae of *Mytilus edulis* were among the most abundant larvae in the Oslofjord (Schram, 1968, 1970), their peak concentration was not as great as in the cohort described by Jørgensen (1981). The estimated grazing of bivalve larvae in Vineyard Sound (Gallager *et al.*, 1994) is similar to that of Jørgensen's estimates, but the species composition was not reported. In the other examples in Table 5, reported peak abundances for single species are much lower. Although concentrations of bivalve veligers of a single species can be high, concentrations sufficient to clear a large proportion of the water daily

Table 4

An abundant cohort of veligers in Isefjord, Denmark; 80 to 90 % Mytilus edulis. Abundances are from Jørgensen (1981); clearance rates are estimated from Sprung (1984b).

Size μm	Number l⁻¹	Larval clearance ml d⁻¹	Proportion of water cleared d⁻¹
90	3150	0.25	0.79
170	445	0.68	0.30
270	93	1.39	0.13

are infrequently encountered. The larval concentrations in Table 5 are lower than concentrations in most laboratory experiments.

CONCENTRATIONS OF LARVAE RELATIVE TO SIMILAR LARVAE OF OTHER SPECIES

The effects of abundant larvae may override intraspecific density-dependent processes for similar but scarcer larvae of other species. The case of abundant veligers of *Mytilus edulis* in the Isefjord can be taken as an example. About 90 % of the bivalve veligers were identified as *M. edulis* and about 10 % as *Mya arenaria*. In so far as veligers of these two species have similar effects, the effects of the concentration of *M. edulis* were more important for *M. arenaria* than were the effects of the concentration of *M. arenaria*. If the veligers of *M. arenaria* cleared about 0.05 of the surrounding water daily, then their impact through clearing particles from suspension was greater than that of many of the other larvae tabulated in this survey. Nevertheless, uncorrelated fluctuations in abundance of *M. edulis* would overwhelm intraspecific density-dependent effects for *M. arenaria* that might arise from their feeding. Similarly, if predators responded to the abundant veligers of *M. edulis* by consuming a larger proportion of the bivalve veligers in general, veligers of *M. arenaria* would also suffer the consequences. Schram (1968, 1970) found a similar dominance of veligers of *M. edulis* over veligers of *M. arenaria* and other bivalves in the Oslofjord.

Similar comparisons could be made for other examples in which larvae of one species dominated the meroplankton. Schram (1968) found enormous numbers of larvae of *Polydora ciliata* and *Polydora antennata* in the inner Oslofjord for much of the year. Although larvae of *P. antennata* were abundant (0.17 l⁻¹ and 6.7 % of the common larvae), *P. ciliata* were even more so (2 l⁻¹ and 78.4 % of the common larvae). The relative abundance of these species varied from 72 % *P. antennata* and 28 % *P. ciliata* to >99 % *P. ciliata* and <1 % *P. antennata* (Fig. 1). The abundances of these two species' larvae were negatively correlated (Spearman rank correlation -0.135) if correlated at all. I do not know whether larvae of *P. antennata* feed on the same materials as larvae of *P. ciliata* or attract the same predators, but if they were involved in the same density-dependent processes, variation in abundance of *P. ciliata* obscured the effects of intraspecific variation of *P. antennata*.

Low abundance of larvae of one species relative to similar larvae of other species could overwhelm density-dependent larval growth or mortality within a species.

SAMPLING BIAS

The larval concentrations reviewed here were peak abundances estimated from net and pump samples. These devices sample large volumes of water and thus average larval abundances over a large volume. Larvae could be locally aggregated. I minimized this bias by selecting peak values in reports on larval concentrations. Nevertheless, if highly localized aggregations are common, then the relevant concentrations of larvae could be much higher than those
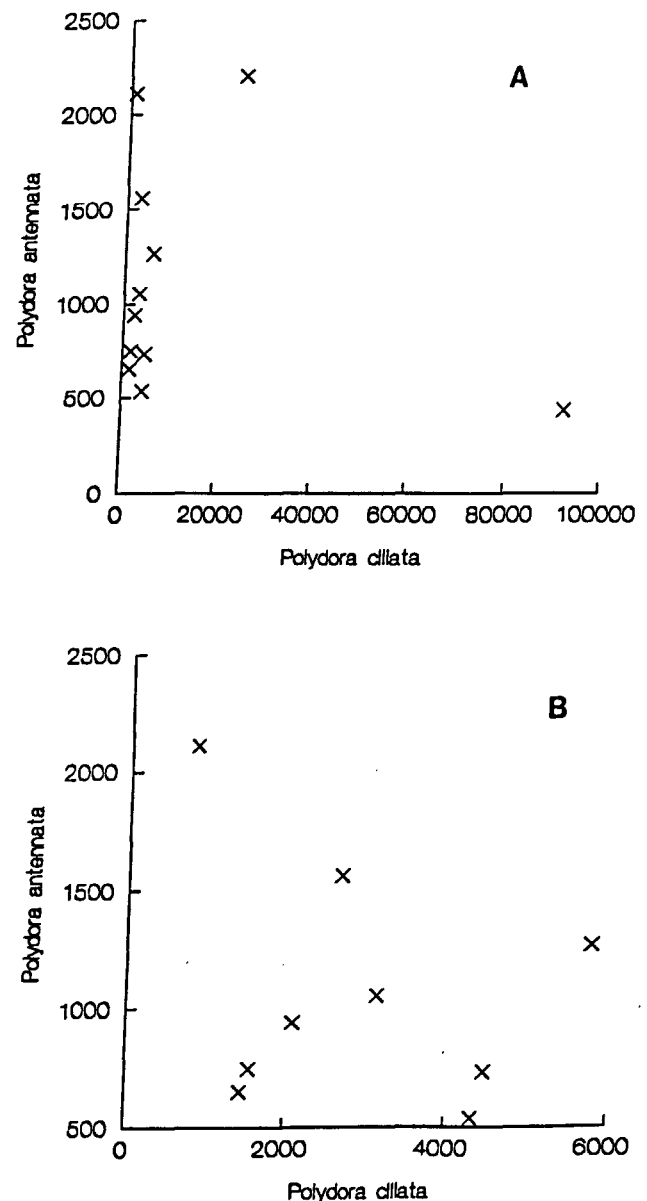

Figure 1

Numbers of larvae of two Polydora *species sampled on different dates in the inner Oslofjord (Schram, 1968). A: samples from all dates. B: samples from the two dates with greatest abundance of* P. ciliata *eliminated to show relative abundances in remaining samples.*

Table 5

Some other reported peak densities of bivalve larvae. Proportion of water cleared is from an assumed clearance rate of 1 ml d⁻¹, which is the rate estimated for a veliger of 218 μm shell length by Sprung's (1984b) regression for Mytilus edulis at 18 °C.

Abundance number l^{-1}	Proportion of water cleared d^{-1}	Species, location, net mesh or count threshold, author
40	4×10^{-2}	*Mytilus edulis*, Oslo Harbor, June, 150 μm, Schram (1970)
3.6	4×10^{-3}	*Mytilus edulis*, Lower Delaware Bay, 241 μm, Maurer *et al.* (1978)
0.87	1×10^{-3}	*Mytilus edulis*, Nakkholmen, August, 125 μm, Schram (1968)
620	0.6	*Mercenaria mercenaria* + other spp., Vineyard Sound, 53 μm, Gallager *et al.* (1994)
4.7	5×10^{-3}	*Anomia simplex*, S. New England Shelf, October, >200 μm, Mann (1985)
2.2	2×10^{-3}	*Placopecten magellanicus*, Georges Bank, October, 85 μm, Tremblay and Sinclair (1990)

estimated from plankton samples. If the aggregations are dominated by single species, then density-dependent growth and mortality are a possibility. Are concentrations sufficiently high for resource competition in local aggregations ?

Sites where larvae may aggregate include surface convergences (Oliver and Willis, 1987; Shanks and Wright, 1987; Kingsford, 1990), layers in density stratified waters (Tremblay and Sinclair, 1990), and the bottom (Sibert, 1981; DeVries *et al.*, 1994). A very high degree of aggregation is needed to change the conclusions based on net and pump samples (Tab. 2, 3, 5). Larvae can be aggregated by a factor of ten or more in slicks as compared to rippled surface water, but the concentrations of feeding larvae were less than one per liter in the samples from slicks tabulated by Kingsford (1990), which were samples with the greatest concentration relative to that in adjacent rippled water. Shanks (1988) found the highest concentrations of larval fish, crustaceans, and polychaetes in convergence zones over internal waves, but none had a mean density exceeding one larva per m², and most densities were far less. There are cases in which multispecies mass spawnings by corals have resulted in mass mortality of embryos or larvae (Simpson *et al.*, 1993), but such prolonged concentrations of planktonic spawn and embryos appear to be rare among marine invertebrates. Sampling techniques such as the video plankton recorder (Davis *et*

al., 1992) can determine whether peak concentrations of larvae are commonly three or more orders of magnitude greater than those indicated by net and pump samples.

Concentration in other planktonic microhabitats is possible. In the samples of Shanks and Edmondson (1990), a large proportion of the competent polychaete larvae (but few precompetent larvae) were associated with marine snow. The total abundance of metazoans on marine snow was less than 0.4 per aggregate. The effect of marine snow on local concentrations of larvae is still unclear.

CONCLUSION

Larvae of most species are at such low concentrations that their effect on their own food supply is expected to be negligible. In addition, for most species and at most places, the combined effect of other planktonic suspension feeders, including other meroplanktonic larvae, is expected to completely obscure any effects of intraspecific variation in abundance.

My discussion of intraspecific density-dependent growth or mortality addressed the impact of larvae on their food supply. Predation and transmission of pathogens also can depend on concentrations of prey or host. Because little is known about the specificity of attacks by predators or pathogens on larvae, I did not speculate on this possible source of density-dependent mortality. A plausible hypothesis for density-dependent mortality from these sources would be constrained by the apparently low densities of larvae within most species.

From existing evidence, density-dependent larval mortality seems implausible for most species of marine invertebrates. I hope that this review will prompt a search for stronger tests of the hypothesis of density-dependent larval mortality or larval growth.

REFERENCES

Achuthankutty C.T., S.R.S. Nair, P. Haridas, M. Madhupratap (1989). Zooplankton composition of the Kalpeni and Agatti atolls, Lakshadweep archipelago. *Indian J. Marine Sciences* **18**, 151-154.

Alves Pekala G. (1980). Nota preliminar sobre a composição do zooplancton do estuário do Rio Paraíbo do Norte, PB, Brasil. *Boletim Inst. Oceanogr. Sao Paulo* **29**, 291-296.

Appelmans T. (1994). Site of particle selection determined from observations of individual feeding larvae of the sand dollar *Dendraster excentricus*. *Limnol. Oceanogr.* **39**, 404-411.

Ayukai T. (1994). Ingestion of ultraplankton by the planktonic larvae of the crown-of-thorns starfish, *Acanthaster planci*. *Biol. Bull.* **186**, 90-100.

Banse K. (1986). Vertical distribution and horizontal transport of planktonic larvae of echinoderms and benthic polychaetes in an open coastal sea. *Bull. Mar. Sci.* **39**, 162-175.

Banse K. (1991). Rates of phytoplankton cell division in the field and in iron enrichment experiments. *Limnol. Oceanogr.* **36**, 1886-1898.

Bhat B.V., T.R.C. Gupta (1983). Zooplankton distribution in the Nethravati-Gurupur Estuary, Mangalore. *Indian J. Mar. Sci.* **12**, 36-42.

Blanner P. (1982). Composition and seasonal variation of the zooplankton in the Limfjord (Denmark) during 1973-1974. *Ophelia* **21**, 1-40.

Bollens S.M. (1988). A model of the predatory impact of larval marine fish on the population dynamics of their zooplankton prey. *J. Plankton Res.* **10**, 887-906.

Cameron R.A., S.S. Rumrill (1982). Larval abundance and recruitment of the sand dollar, *Dendraster excentricus*. *Mar. Biol.* **71**, 197-202.

Champalbert G. (1993). Plankton inhabiting the surface layer of the southern and southwestern lagoon of New Caledonia. *Mar. Biol.* **115**, 223-228.

Cushing D.H. (1983). Are fish larvae too dilute to affect the density of their prey ? *J. Plankton Res.* **5**, 847-854.

Davis H.C., R.R. Guillard (1958). Relative value of ten genera of micro-organisms as food for oyster and clam larvae, *Fish. Bull. U. S. Fish Wildl. Serv.* **58**, 293-304.

Davis C.S., S.M. Gallager, A.R. Solow (1992). Microaggregations of oceanic plankton observed by towed video microscopy. *Science* **257**, 230-232.

DeVries M.C., R.A. Tankersley, R.B. Forward Jr., W.W. Kirby-Smith, R.A. Luettich Jr. (1994). Abundance of estuarine crab larvae is associated with tidal hydrologic variables. *Mar. Biol.* **118**, 403-413.

Ebenman B. (1992). Evolution in organisms that change their niches during the life cycle. *Am. Nat.* **139**, 990-1021.

Emlet R.B. (1986). Larval production, dispersal, and growth in a fjord: a case study on larvae of the sand dollar *Dendraster excentricus*. *Mar. Ecol. Prog. Ser.* **31**, 245-254.

Fenaux L., M.F. Strathmann, R.R. Strathmann (1994). Five tests of food-limited growth of larvae in coastal waters by comparisons of rates of development and form of echinoplutei. *Limnol. Oceanogr.* **39**, 84-98.

Ferrari I., V.U Ceccherelli., M.G. Mazzocchi (1982). Structure du zooplancton dans deux lagunes du Delta du Pô. *Oceanologica Acta* **5**, 4 suppl., 293-302.

Fortier L., R.P. Harris (1989). Optimal foraging and density-dependent competition in marine fish larvae. *Mar. Ecol. Prog. Ser.* **51**, 19-33.

Gallager S.M., C.J. Langdon, K.D. Stolzenbach, L. Davis, D.K. Stoecker (1988). High-speed video analysis of particle capture by a ciliated suspension feeder. *EOS* **69**, 1086.

Gallager S.M., J.B. Waterbury, D.K. Stoecker (1994). Efficient grazing and utilization of the marine cyanobacterium *Synechococcus* sp. by larvae of the bivalve *Mercenaria mercenaria*. *Mar. Biol.* **119**, 251-259.

Hai T.L. (1985). Evolution saisonnière du zooplancton dans trois sites peu profonds de Thau, une lagune Nord-Méditerranéenne. *Hydrobiologia* **128**, 161-174.

Hansen B. (1991). Feeding behaviour in larvae of the opisthobranch *Philine aperta*. II. Food size spectra and particle selectivity in relation to larval behaviour and morphology of velar structures. *Mar. Biol.* **111**, 263-270.

Hansen B., K.W. Ockelmann (1991). Feeding behaviour in larvae of the opisthobranch *Philine aperta*. I. Growth and functional response at different developmental stages. *Mar. Biol.* **111**, 255-261.

Hart M.W. (1993). Size, larvae, and videotape: causes and consequences of variation in suspension-feeding rates of echinoderm larvae. Ph.D. Thesis, University of Washington, Seattle, 149 p.

Hart M.W., R.R. Strathmann (1994). Functional consequences of phenotypic plasticity in echinoid larvae. *Biol. Bull.* **186**, 291-299.

Hart M.W., R.R. Strathmann (1995). Mechanisms and rates of suspension-feeding, in: *Ecology of Marine Invertebrate Larvae*, ed. by L. R. McEdward. CRC Press, Boca Raton, 193-221.

Hilborn R., C.J. Walters (1992). *Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty*, Chapman and Hall, New York, 570 p.

Hopkins T.L. (1977). Zooplankton distribution in surface waters of Tampa Bay, Florida. *Bull. Mar. Sci.* **27**, 467-478.

Istock C.A. (1967). The evolution of complex life cycle phenomena: an ecological perspective. *Evolution* **21**, 592-605.

Jørgensen C.B. (1981). Mortality, growth and grazing impact of a cohort of bivalve larvae *Mytilus edulis* L. *Ophelia* **20**, 185-192.

Kamiyama T. (1994). The impact of grazing by microzooplankton in northern Hiroshima Bay, the Seto Inland Sea, Japan. *Mar. Biol.* **119**, 77-88.

Kingsford M.J. (1990). Linear oceanographic features: A focus for research on recruitment processes. *Aust. J. Ecol.* **15**, 391-401.

Kiørboe T., P. Munk, K. Richardson, V. Christensen, H. Paulsen (1988). Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Mar. Ecol. Prog. Ser.* **44**, 205-219.

Leggett W.C., E. Deblois (1994). Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages ? *Neth. J. Sea Res.* **32**, 119-134.

Lonsdale D.J., B.C. Coull (1977). Composition and seasonality of zooplankton of North Inlet, South Carolina. *Chesapeake Science* **18**, 272-283.

Mann R. (1985). Seasonal changes in the depth distribution of bivalve larvae on the southern New England shelf. *J. Shellfish. Res.* **5**, 57-64.

Maurer D., L. Watling, R. Lambert, A. Pembroke (1978). Seasonal fluctuation of zooplankton populations in lower Delaware Bay, USA. *Hydrobiologia* **61**, 149-160.

McEdward L.R., R.R. Strathmann (1987). The body plan of the cyphonautes larva of bryozoans prevents high clearance rates: comparison with the pluteus and a growth model. *Biol. Bull.* **172**, 30-45.

Munk P., T.G. Nielsen (1994). Trophodynamics of the plankton community at Dogger Bank: predatory impact by larval fish. *J. Plankton Res.* **16**, 1225-1245.

Myers R.A., N.G. Cadigan (1993). Density-dependent juvenile mortality in marine demersal fish. *Can. J. Fish. Aquat. Sci.* **50**, 1576-1590.

Myers R.A., A.A. Rosenberg, P.M. Mace, N. Barrowman, V.R. Restrepo (1994). In search of thresholds for recruitment overfishing. *ICES J. Mar. Sci.* **51**, 191-205.

Nielsen T.G., T. Kiørboe (1994). Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. *Limnol. Oceanogr.* **39**, 508-519.

Oshurkov V.V., M.B. Shilin, I.V. Oksov, B.R. Smirnov (1982). Seasonal dynamics of meroplankton in Chupa Inlet (White Sea). *Soviet J. Mar. Biol.* **8**, 1-8.

Oliver J.K., B.L. Willis (1987). Coral-spawn slicks in the Great Barrier Reef: preliminary observations. *Mar. Biol.* **94**, 521-529.

Pedrotti M.L. (1993). Spatial and temporal distribution and recruitment of echinoderm larvae in the Ligurian Sea. *J. Mar. Biol. Ass. U.K.* **73**, 513-530.

Pennington J.T. (1986). Seasonal population dynamics of invertebrate meroplankton of San Juan Channel, Washington, and studies on patterns of loss from larval populations by predation. Ph.D. Thesis, University of Alberta, Edmonton, 237 p.

Rhodes E.W., W. S. Landers (1973). Growth of oyster larvae, *Crassostrea virginica*, of various sizes in different concentrations of the chrysophyte, *Isochrysis galbana*, *Proc. Natl. Shellfish. Assoc.* **63**, 53-59.

Rivkin R.B., M.R. Anderson, D.E. Gustafson Jr. (1991). Ingestion of phytoplankton and bacterioplankton by polar and temperate echinoderm larvae. *Antarctic Journal* **26**, 156-158.

Scheltema R.S. (1986). On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. Mar. Sci.* **39**, 290-322.

Schram T.A. (1968). Studies of the meroplankton in the inner Oslofjord. I. Composition of the plankton at Nakkolmen during a whole year. *Ophelia* **5**, 221-243.

Schram T.A. (1970). Studies of the meroplankton in the inner Oslofjord. II. Regional differences and seasonal changes in the specific distribution of larvae. *Nytt Magasin for Zoologi* **18**, 1-21.

Shanks A.L. (1988). Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. *Fishery Bulletin* **86**, 703-714.

Shanks A.L., E.W. Edmondson (1990). The vertical flux of metazoans (holoplankton, meiofauna, and larval invertebrates) due to their association with marine snow. *Limnol. Oceanogr.* **35**, 455-463.

Shanks A.L., W.G. Wright (1987). Internal-wave mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *J. Exp. Mar. Biol. Ecol.* **114**, 1-13.

Shepherd J.G., D.H. Cushing (1980). A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *J. Cons. Int. Explor. Mer.* **39**, 160-167.

Sibert J.R. (1981). Intertidal hyperbenthic populations in the Nanaimo Estuary. *Mar. Biol.* **64**, 259-265.

Simpson C.J., J.L. Cary, R.J. Masini (1993). Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs* **12**, 185-191.

Sinclair M. (1988). *Marine Populations. An Essay on Population Regulation and Speciation.* University of Washington Press, Seattle, 252 p.

Sprung M. (1984). Physiological energetics of mussel larvae (Mytilus edulis). I. Shell growth and biomass. *Mar. Ecol. Prog. Ser.* **17**, 283-292.

Sprung M. (1984*b*). Physiological energetics of mussel larvae (Mytilus edulis). II. Food uptake. *Mar. Ecol. Prog. Ser.* **17**, 295-305.

Sprung M. (1994). High larval abundances in the Ria Formosa (Southern Portugal) - methodological or local effect ? *J. Plankton Res.* **16**, 151-160.

Stone C.J. (1989). A comparison of algal diets for cirripede nauplii. *J. Exp. Mar. Biol. Ecol.* **132**, 17-40.

Strathmann R.R. (1971). The feeding behavior of planktotrophic echinoderm larvae: mechanisms, regulation, and rates of suspension-feeding. *J. Exp. Mar. Biol. Ecol.* **6**, 109-160.

Strathmann R.R. (1987). Larval feeding, in: *Reproduction of Marine Invertebrates*, Vol. 9, ed. by A.C. Giese, J.S. Pearse, and V.B. Pearse. Blackwell, Palo Alto, 465-550.

Tremblay M.J., M. Sinclair (1990). Sea scallop *Placopecten magellanicus* larvae on Georges Bank - vertical distribution in relation to water column stratification and food. *Mar. Ecol. Prog. Ser.* **61**, 1-15.

Valdes J.L., M.R. Roman, M.T. Alvarez-Ossorio, A.L. Gauzens, A. Miranda (1990). Zooplankton composition and distribution of the coast of Galicia. *J. Plankton Res.* **12**, 629-643.

White J.R., M.R. Roman (1992). Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **86**, 251-261.

Williams R., N.R. Collins (1986). Seasonal composition of meroplankton and holoplankton in the Bristol Channel. *Mar. Biol.* **92**, 93-101.

Yoshioka P.M. (1982). Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. *Ecology* **63**, 457-468.

Youngbluth M.J. (1979). The variety and abundance of zooplankton in the coastal waters of Puerto Rico. *Northeast Gulf Science* **3**, 15-26.