

LIFE DIAGRAM PATTERNS IN BENTHIC
POLYCHAETES

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Abstract.—Life diagrams in polychaetes can be grouped into three patterns. One pattern, including annual species, shows large reproductive efforts, small eggs and planktotrophic larvae. A second pattern, including the perennial species, shows low reproductive efforts, moderately large to large eggs, and non-planktotrophic development. The third pattern includes the multi-annual species, shows high reproductive effort, moderately large eggs, and non-planktotrophic development. These patterns may be in part systematically related to the environment in which the different species of polychaetes are found, but also appear related to a potential need for maintaining small cohesive reproductive units.

The study of life diagrams can be done from several points of view. A veritable jungle of modelling studies of various phases of life diagrams has been published (reviewed by Menge 1975, and Stearns 1976). General problems with modelling have been reviewed recently by Pielou (1981) and will not be considered here. It appears intuitively obvious that a certain factual base of observations must be available to model-builders so that models represent something known to occur with a frequency higher than zero in nature. Conceptual models do not necessarily have to be testable *in toto*, but at least certain facets should be available for testing. The lifespan of an individual polychaete may be as short as a few weeks (*Ophryotrocha* spp.) or last several years (*Eunice* spp.). A basic assumption of this paper is that knowledge of the lifespan of any polychaete species can be used to predict features in the life diagram of that species, and conversely, that information about certain life diagram features, such as brood size or egg size, can be used to predict general life habits and longevity of a given species.

The primary object of this study is to review the few cases for which information is available to test the assumption. A secondary purpose is to review some of the literature on the topic. Thirdly, various predictions are made about unknown features of life diagrams for selected species based on the available information, and suggestions are made as to how these predictions can be tested.

The terms *life cycle* or *life history* are usually defined as a description of the life of an individual starting at release from the parental organism and ending at death. Both terms have unfortunate implications. For example, the sequence of events is only in a formal sense cyclic since all individuals that go through the "cycle" are different (see Wiley and Brooks 1982:1-3), except perhaps in a few cloning forms and even in these, postparturition selection may "change" the clones from one release (spawning) episode to the next. The term cycle implies a static, non-evolutionary point of view. This concept can be useful, but will aid little in explaining differing powers of ecological and geographical dispersal. The term "history," as used in such combinations as natural history, implies a description of past events with little heuristic power. The term has also frequently been used to cover the first part of ontogenesis up to reproductive maturity. The

information yielded by ontogenetic study of a given species has turned out to be useful as a predictor of ontogenesis in phylogenetically or ecologically related taxa. The word diagram lacks some of the problematic implications of the two other terms. It is clearly a theoretical, formal term and implies a level of abstraction useful for making testable predictive statements. The above terminological problems were first pointed out to me by Mr. Bill Kennedy.

Most studies on polychaete life diagrams have focused on a single species, or one part of the diagram has been studied for several, usually taxonomically related species (cf. papers cited in Schroder and Hermans 1975). Reviews, such as the very extensive one issued by Schroder and Hermans (1975) have usually focused on detailing the complex factual information necessary for a more theoretical approach. In the review quoted, however, the format did not allow much freedom to explore the theoretical implications.

Trendall (1982) pointed out that in mosquito fish, the different life diagram traits were not necessarily correlated from one locale to another. For this reason, life diagrams must be characterized based on a single population; possibly, for most species, differences between populations in life diagram features will be less than differences between species, but this cannot be assumed *a priori*. The path of generalizations about life diagrams leads then from a study of single populations, via comparisons of diagrams within species, to that between species and between higher taxa. In this study it is assumed that differences among populations are less than differences among species. The study is based on information about single populations, but it is assumed that the diagram found for a population is characteristic of the species as a whole.

The sequence of events in the life of a number of specimens of a single species from fertilization to death may be generalized into a *life diagram* for that species. A comparison of life diagrams for several species may be generalized into a presumably limited number of *life diagram patterns*. A life diagram pattern is thus a second-level abstraction, rather than a primary abstraction. The published literature makes it amply clear that a distinction between the two levels of abstraction has not been made. Life diagram patterns do not necessarily follow taxonomic lines, even if a primary testable prediction for any species would be that its life diagram ought to be similar to that of a related species. Life diagram patterns may follow habitat requirements and a secondary set of hypotheses for a given species might be associated with this feature. The usefulness of separating between these two levels of abstraction thus lies in the possibilities it gives for making different sets of predictions.

Any event in the life diagram of any species can only be wholly understood in connection with all other events in the life of each organism. In other words, the life diagram represents a set of co-adapted features consisting of several partially distinguishable stages or phases, where any phase may be studied separately, but where its significance may be understood only as part of the whole diagram.

Life Diagram Events

The life of any organism is a continuum. For the purposes of analysis, this continuum may be separated into a series of definable events, with the caveat that each of the defined events usually is not distinctly separable from the previous event or from the following event but forms part of the continuum. For the

purpose of this discussion nine distinct life diagram events are recognized and defined. The physical location of each event is of primary importance, not least since the location is frequently associated with one or another axis of the life diagram (e.g., small egg-size is frequently correlated with pelagic early development; for example see Thorson 1950).

Spawning and fertilization.—Spawning may take place in the open water, in a burrow or tube, or into an eggmass, or the eggs may be retained in the body cavity of the female so that internal development takes place (Smith 1950). Eggs spawned inside a tube may be grouped in capsules, as in spionids (Blake 1969), or they may occur singly in a string, or stored in some other fashion (Knight-Jones *et al.* 1972). Egg sizes may vary from about 30 μm to about 2–3 mm in diameter. The eggs are usually somewhat flattened or disc-shaped. Fertilization usually appears closely associated with the spawning of the eggs and is assumed to take place when the eggs are released. The process has been poorly studied and nothing is known of the location of fertilization for most species.

Pre-release development.—The development prior to release of the larvae is usually based on energy contained within the egg-membrane, this part of the life diagram being fueled by yolk supplied by the parent. Early development usually takes place wherever fertilization took place. Several species do not have true larvae; the phase is here taken to include a shorthand description of the early development prior to the release from the egg-membrane, or to the transformation of that membrane into part of the larval or juvenile cuticle.

Larval stage.—This stage includes a number of pre-metamorphic, post-hatching developmental phases, whether they are true trochophores or not. These phases may be feeding larvae, in which case they may feed in any one of several different environments. However, most feeding polychaete larvae are planktotrophic in that they feed pelagically, usually on phytoplankton. Other larvae, such as the encapsulated spionid larvae, are adelphophagic, feeding on eggs present in the same capsule. In this particular kind of parental provisioning, a series of eggs are laid within a single capsule, but only one or a few larvae survive to hatching (Blake 1969).

Usually, but not invariably, feeding larvae are pelagic while non-feeding larvae keep close to or on the bottom (Schroder and Hermans 1975). Non-feeding larvae are usually morphologically rather different from the characteristic trochophore, but vary widely among themselves. For example, the barrel-shaped larvae in the super-family Eunicea have short apical tufts of cilia and a broad band of short cilia around the middle. At the time of release from the parental tube, they are usually poorly differentiated internally (Akesson 1967). Orbiniid larvae are completely covered with short cilia (Anderson 1959, 1961, 1966), and recognition of the prototrochal cilia can be difficult.

The length of the trochophoral stage varies tremendously. Certain spirorbids are competent to settle at the time of release (Beckwitt 1979). In contrast, certain sabellariids may remain pelagic for several months (reviewed by Mauro 1975). Perhaps the most common pattern is for the larvae to become competent to settle fairly rapidly, for example after a 10-day stay in the plankton, with the heavy settlement following after an additional 10 days in the plankton (Thorson 1946), but the larvae may be able to stay in the plankton for as much as several weeks (Wilson 1968).

Metamorphosis.—Most polychaetes undergo a gradual metamorphosis in which the posterior half of the larva elongates and becomes segmented, with setae forming in each segment (Schroder and Hermans 1975). Two to three recognizable setigers are usually formed before juveniles settle out of the plankton, but in some polychaetes, especially spionids, as many as 20 setigers may be present while juveniles are still in the plankton (Blake 1969, Hannerz 1956).

The pattern of metamorphosis is rather similar in both feeding and non-feeding larvae, but is usually less drastic in the latter since they usually do not form complex larval structures that have to be modified for adult use. In most species the start of the metamorphic events appears to be under endogenous control in that formation of segments and setae start while individuals are still in the larval habitat. The process is however frequently arrested after the first few segments are formed, and the remainder of the process appears to be triggered when the larvae contact a suitable substrate. In nearly all polychaetes the larval tissues are resorbed with no apparent discard of material at metamorphosis. Metamorphosis is discussed in detail by Schroder and Hermans (1975).

Establishment in adult habitat.—Most polychaetes appear capable of settling after the first few setigers have formed. However, some species can settle in typical larval configuration while others remain in the plankton until they have attained nearly adult configuration. The level of habitat selectivity appears to vary from species that are highly selective (Wilson 1954, 1955) to species that appear to follow the Thorsonian larval-rain model (Thorson 1950). After settlement all polychaetes will start feeding on food types, if not sizes, used by adults of the species. Species with planktotrophic larvae will at this point also shift to the adult food, which can be widely different from the phytoplankton consumed by the larvae.

Growth phase.—Little is known about the phase of life from settlement to the onset of sexual maturity. At settling most species are only a fraction of their adult length, and densities at settlement may be entirely different from adult population patterns. Density regulation in the form of post-settlement dispersal or mortality must take place. Most species are capable of moving from one location to another, even the so-called sessile taxa (see Dean 1978a, b) so the growth phase may represent a hidden small-scale dispersal phase.

Gamete maturation.—In most polychaetes early development of the sexual products takes place in gonads suspended in the coelomic cavity, with late development occurring while the sex cells are free in the coelom (Schroder and Hermans 1975). Release of sex cells from the gonads may take place as a single event, or be spread out over a longer period of time. Parallel to the late phases of gamete maturation, changes in adult morphology may also signal the onset of sexual maturity. Such changes are usually most drastic in semelparous species, but cyclic changes may also take place in iteroparous forms.

Spawning.—Polychaetes may be semelparous or iteroparous. Specimens of iteroparous species may spawn repeatedly within a single spawning season, or may spawn only once within a single season. Most polychaete species appear to have protracted spawning periods, lasting for several weeks to months; a few species are known to have extremely limited, synchronized spawning, such as the palolo worm, *Palola viridis* (e.g., Hofmann 1974). While the spawning patterns of several swarming polychaetes have been well publicized, most species

do not swarm, but spawn in or near the adult habitat. A number of tubicolous forms spawn within their tubes and burrowing forms may form temporary spawning burrows, leaving their spawn there.

Senescence and death.—Virtually nothing is known about typical causes of death in iteroparous polychaetes. Most semelparous forms may die upon spawning, and in the swarming forms tissues of several major organ-systems have been reported to be resorbed before the spawning takes place (Schroder and Hermans 1975). Certain semelparous forms, such as some spionids, appear to survive the spawning and remain in their tubes with the developing embryos for some period of time.

Material and Methods

The material available for study is extremely limited, in that most of the different kinds of information indicated by the listing of life diagram events must be available and studied in a single population of a species.

Hannan *et al.* (1977) in a study of life histories of benthic invertebrates of Monterey Bay included information on larval development, the size of the reproducing females and the total number of eggs present. Species studied included *Ameana occidentalis*, *Lumbrineris luti*, *Magelona sacculata*, *Mediomastus californiensis*, *Nothria elegans*, *Prionospio cirrifera* and *P. pygmaea*.

Emerson (1975) studied the population ecology of *Diopatra ornata* at Santa Catalina Island off southern California and included sufficient measurements to allow calculation of the necessary parameters. Beckwitt (1979) in a study of the population ecology of spirorbid polychaetes from southern California did a series of experiments on settlement and population structure allowing the inclusion of data for *Janua brasiliensis* and *Pileolaria pseudomilitaris*.

Information on the reproductive biology of onuphid polychaetes has been gathered in the vicinity of the Smithsonian Marine Station at Link Port, Florida, at Bermuda, and in Belize; the following species have been studied in some detail: *Kinbergonuphis simoni* from Florida, *Mooreonuphis jonesi* at Bermuda, and *K. pulchra* in Belize. Some information is available for additional species from Florida, and this material is used to make some testable predictions about missing data.

For each species the following information was recorded: 1. Size of the reproducing female (numbers of setigers as well as length and width measurements). 2. Average egg-size. 3. Numbers of eggs produced by a female in a single reproductive event. 4. Number and distribution of reproductive events in the life of a single individual. 5. Estimated length of life for a single individual.

Data are presented in tables and illustrations and compared to information otherwise available in the literature.

The following biological notes indicate the basic habitat and general geographical dispersal of principal species treated in this paper. Table 1 reviews some basic life diagram parameters for these species.

Ameana occidentalis Hartman (1942) (family Terebellidae) lives in temporary burrows in sandy and muddy environments from intertidal zones to the edge of the continental shelf or a little beyond; it is known from southern and central California, but may also be present along the whole northwest Pacific coast.

Identification of species in the genus is problematic and the exact distribution is currently difficult to assess.

Diopatra ornata Moore (1910) (family Onuphidae) is tubicolous and lives at shelf and upper slope depths in sandy and muddy environment in the eastern Pacific Ocean. Emerson (1975) did a large-scale study of a single population of *D. ornata* from Santa Catalina Island.

Janua brasiliensis (Grube, 1871) (family Spirorbidae) is a small, spirally coiled worm living in a calcareous tube. It is widely dispersed in warm waters in very shallow subtidal and intertidal areas. Beckwitt (1979) examined it as part of a study of intertidal spirorbids from southern California.

Kinbergonuphis pulchra (Fauchald, 1981) (family Onuphidae) lives in relatively poorly constructed tubes in shallow subtidal areas. It is currently known only from sandy areas inside the outer edge of the barrier reef off Belize, Central America.

Kinbergonuphis simoni (Santos, Day, and Rice, 1981) (family Onuphidae) lives in poorly constructed tubes in shallow subtidal and intertidal areas in sand. It is known from both sides of peninsular Florida, and is common in bays and inlets.

Lumbrineris luti Berkeley and Berkeley (1945) (family Lumbrineridae) lives in sandy and muddy areas at shelf depths along the eastern Pacific Ocean. It does not build tubes but burrows through the substrate.

Magelona sacculata Hartman (1961) (family Magelonidae) lives in sandy substrates at shelf depths off southern and central California. It does not build a permanent tube or burrow, but appears to move through the substrate more or less continuously.

Mediomastus californiensis Hartman (1944) (family Capitellidae) was originally described from California in shallow muddy environments, but has since been reported widely from both coasts of the Americas. It builds semi-permanent burrows and appears tolerant of considerable environmental abuse in that it frequently is present in harbors and similar high-organic environments (Hannan *et al.* 1977).

Mooreonuphis jonesi Fauchald (1982) (family Onuphidae) is the only onuphid known from shallow water in Bermuda. It is common in sand and coral debris and builds tubes which are covered externally with coral and shell fragments.

Nothriu elegans (Johnson, 1897) (family Onuphidae) is known from shallow subtidal to deep shelf depths off the west coast of the United States and Canada; it is tubicolous and especially common in relatively clean sandy environments.

Pileolaria pseudomilitaris (Thiriot-Quievreux, 1965) (family Spirorbidae) appears to be widespread in warm waters in intertidal and shallow subtidal areas; it is small, spirally coiled and enclosed in a calcareous tube. It was studied in southern California by Beckwitt (1979).

Prionospio cirrifera (Wiren, 1883) (family Spionidae) was originally described from shallow water in the Arctic Ocean and has since been widely reported. It is possible that material studied by Hannan *et al.* (1977) should be referred to by another name (Nancy Maciolek personal communication), but since all specimens came from a single area and were studied over a long period of time, it appears safe to assume that they represent a single species. *Prionospio cirrifera* builds a small tube which it is capable of leaving, and has been reported from a variety

Table 1.—Some ecological characteristics of polychaetes considered in the analysis. The columns are: 1. Longevity; 2. Motility pattern of adults; 3. Feeding pattern of larvae.

	1	2	3
<i>Ameana occidentalis</i>	annual	discretely motile	feeding
<i>Diopatra ornata</i>	perennial	sessile	non-feeding
<i>Janua brasiliensis</i>	multiannual	sessile	non-feeding
<i>Kinbergonuphis pulchra</i>	perennial	sessile	non-feeding
<i>Kinbergonuphis simoni</i>	perennial	sessile	non-feeding
<i>Lumbrineris luti</i>	perennial	motile	non-feeding
<i>Magelona sacculata</i>	annual	motile	feeding
<i>Mediomastus californiensis</i>	multiannual	discretely motile	non-feeding
<i>Mooreonuphis jonesi</i>	perennial	sessile	non-feeding
<i>Onuphis elegans</i>	perennial	sessile	non-feeding
<i>Pileolaria pseudomilitaris</i>	multiannual	sessile	non-feeding
<i>Prionospio cirrifera</i>	multiannual	discretely motile	feeding
<i>Prionospio pygmaea</i>	multiannual	discretely motile	feeding

of different environments. The particular form studied here is present along the eastern Pacific Ocean in muddy to sandy environments at shelf depths.

Prionospio pygmaea Hartman (1961) (family Spionidae) was originally described from southern California, and while the same taxonomic considerations apply to this as to the preceding species, it is more likely that it is currently referred to by its correct name. It is known from southern and central California in sandy and muddy environments at shelf and slope depths. Like its congener, it builds small, semi-permanent tubes.

Results

Table 2 shows the measured and calculated values for all species for which adequate data were available. Table 3 reviews information available for another eight species, for which some information may be missing or an inadequate number of specimens has been examined.

The lifetime reproductive effort per female varies in a systematic fashion (Fig. 1). Perennial species, defined as those that reproduce in at least two different growth seasons, have consistently low lifetime investments. For all species examined it represents less than 10% of the volume of the females and is probably overestimated since it was assumed that all individuals were in their first reproductive season and would not grow before the next reproductive event. This assumption is known to be incorrect for *Diopatra ornata* and *Mooreonuphis jonesi* (Emerson 1975; Fauchald 1982), but cannot be corrected without knowledge of the exact age of all females examined.

The two annual species examined have considerably higher lifetime reproductive efforts, representing more than 20% of the volume of the reproducing females. The reproductive effort is underestimated in that it has been assumed that females of both species reproduce only once and die after reproduction. Some annual species are known to partition their spawning into several shorter bursts, with regeneration of the coelomic oocytes between events (Schroder and Hermans 1975). The available data did not make it possible to estimate whether or not either species shows such patterns.

Table 2.—Life diagram characteristics for the species of polychaetes considered in the analysis. The columns are: 1. Total number of setigers; 2. Total length in mm; 3. Maximal width in mm; 4. Largest egg-diameter in micrometer; 5. Smallest egg-diameter in micrometer; 6. Volume of a single egg in 10⁶ cubicmicrometers; 7. Numbers of eggs in a single spawn; 8. Volume of eggs in a single spawn in 10⁶ micrometers; 9. Numbers of spawning events per female per lifetime; 10. Lifetime volume of eggs per female in 10⁶ cubicmicrometers; 11. Volume of adult female in 10⁶ cubicmicrometers; 12. Fecundity per female per lifetime, measured as the relative volume of eggs per female per lifetime, in parts per hundred.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Amaena occidentalis</i>	—	100	4.5	210	158	2.77	14,000	38,792.39	1	38,792.39	159,043.13	24.39	Central California
<i>Diopatra ornata</i>	380	500	3.0	235	176	3.90	900	3510.00	4	14,040.00	3,534,291.74	.40	Southern California
<i>Janua brasiliensis</i>	—	—	—	—	—	10.00	15	150.00	24	3649.50	3000.00	121.65	Southern California
<i>Kinbergonuphis pulchra</i>	191	67.41	.95	331	248	10.67	74	789.59	3	2368.76	47,781.68	4.96	Belize
<i>Kinbergonuphis simoni</i>	167	56.22	.90	356	267	13.34	46	613.44	3	1840.33	35,765.62	5.15	Florida
<i>Lambrineris luiti</i>	—	200	2.36	100	75	.29	500	145.30	2	290.60	10,618.58	2.74	Central California
<i>Magelona sacculata</i>	—	30	.60	130	98	.65	3000	1951.16	1	1951.16	8482.30	23.00	Central California
<i>Mediomastus californiensis</i>	—	15	.50	80	60	.15	1500	226.19	1	226.19	294.52	76.80	Central California
<i>Mooreonuphis jonesi</i>	122	35.40	.87	164	123	1.29	22	28.81	3	86.42	21,044.16	.41	Bermuda
<i>Onuphis elegans</i>	—	300	2.94	240	180	4.07	789	3212.42	4	12,849.67	2,036,600.27	.63	Central California
<i>Pileolaria pseudomilitaris</i>	—	—	—	—	—	15.0	—	220.00	24	4866.6	5000.00	97.33	Southern California
<i>Prionospio cirrifera</i>	—	13	.50	30	22	.01	500	3.89	1	3.89	255.25	1.49	Central California
<i>Prionospio pygmaea</i>	—	11	.50	60	45	.06	500	31.10	1	31.10	215.98	14.40	Central California

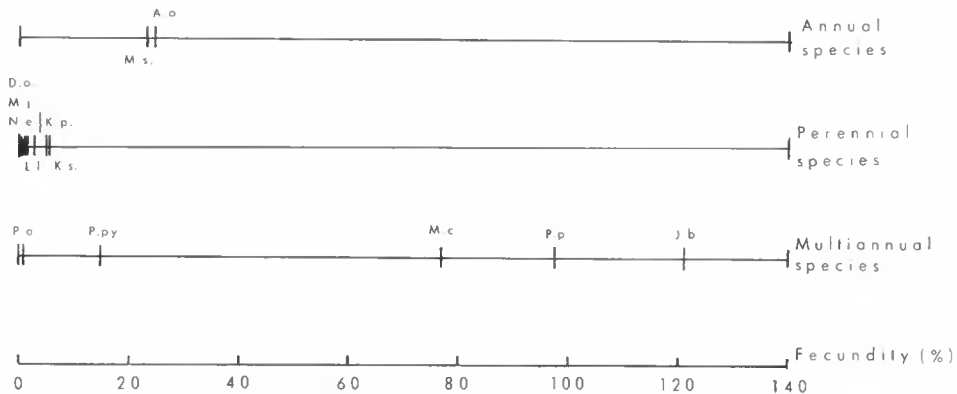


Fig. 1. Diagram showing the relative fertility of annual, perennial and multiannual species. The fecundity measure is in per cent of the total volume of the female. The species are: A.o., *Ameana occidentalis*; D.o., *Diopatra ornata*; J.b., *Janua brasiliensis*; K.p., *Kinbergonuphis pulchra*; K.s., *K. simoni*; L.l., *Lumbrineris luti*; M.s., *Magelona sacculata*; M.c., *Mediomastus californiensis*; M.j., *Mooreonuphis jonesi*; N.e., *Onuphis elegans*; P.p., *Pileolaria pseudomilitaris*; P.o., *Prionospio cirrifera*; P. py., *Prionospio pygmaea*.

Multiannual species, defined as those species that go through two or more generations in a single growth season, show a great deal of variability. Three taxa, a capitellid and two spirorbids, have extremely high lifetime reproductive efforts, above 75% in all three cases; two spionids show low to moderate reproductive efforts. In the case of the two spirorbids, it is known that a single individual may produce up to 24 batches of eggs in a lifetime (Beckwitt personal communication). Spirorbids live in an unstable environment, so at least some of these egg-batches probably remain unrealized in the life of any given female. The resulting reduction in reproductive effort could be considerable, but even if one half of the possible egg-batches were skipped, the lifetime reproductive effort would still be more than twice that for any annual or perennial species. It was assumed that the two spionids breed only once, as the most conservative estimate possible. If in fact each female breeds twice, the reproductive effort per female will increase above the level of the annual species and be close to the level of the two spirorbids.

Comparing information in Tables 1 and 2 leads to some interesting conclusions. Three major life diagram patterns appear to be present. One, represented by annual species, shows large reproductive efforts, moderately large eggs, and planktotrophic larvae. The second pattern, represented by perennial species, shows low reproductive efforts, moderately large to large eggs and a non-planktotrophic development. The third pattern, represented by the multiannual forms, shows a (probable) high reproductive effort, relatively small eggs, and a non-planktotrophic development. These patterns are indicated in Figure 2 as Pattern I and Patterns IIa and IIb. The two latter patterns appear related in that both include forms that lack planktotrophic larvae and any organized larval or adult dispersal phase.

Another interesting point is that both perennial and multi-annual forms are relatively sedentary as adults. Onuphids, which make up the bulk of the perennial

Table 3.—Life diagram features for selected species of polychaetes for which inadequate data are available for complete determination of life diagram pattern. The columns are: 1, Total number of setigers; 2, Total length in millimeters; 3, Maximum width in millimeters; 4, Greatest egg diameter in micrometers; 5, Smallest egg diameter in micrometers; 6, Volume of a single egg in 10⁶ cubicmicrometers; 7, Numbers of eggs in a single spawning event; 8, Volume of eggs in a single spawning event in 10⁶ cubicmicrometers; 9, Numbers of spawning events in the life of a female; 10, Life-time volume of eggs for a single female in 10⁶ cubicmicrometers; 11, Total volume of the females in 10⁶ cubicmicrometers; 12, Lifetime fecundity for each female in %; 13, Locality from which the sampled specimens were taken, comments.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Axiotrella</i> sp. specimen 1.	13	54.0	1.5	185	138	1.85	500	927.37	1	927.37	—	—	Florida, incomplete
Specimen 2	16	58.0	1.0	243	183	4.22	500	2110.15	1	2110.15	—	—	Florida, incomplete
Specimen 3	17	50.56	1.6	270	202	5.78	480	2775.75	1	2775.75	101,656.91	2.73	Florida
Specimen 4	16	53.60	1.6	226	169	3.57	500	1785.12	1	1785.12	—	—	Florida, incomplete
<i>Capitella capitata</i> sp. 1	15	4.32	.32	120	90	—	—	—	—	—	—	—	Florida, incomplete
<i>Diapatra cuprea</i> specimen 1	83	48.0	2.0	183	137	1.81	3182	5760.14	4	23,040.58	—	—	Florida, incomplete
Specimen 2	148	67.0	2.0	197	147	2.26	1600	3616.00	4	14,464.00	210,486.71	6.87	Florida
<i>Eteone lactea</i> specimen 1	107	33.60	.80	95	72	.26	1200	306.21	1	306.21	16,919.36	1.81	Florida
Specimen 2	187	40.80	1.12	98	73	.28	1300	362.82	1	362.82	40,196.30	.90	Florida
<i>Glycinde solitaria</i> sp. 1	190	16.80	.96	87	65	.23	900	208.46	1	208.46	1158.12	18.00	Florida
<i>Haploscoplos fragilis</i>													
Specimen 1	127	52.5	2.5	150	112	.99	1800	1781.28	1	1781.28	257,217.90	.69	Florida
Specimen 2	80	18.72	1.12	135	101	.72	400	286.28	1	286.28	18,443.01	1.55	Florida
<i>Magelona</i> sp. specimen 1	70	25.6	1.92	140	105	.81	1750	1414.31	1	1414.31	74,119.47	1.91	Florida, in reg.
<i>Ouaphis eremita oculata</i>													
Specimen 1	—	32.96	1.60	211	158	2.45	—	—	4	—	—	—	Florida
<i>Ophelina</i> sp. specimen 1													
Specimen 1	50	36.5	1.5	96	72	—	—	—	—	—	—	—	Florida
<i>Owenia fusiformis</i>													
Specimen 1	18	24.80	1.12	105	79	.34	2500	844.75	1	844.75	24,433.05	3.46	Florida
<i>Sireblosoma crassibranchia</i>													
Specimen 1	70	49.60	2.40	221	166	3.16	4000	126,020.41	1	12,620.41	224,385.11	5.62	Florida
Specimen 2	52	32.80	2.72	173	130	1.41	—	—	—	—	—	—	Florida, incomplete
Specimen 3	57	61.44	2.40	184	138	1.83	4000	—	—	—	—	—	Florida, incomplete
Specimen 4	53	48.96	2.88	196	147	2.20	—	—	—	—	—	—	Florida, incomplete

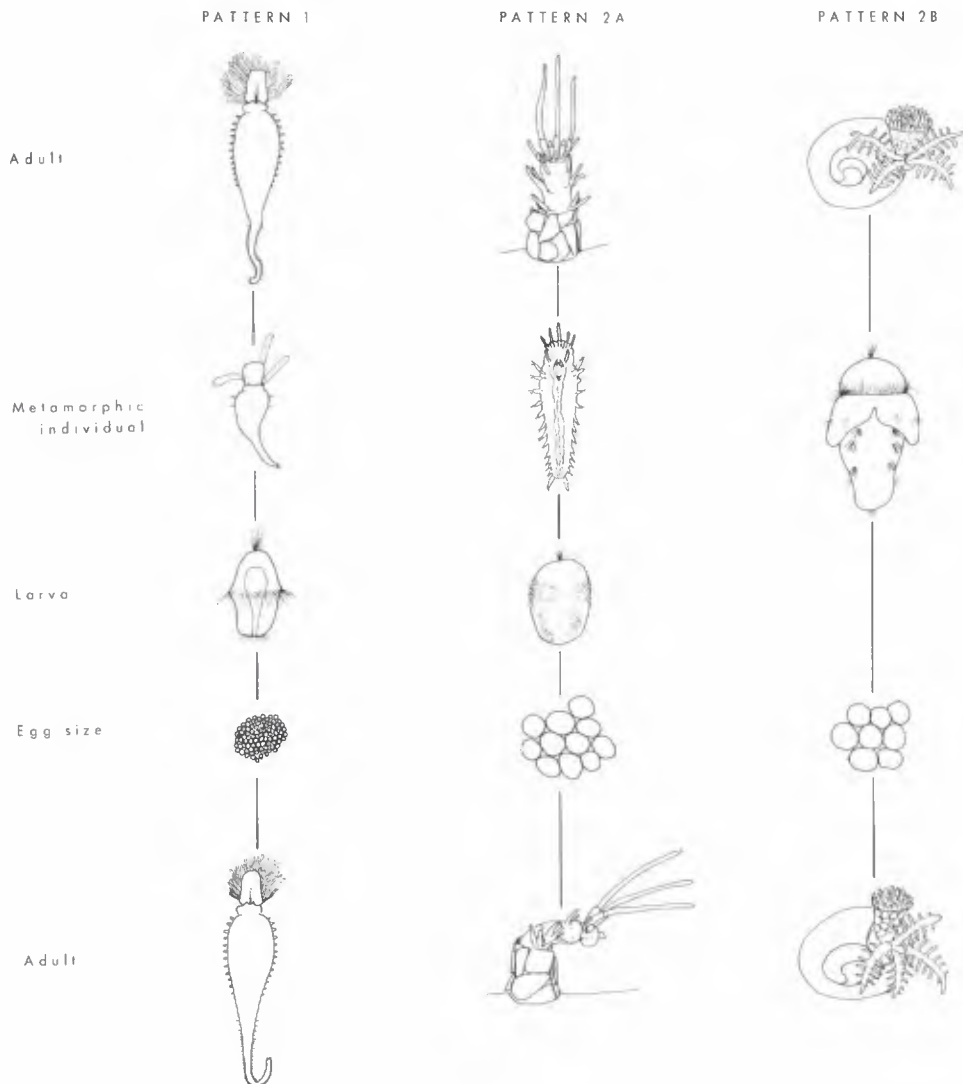


Fig. 2. Life diagram patterns for 3 selected species of polychaetes. The species are from left to right: *Amaeana occidentalis*, *Kinbergonuphis simoni* and *Pileolaria pseudomilitaris*. The patterns are discussed further in the text.

species examined, are all tubicolous. These species also appear to have lost the pelagic dispersal stage in that they have non-feeding, benthic larvae that are capable of settling immediately upon release (Emerson 1975; Fauchald personal observations). *Kinbergonuphis simoni* and *Mooreonuphis jonesi* both brood their young and release them from the parental tube at the 10- (or more) setiger stage (Fauchald 1982 and personal observations). Beckwitt (1979) demonstrated that specimens of the two spirorbid species were capable of settling immediately upon release from the parental tube.

Discussion

The benthopelagic life-cycles of marine invertebrates are usually discussed in terms of fitness of the species, expressed as the number of offspring of each female (cf. Caswell 1980, 1981). The reduction in length of the pelagic phase of the life diagram was considered an exceptional, relatively rare phenomenon by Caswell (1981) who demonstrated under what conditions selection for a reduced larval life might take place. In fact, a variety of marine invertebrates including prosobranch snails, all benthic peracarid crustaceans, and various polychaetes show a loss of the pelagic life-phase, so the pattern can hardly be considered exceptional. Furthermore, among the polychaetes a variety of otherwise unrelated groups show a reduction in the length of larval life; presumably this loss has occurred independently in each of these groups.

The life-diagram patterns of polychaetes identified above appear difficult to fit with the fitness theory for a variety of reasons. First, the large, perennial forms among the polychaetes usually show reduced motility as adults (Fauchald and Jumars 1979); second, these same species also show reduced motility as larvae and appear to lack a dispersal phase altogether. In contrast, annual forms, which also include a number of large species, are frequently highly motile both as larvae and as adults. The multiannual forms probably show the high reproductive effort expected by theory (the Pianka version of McArthur and Wilson's r- and K-selection theory, Pianka 1970), but do not agree with that theory in that neither larvae nor adults have high dispersal abilities and the reproductive effort is channeled into a few highly developed larvae rather than into the numerous broadcast offspring predicted by the theory.

Shields (1982) in a discussion of the maintenance of sexual reproduction, stated that most life-diagram theory is based on the assumption that most species have large, panmictic populations and that in such populations the maintenance of sex leads to what Williams (1975) referred to as the cost of meiosis. A highly fit genotype that arises through sexual reproduction will very probably be lost to the next generation through well documented genetic processes. According to Shields (1982) asexual reproduction, which would initially keep the highly fit genotype intact, eventually would lead to a ratcheting of mutations, spreading them through the population. Shields pointed out that in relatively small populations of related organisms, sexual reproduction will stabilize a successful genome and will tend to weed out deleterious mutations. Thus maintenance of sex in these forms, while of long-term importance in evolution, is basically a conservative feature allowing a small, successful population to maintain itself while conditions remain reasonably stable (in ecological time) but to retain the evolutionary flexibility that sexual reproduction implies in evolutionary time.

The explanation for the loss of a larval dispersal phase in the perennial sessile polychaetes appears to involve a Shieldian inbreeding: the loss of a dispersal phase simply is a means of maintaining a cohesive, small interbreeding population so that a successful genome can be maintained. The loss of larval life then does not involve individual fitness *per se*; Caswell's fitness argument presumably works for relationships within each population, but the overriding feature, the maintenance of a small interbreeding population, has been the determining factor in losing the dispersal phase.

The loss of dispersal in multi-annual forms may be related to the habitat these forms usually occupy. These forms usually occur in relatively ephemeral environments. Clearly, disturbed patches are distributed in a statistically predictable fashion. For example, soft muddy and sandy bottoms in middle-shelf environments are usually stable, and few disturbances occur. However, one or a few major storm-systems will sweep over most coastlines from time to time and the waves from these systems will disturb bottom sediments in water deeper than that reached by normal wave-trains. An interrupted band of disturbed soft sediments is thus created along many coast-lines, but it is impossible to predict exactly where the disturbance will come in a given year: we know that the disturbance will come, in a statistical sense, but cannot predict exactly where nor when. Most of the multi-annual forms are small, and may themselves be moved around with the disturbed sediments. Further, if the "life-expectancy" of a disturbed patch is longer than the life-expectancy of specimens of the species occupying the patch, then it is clearly to the advantage of the occupying species to see to it that its offspring do not get dispersed much beyond the outlines of the patch. The net effect of this ecological determinant will be exactly the same as for the perennial species in that each actually interbreeding population will remain small, and specimens found close to each other have a high probability of being closely related as well.

The annual species have retained large numbers of small offspring and the larvae may spend a long time in the plankton. It is possible that these taxa have very large, panmictic populations and thus fulfill the criteria for maintenance of sex indicated by Williams (1975); however, there may also be valid ecological reasons why large numbers of larvae are maintained among these taxa. Provided that adults die after breeding, each population of larvae that settle will have to settle in an environment where the presence of adults of the same species cannot be used as a cue in settlement. However, Wilson (1954, 1955) demonstrated that the larvae of *Ophelia bicornis* are attracted to sand where adults have been present, reducing the chance-settlement in this particular species. It is also possible that taxa in this category are unspecific in their ecological requirements and may be presently found in extensive environments, such as sandy and muddy bottoms with variable grain size, organic content, and depth. Under these circumstances, it would be to the advantage of the species to spread its larvae as widely as possible and thus to maintain maximum genetic flexibility.

The result of this study points out, that while the life-diagram theory as it has developed probably is correct, other features must be taken into account, and that the extremely heavy focus of the life-diagram theory on fitness and with the hidden assumption of large, panmictic populations, has made the investigators overlook the consequences of the fact that many animals occur in small, isolated or partially isolated populations in which a successful genome is being maintained by a loss of dispersal mechanisms. The pattern developed here is not universal: a great number of polychaetes do in fact disperse over wide areas and do have larvae that live for a long period of time in the plankton (Wilson 1968; Scheltema 1974), but a surprisingly large number of species appear to shorten the larval life, either by spawning into an egg-mass (lumbrinerids, maldanids, terebellids), by brooding (onuphids, serpulids, spionids) or even by direct development (nereidids). In these cases, I believe the best interpretation of the curtailment of long

larval life lies in the attempt at maintaining small breeding populations, rather than in any optimization of fitness in terms of numbers of offspring. A second interpretation might be that the curtailment of larval life reduces larval wastage if the adult environment is hard to find and patchy. Note that these two explanations may simultaneously be correct. I believe that the fitness theory as currently conceived might have great value in explaining differences between individual organisms within a confined environment.

The reduction in lifetime reproductive effort in the perennial species indicates that for these species, most of which are large (for polychaetes) a larger fraction of the energy consumed has been shifted to growth rather than to reproduction. This is especially striking when comparing the lifetime reproductive effort of similar sized onuphids which are perennial, with the annual terebellids.

The findings of this study are consistent with the review by Schaffer and Gadgil (1975) of higher plants. In some respects the coincidence may be fortuitous since the present emphasis has been on the role of reduced larval dispersal in maintaining a cohesive genetic structure in the population, rather than on the selection for an optimal life diagram emphasized by Schaffer and Gadgil (1975). It may be competitively of so great importance for a population to maintain genetic cohesiveness that selection for other features in the short term becomes trivial.

As indicated by Trendall (1982) different life diagram traits may not at all be closely correlated to each other. The idea of a life diagram for all populations of species may be spurious: each population, with the constraints built into the basic morphology and development of the taxon, may adapt the life diagrams to the local conditions under which the population survives. Despite this caveat, it appears that the polychaetes investigated so far can be fitted into the three patterns described above.

Very few of the 15,000+ known species of polychaetes were taken into account in erecting this system of life diagram patterns. An attempt was made at having as many and as varied morphological forms represented as possible, but inevitably, the few species examined represent a biased sample including species for which data could be easily gathered or were already present in the literature. The detailed structure of the life diagram patterns for polychaetes may change, but the basic outline will probably remain similar to the one detailed above.

Some Predictions

For the last several years I have been following the reproductive activity of selected species of polychaetes in the vicinity of the Smithsonian Marine Station at Link Port, Florida. For some species I have gathered sufficient information to include them among the species listed above. However, for most of them I have either inadequate numbers of specimens or some pieces of information cannot be gathered with the techniques I am using.

Table 3 reviews information for these taxa. Based on life-diagram patterns I outlined above, I believe the following statements will, when tested, describe the situation for these species.

Two of the species for which I have been gathering data are onuphids, *Onuphis eremita oculata* Hartman (1951) and *Diopatra cuprea* (Bosc, 1802). For both species I lack crucial data, but the average egg-sizes for both indicate that the

life diagram for each should be similar to that found for other onuphids, with low reproductive effort, small numbers of eggs and lack of pelagic larvae, or at least tube-brooding until larvae are competent to settle.

Axiothella sp., a maldanid, is known to discharge eggs into an eggmass; the egg-size and average numbers of eggs per batch indicate a reduced larval development, without a feeding larval stage. The reproductive effort of the only complete female sampled indicates that the species should live for at least two seasons.

Glycinde sp., a goniadid, has a relatively high reproductive effort combined with small eggs; it is suspected that this species may be annual and have a pelagic, planktotrophic larva.

Streblosoma sp. of the family Terebellidae, has relatively large eggs, and moderately high reproductive effort. Related species are known to spawn into a loosely organized egg-mass, which deteriorates rapidly and releases larvae, which, while they may be planktotrophic, are capable of settling shortly after release from the egg mass. Based on the available information, it appears that *Streblosoma* will show a similar pattern. The species may be an annual.

The capitellids studied by Grassle and Grassle (1974, 1976) show a bewildering array of different life-diagrams. Some taxa have planktotrophic larvae, others have a reduced larval life or direct development, the average egg-diameters appear well correlated with the developmental pattern exhibited (see also Schroder and Hermans 1975, and Hermans 1979). The consequences in terms of life-diagrams are that the forms with a planktonic larva are capable of dispersing rapidly and widely, whereas the forms without such larvae are capable of building up larger populations once a suitable habitat has been located. The only specimen of *Capitella* measured in the current study had large eggs and thus should belong to the taxa with a reduced larval development. The different recruitment strategies of the capitellids may well determine longevity and thus differential resource utilization by each species, and may thus explain why the Grassles found more than a single species in a sample in certain areas off Massachusetts.

Two specimens of *Haploscoloplos fragilis* measured during the current study show egg sizes similar to those measured for *Scoloplos armiger*, another orbiiniid, by Anderson (1959). The reproductive effort is very low and very few segments contained eggs in both specimens. It is suggested that this orbiiniid shows a mixed strategy: the larvae are planktotrophic, but the individual specimens live for at least two seasons or alternatively, are capable of spawning more than once, each well separated out in the life of the female. The two individuals, both complete, are very different in size, indicating that perhaps the latter alternative may be the correct one.

A single specimen of a species of *Ophelina* was measured. The egg diameters are similar to those measured for *Armandia bioculata* by Hermans (1979) and it is predicted that the life diagram will be characteristic of an annual species, with high reproductive effort, small, planktotrophic larvae and relatively lengthy planktonic life.

Another interesting prediction is related to the structure of the deep sea benthos. The dominating benthic forms at least among the polychaetes in deep water are all forms that fit with the pattern found above for multi-annual forms (see Hartman 1965, Hartman and Fauchald, 1971). The shallow water multi-annual

forms are associated with areas of randomly disturbed sediments or other unstable, unpredictable environments. The dominance of species with a similar life diagram in the deep sea benthos indicates that a similar disturbance pattern may be present in the apparently stable deep sea benthos. As indicated by Dayton and Hessler (1972) this disturbance is very probably biological in nature.

Acknowledgments

This study started with a lecture I gave during the class in polychaete biology at Catalina Marine Science Center, University of Southern California, in 1979. Bill Kennedy and Fred Piltz, the assistants in that class, and also the students encouraged me to develop the topic further; particularly Bill Kennedy was instrumental in getting me started. The reaction to a paper I gave at the annual meeting of American Society of Zoologists in Tampa indicated that the material would create a great deal of interest, if not agreement. Various versions of the paper have been read by Meredith L. Jones, Mary E. Rice, Peter A. Jumars, Kirk Fitzhugh, and David E. Russell, all of whom gave their candid opinions but should not be held responsible for its content.

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