## Sexual reproduction and larval biology



## Animals are life cycles



Fig. 1. A collage of some invertebrate larval forms showing variations in shapes and patterns of ciliation
 Larvae are Garang 1928); D (afer Garstang, 1928), D, polychate nect (as0), ( 1972); 1972); I, gastropod veliger (after Dawydof, 1940a); J, nemertean pilidium (after Dawydoff, 1940b); K, sipunculid pelagosphera (after Jägersten, 1972); L, cnidarian planula (Emlet, personal observation); M, enteropneust hemichordate, nonfeeding (after Burdon-Jones, 1952); N, enteropneust tornaria (after Strathmann and Bonar, 1976); O, entoproct (after Jägersten, 1972); P, inarticulate brachiopod (after Jägersten, 1972); Q, archeogastropod trochophore (after Kessel, 1964); R, holothuroid auricularia (after Strathmann, 1971); S, ophiuroid pluteus (after Strath mann, 1971).

Modes of Sexual Reproduction

|  | Sexes ${ }^{1}$ | Broad | ast Spawn? | Brood? ${ }^{\text {2 }}$ |
| :---: | :---: | :---: | :---: | :---: |
| Porifera | d, H |  | Yes ${ }^{3}$ | +++ |
| Cnidaria | D, h |  | Yes ${ }^{3}$ | +++ |
| Ctenophora | d, $\mathbf{H}$ |  | Yes | + |
| Platyhelminthes | d, H | C |  | + |
| Nemertea | D, h |  | Yes | + |
| Nematoda | D, h | C |  | ++ |
| Annel. Polychaeta | D, h |  | Yes | ++ |
| Sipuncula | D, h |  | Yes | + |
| Mollusca | D, H | $\mathrm{C}^{4}$ | Yes | ++ |
| Arthro. Crustacea | D, H | C |  | +++ |
| Hexapoda | D, h | C |  | +++ |
| Phoronida | d, H |  | Yes ${ }^{3}$ | ++ |
| Bryozoa | d, H |  | $\because \mathrm{Yes}^{3}$ | ++ |
| Brachiopoda | D, h |  | Yes ${ }^{3}$ | ++ |
| Echinod. | D, h |  | Yes | ++ |
| Hemichordata | D |  | Yes | - |
| Urochordata | D, h |  | Yes | ++ |

${ }^{1}$ Sexes: $\mathrm{D}=$ dioecious, $\mathrm{H}=$ hermaphrodite, lower case = rare.
${ }^{2}$ Brooding: embryo development encapsulated or on adult body
${ }^{3}$ Typically or often only male spawns.
$\mathrm{C}=$ copulation (or other direct gamete exchange)
${ }^{4}$ All cephalopods, most gastropods.

Modes of habitat use

"holopelagic"
"holobenthic"


## Modes of sexuality



Modes of fertilization


Fig. 4. Percentage of eggs fertilized as a function of spawn-ing-group size and degree of aggregation. Solid bars are dispersed treatments; hatched bars are aggregated treatments.

Broadcast spawning

Insemination



## Early development in...bryozoans



## Presence of metamorphosis and typical larval forms


molusca


|  | Metamorphosis? |  | Typical larva |
| :---: | :---: | :---: | :---: |
| Porifera |  | Yes | amphiblastula |
| Cnidaria |  | Yes | planula |
| Ctenophora |  | Yes | cydippid |
| Platyhelminthes |  | Yes | Muller's, cercariae |
| Nemertea |  | Yes | pilidium |
| Nematoda | No |  |  |
| Nematomorpha |  | Yes | gordoiod |
| Acanthocephala |  | Yes | acanthor |
| Rotifera |  | Yes |  |
| Annel. Polychaeta |  | Yes | trochophore |
| Sipuncula |  | Yes | trochophore |
| Mollusca |  | Yes | trochophore, veliger |
| Arthro. Crustacea Hexapoda |  | Yes | nauplius, zoea caterpillar,grub,maggot |
| Phoronida |  | Yes | actinotrocha |
| Bryozoa |  | Yes | cyphonautes, coronate |
| Brachiopoda |  | Yes | articulate larva |
| Kamptozoa |  | Yes |  |
| Echinod. Oph,Ech |  | Yes | pluteus |
| Ast, Hol |  | Yes | bipinnaria; auricularia |
| Hemichordata |  | Yes | tornaria |
| Urochordata |  | Yes | tadpole |
| Chaetognatha | No |  |  |
| Onychophora | No |  |  |
| Gastrotricha | No. |  |  |
| Kinorhyncha | No |  |  |
| Loricifera |  | Yes | Higgins |
| Tardigrada | No |  |  |
| Priapulida |  | Yes | Lorica |




CHORDATA


Metamorphosis in three echinoderm classes


Echinoid pluteus


Asteroid bipinnaria


## Some examples of metamorphosis

polychaetes

1.

barnacles


1. Attached cyprid.


Metamorphosis of acorn barnacle, Balanus amphitrite. (After Barnard and Lane)

2. Shedding of larval exoskeleton.

phoronids

metatroch


## Direct and indirect development in terrestrial insects


(b)
(a)
(a) Hemimetabolous development of a grasshopper.
(b) Holometabolous development in the silkworm moth.


## Who wants to be a larval biologist?



## Who wants to be a larval biologist?



## Who wants to be a larval biologist?



## Who wants to be a larval biologist?


barnacle


## Who wants to be a larval biologist?



## Who wants to be a larval biologist?



## Who wants to be a larval biologist?



## Who wants to be a larval biologist?


brachiopod


## Who wants to be a larval biologist?



## Who wants to be a larval biologist?




## Who wants to be a larval biologist?



## Who wants to be a larval biologist?


hemichordate

Animals are life cycles


## Life-history evolution of marine invertebrates

## the "time-fecundity model"

life-history strategies
fewer chances
short time in plankton

more chances
long time in plankton
 $\begin{array}{lll}\dagger & \uparrow & \uparrow \\ 0 & 0 & \ominus\end{array}$ "schmoo"
consequences of investment in
different egg sizes

Risks of time in the plankton


Consequences for egg size evolution of:

- Food supply?
- Predation risk?
- Offshore currents?


Heliocidaris tuberculata
H. erythrogramma

