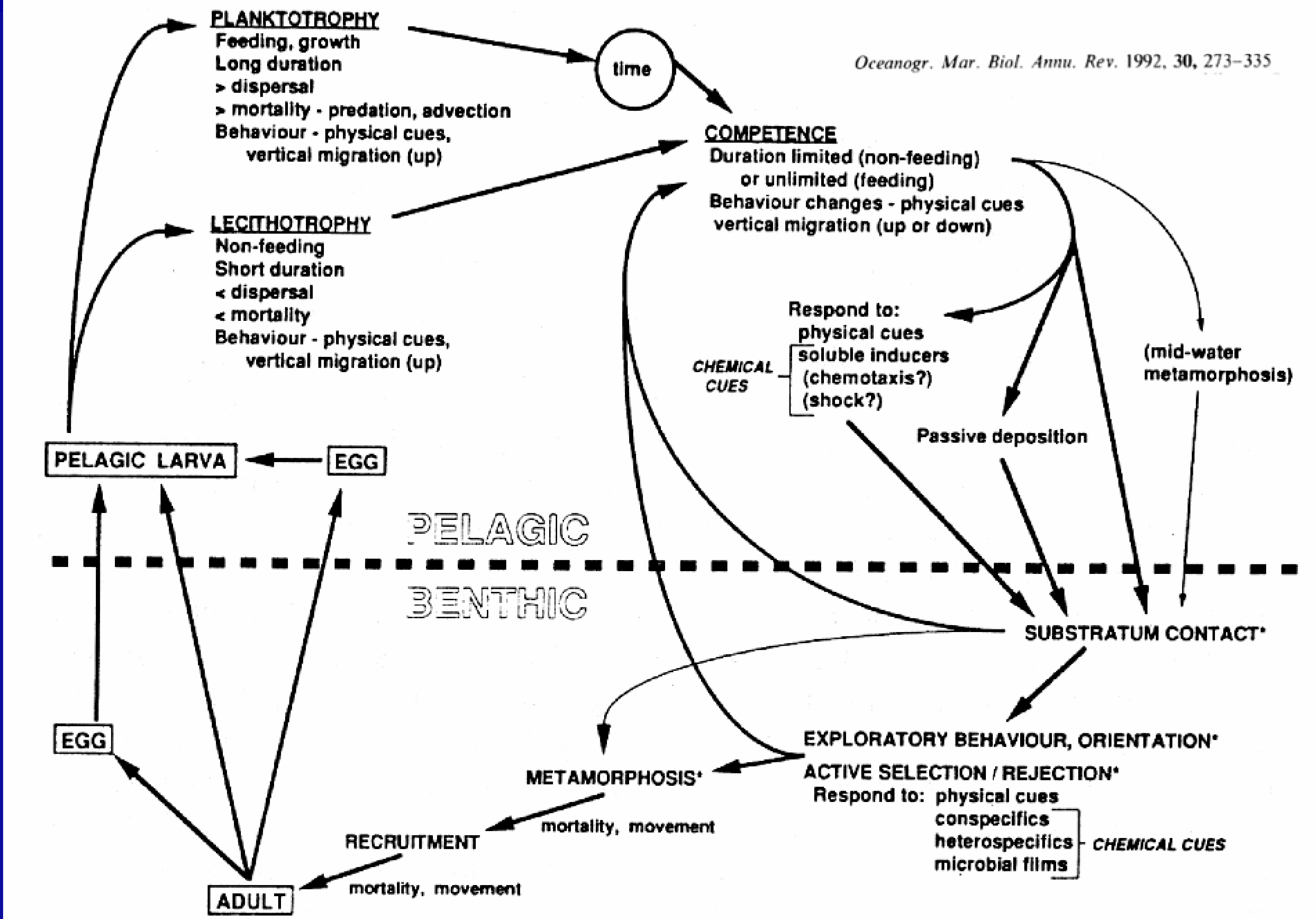
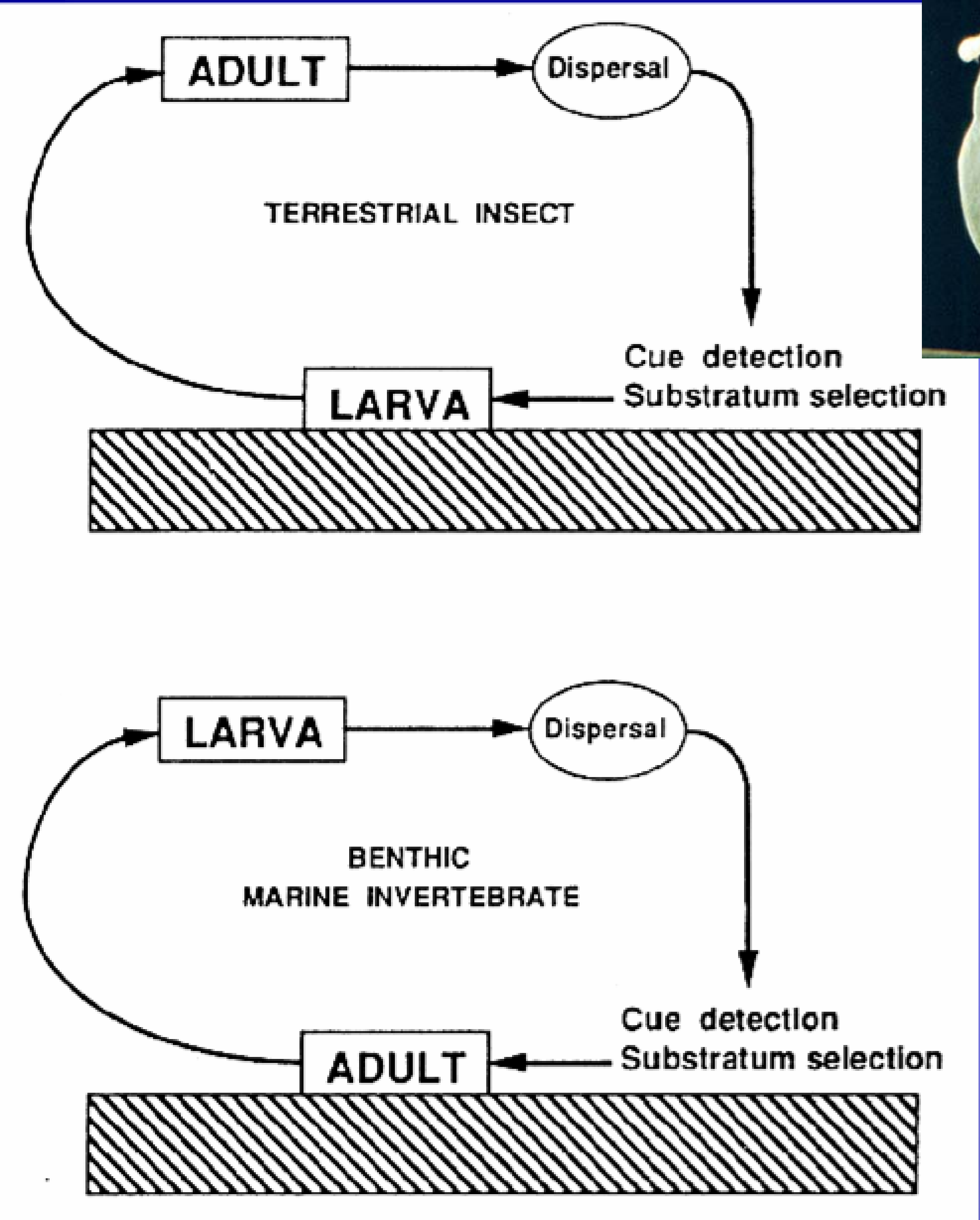
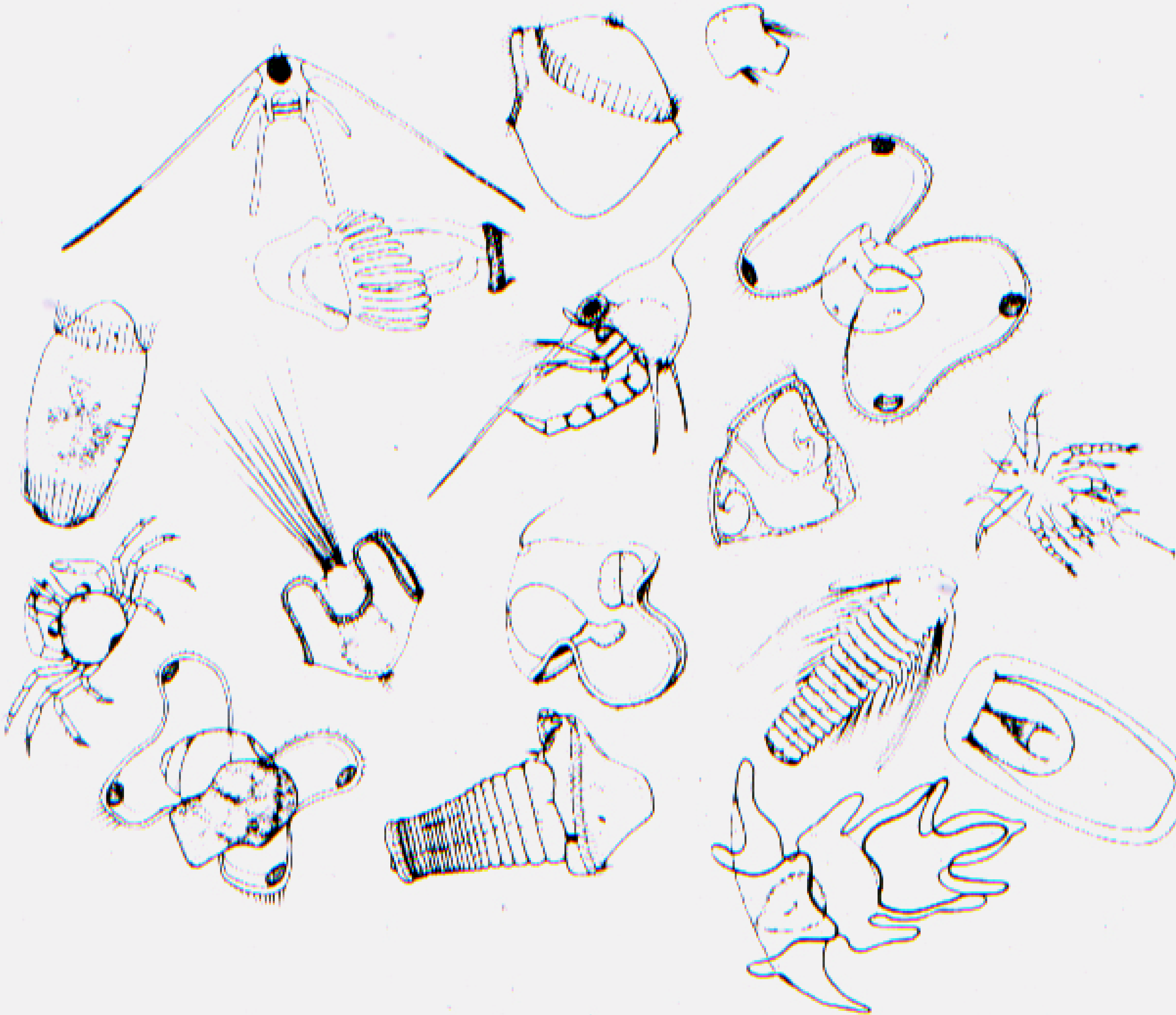
CHEMICAL ECOLOGY OF MARINE INVERTEBRATE LARVAL SETTLEMENT

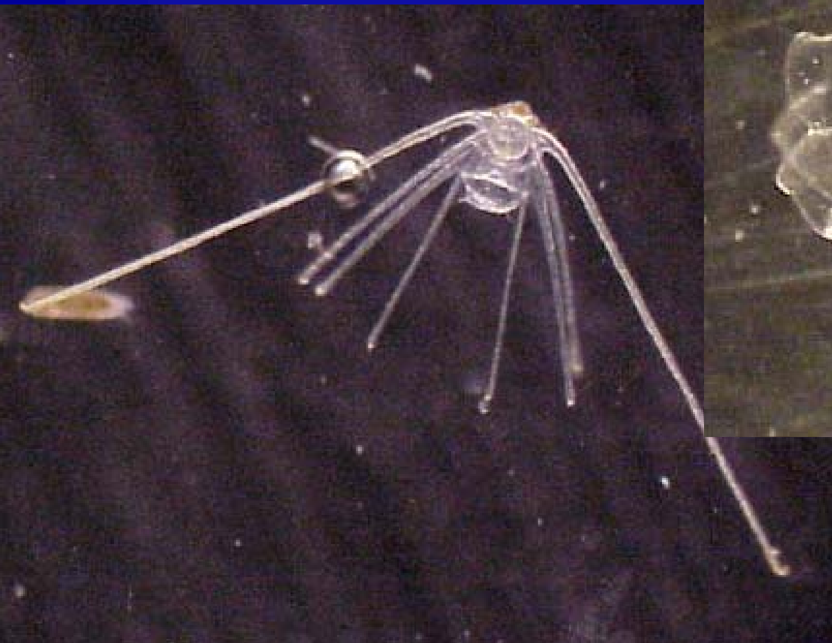
- Biofouling: control of settlement
- Aquaculture: shell-fisheries
- Ecological: distribution and abundance of benthos

Oceanogr. Mar. Biol. Annu. Rev. 1992, 30, 273–335

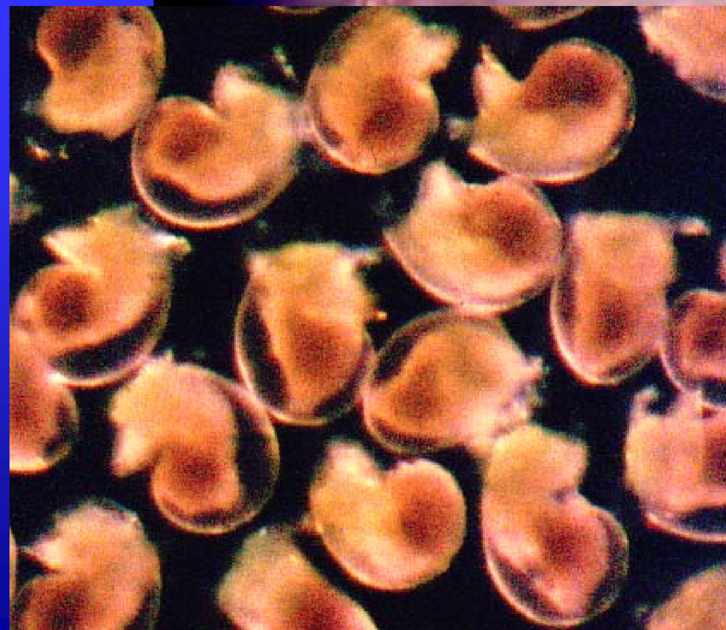



ADULT
Dispersal
TERRESTRIAL INSECT
Cue detection
Substratum selection
LARVA
LARVA
Dispersal
BENTHIC
MARINE INVERTEBRATE
Cue detection
Substratum selection
ADULT









CATEGORIES OF SPECIFICITY:

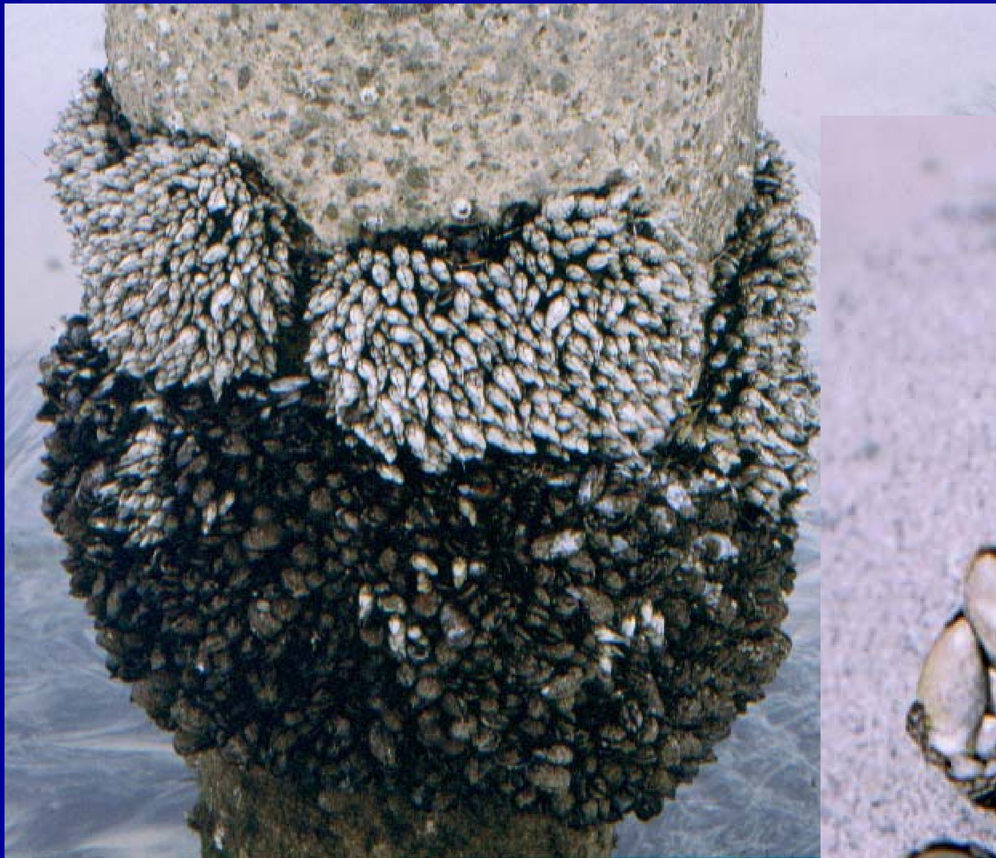
1) settlement on biofilms (sediment)

2) gregarious settlement - conspecifics

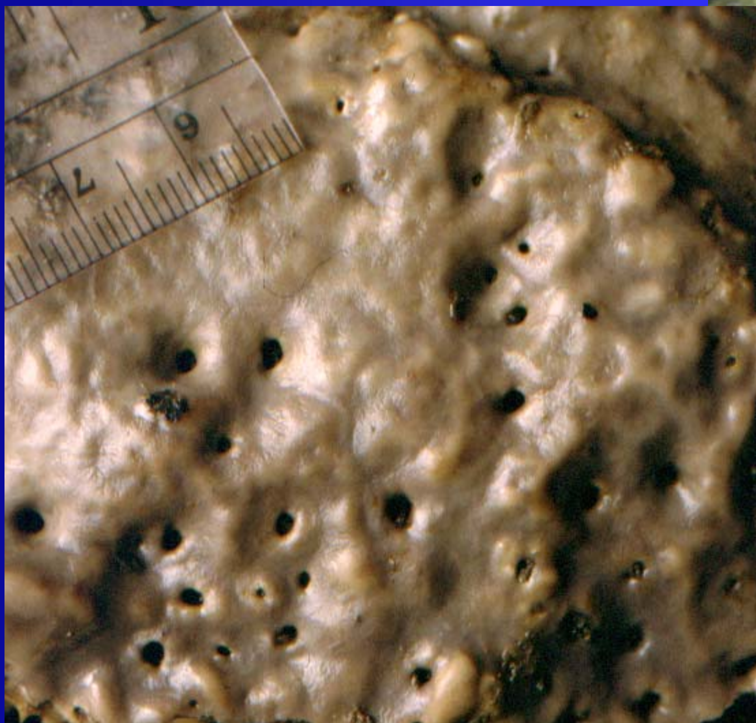
3) associative settlement - prey, hosts

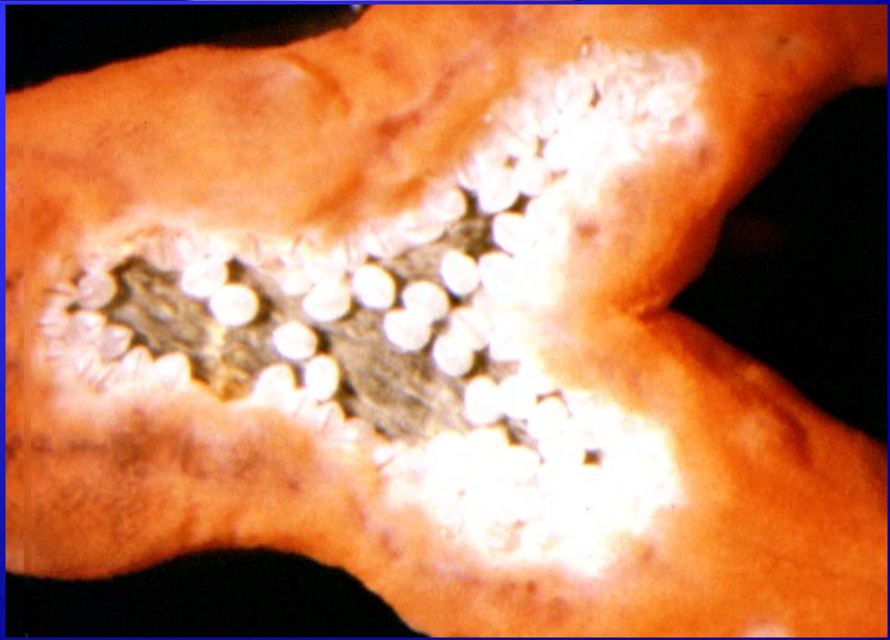
Barnacles exhibit all categories

Physical cues are important too

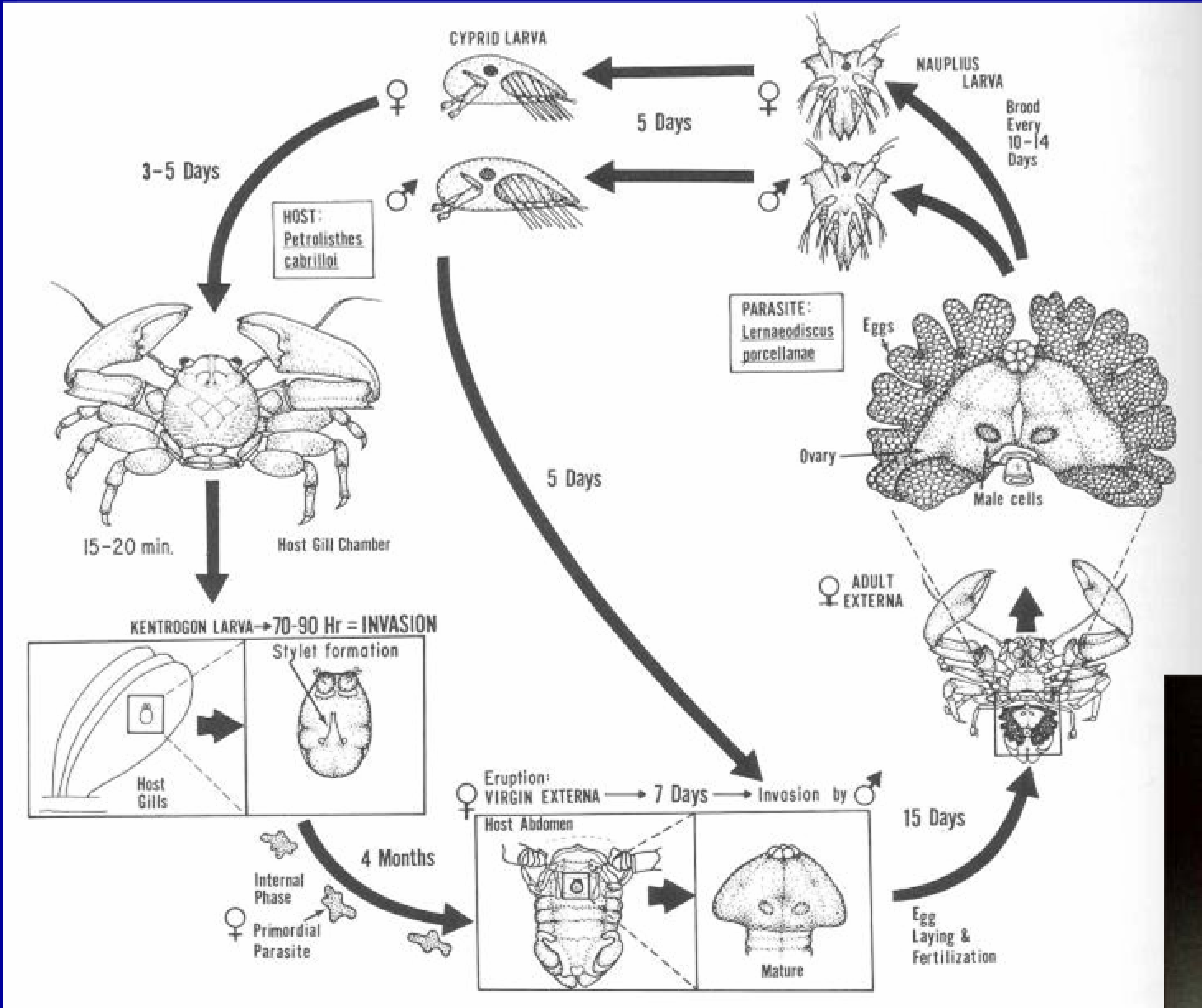






Conopea galeatus on *Lophogorgia chilensis*



Courtesy University of California, Santa Barbara

Associative settlement



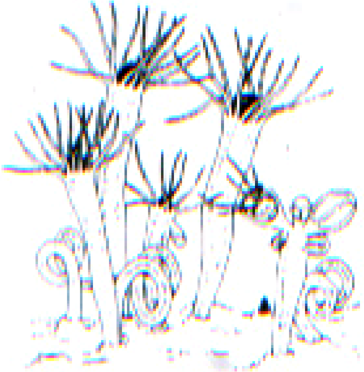
Gregarious settlement

GREGARIOUS SETTLEMENT

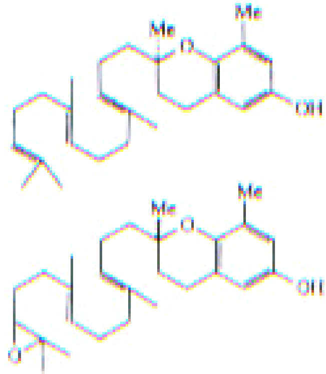
Species	Substratum	Detection	Cue
Barnacles	conspecific	surface	proteinaceous?
Balanus			arthropodin?
Semibalanus			actin?
Oysters	conspecifics		
Crassostrea	“settlement”	soluble	DOPA/melanin?
Ostrea			ammonia?
			tripeptide?
	-metamorphosis	surface	bacterial?
Tubeworm	conspecifics	surface	cement peptide?
Phragmatopoma			DOPA?
			FFAs?
Hydroides	conspecifics?	surface	bacteria?

ASSOCIATIVE SETTLEMENT

Species	Substratum	Detection	Cue
Nudibranch *Phestilla*	corals *Porites*	soluble	? (30 years!!)
Abalone *Haliotis*	crustose red algae	surface	GABA? peptide?
	adult mucus / microbial film		
Coral *Agaricia*	crustose red algae	surface	carbohydrate?
Sea urchin *Holopneustes*	red alga *Delisea*	soluble?	carbohydrate: floridoside + isethionic acid

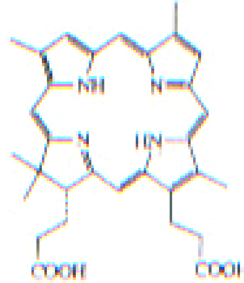


δ-tocotrienol and epoxide
Nishihira, 1968
Kato *et al.*, 1975

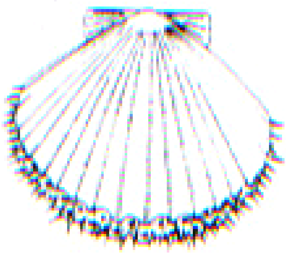


Coryne uchidai - hydroid
Substratum: Sargassaceae - brown algae

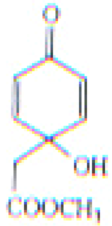
bonellin
Sorby, 1875
Pelter *et al.*, 1978



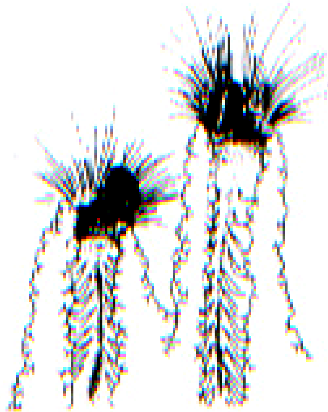
Bonellia viridis - echiuran worm
Substratum: conspecifics



jacaranone
Yvin *et al.*, 1985
Cochard *et al.*, 1989



Pecten maximus - bivalve mollusc
Substratum: *Delesseria sanguinea* - red alga



unsaturated free fatty acids
Pawlik, 1986
Pawlik and Faulkner, 1986

$CH_3(CH_2)_5CH{=}CH(CH_2)_7COOH$

$CH_3(CH_2)_4CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$

$CH_3(CH_2)_4(CH{=}CHCH_2)_3CH{=}CH(CH_2)_3COOH$

$CH_3CH_2(CH{=}CHCH_2)_4CH{=}CH(CH_2)_3COOH$

Phragmatopoma lapidosa - polychaete worm
Substratum: conspecific tubes

A “natural” chemical cue that *induces* or *deters* settlement can be demonstrated to exist:

1) on or near the substratum

2) at effective concentrations

3) under natural conditions

Problems with assays of potential settlement inducers or antifouling compounds:

1) extracts or compounds “pooled” on a surface at high concentrations

2) physical characteristics of surface are altered

3) compounds solubilized in still water at unnaturally high concentrations

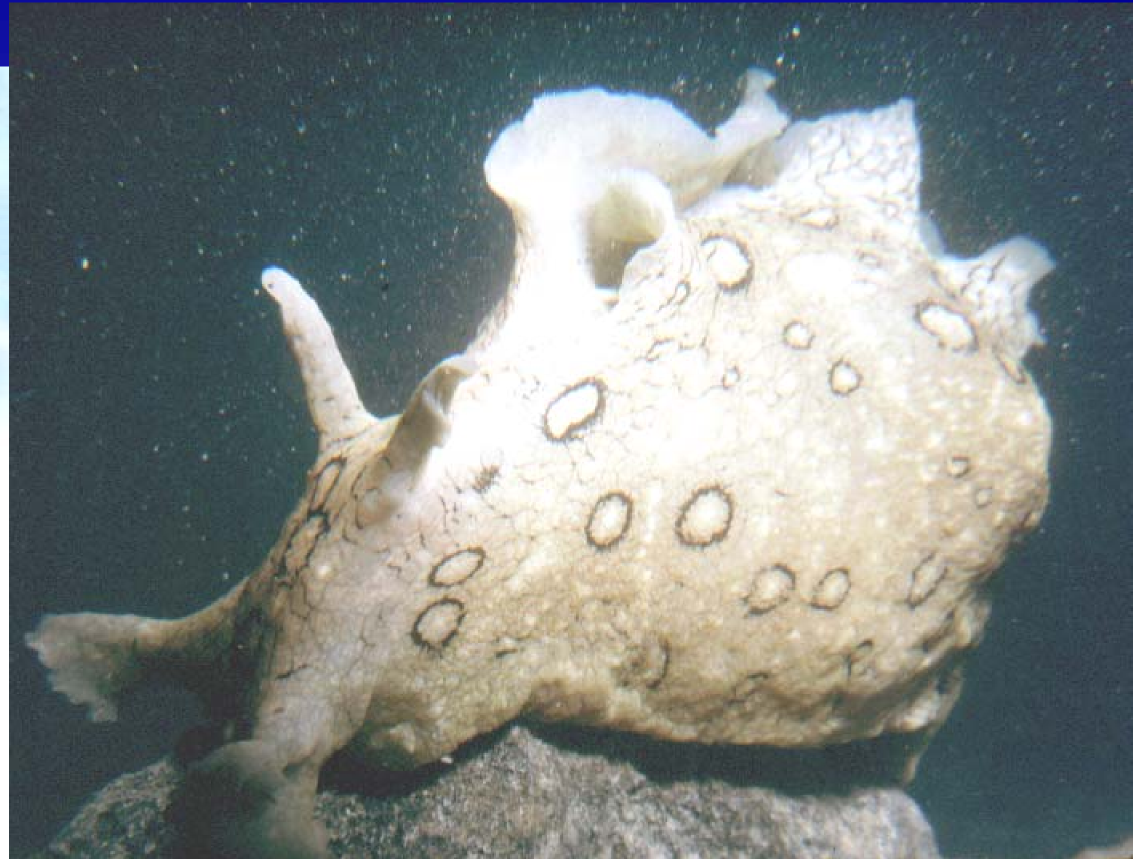
4) long-term, whole larva assays are subject to artifact

Why is it so difficult to isolate the natural chemical cues that affect marine invertebrate larvae?

1) Larvae are small, planktonic
2) Sensory organs are multifunctional
3) Water flow is complex
4) Cues are multiple and hierarchical

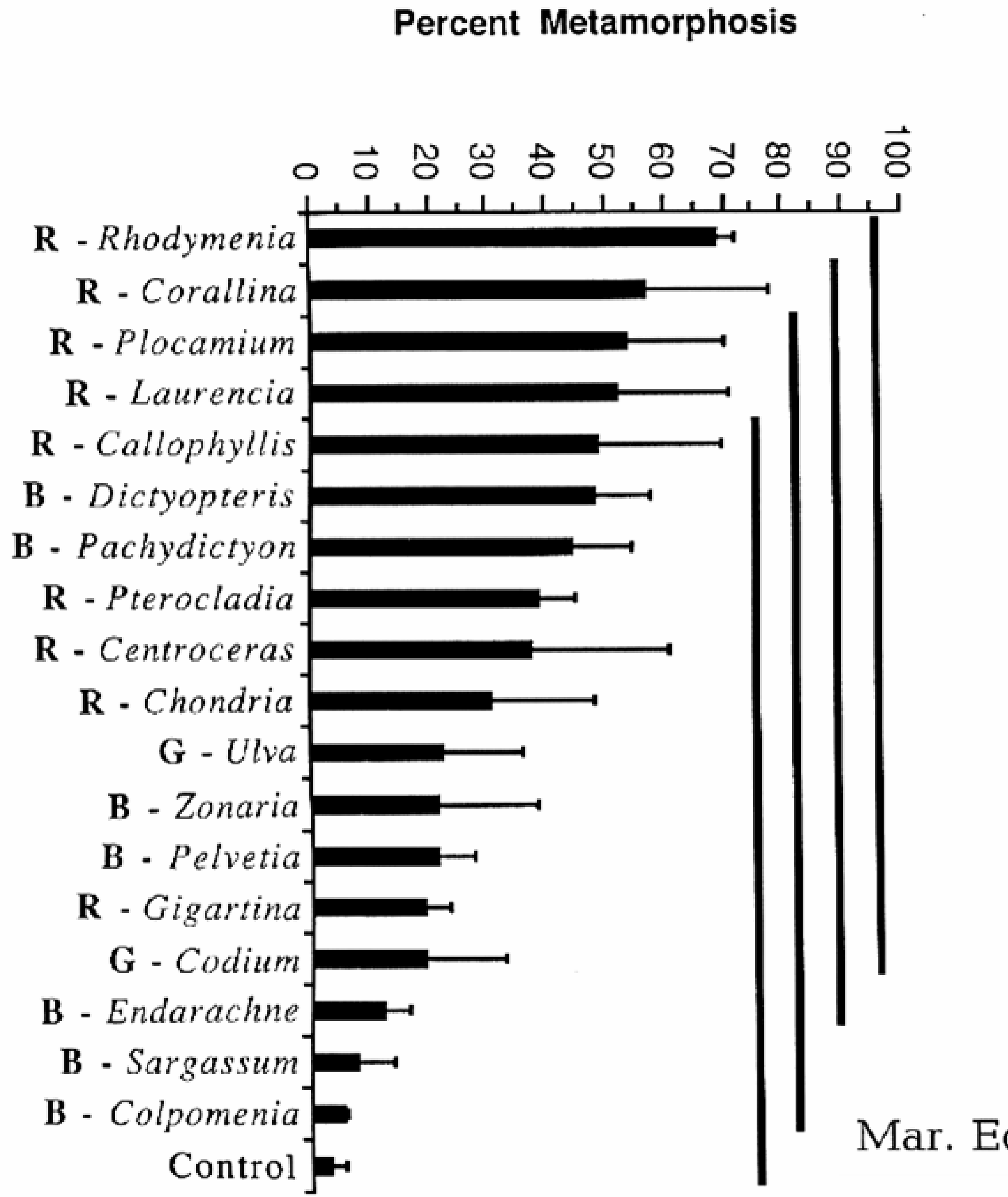
“It is evident that there is need for new viewpoints, for more observations and, perhaps, for team-work between various disciplines not only of biology but of physics and chemistry as well before there will be a clearly acceptable hypothesis of metamorphosis. Only the beginnings have been made in this interesting field.”

W.F. Lynch (1961): Extrinsic factors influencing metamorphosis in bryozoan and ascidian larvae. *Amer. Zool.* 1: 59-66.



***Aplysia* spp.**


PYREX
7/20/87

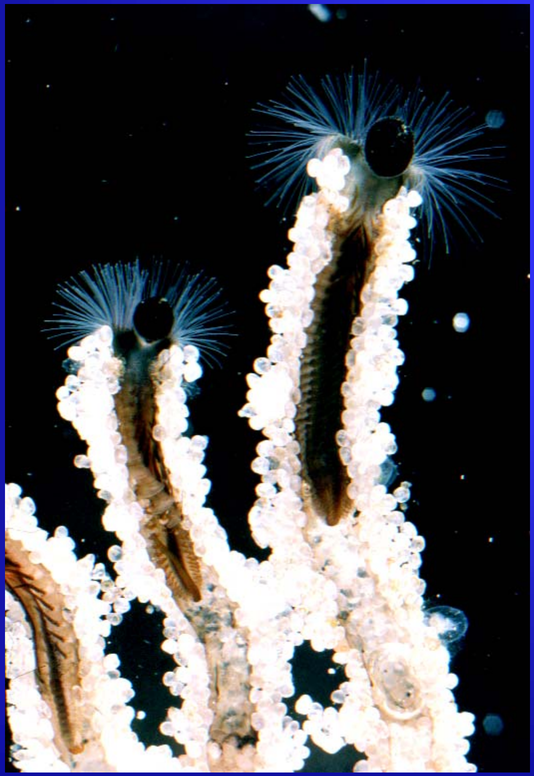
Non specific --

but, for a mobile consumer, getting in the proper habitat may be a sufficient trade-off

Mar. Ecol. Prog. Ser. 51: 195–199, 1989

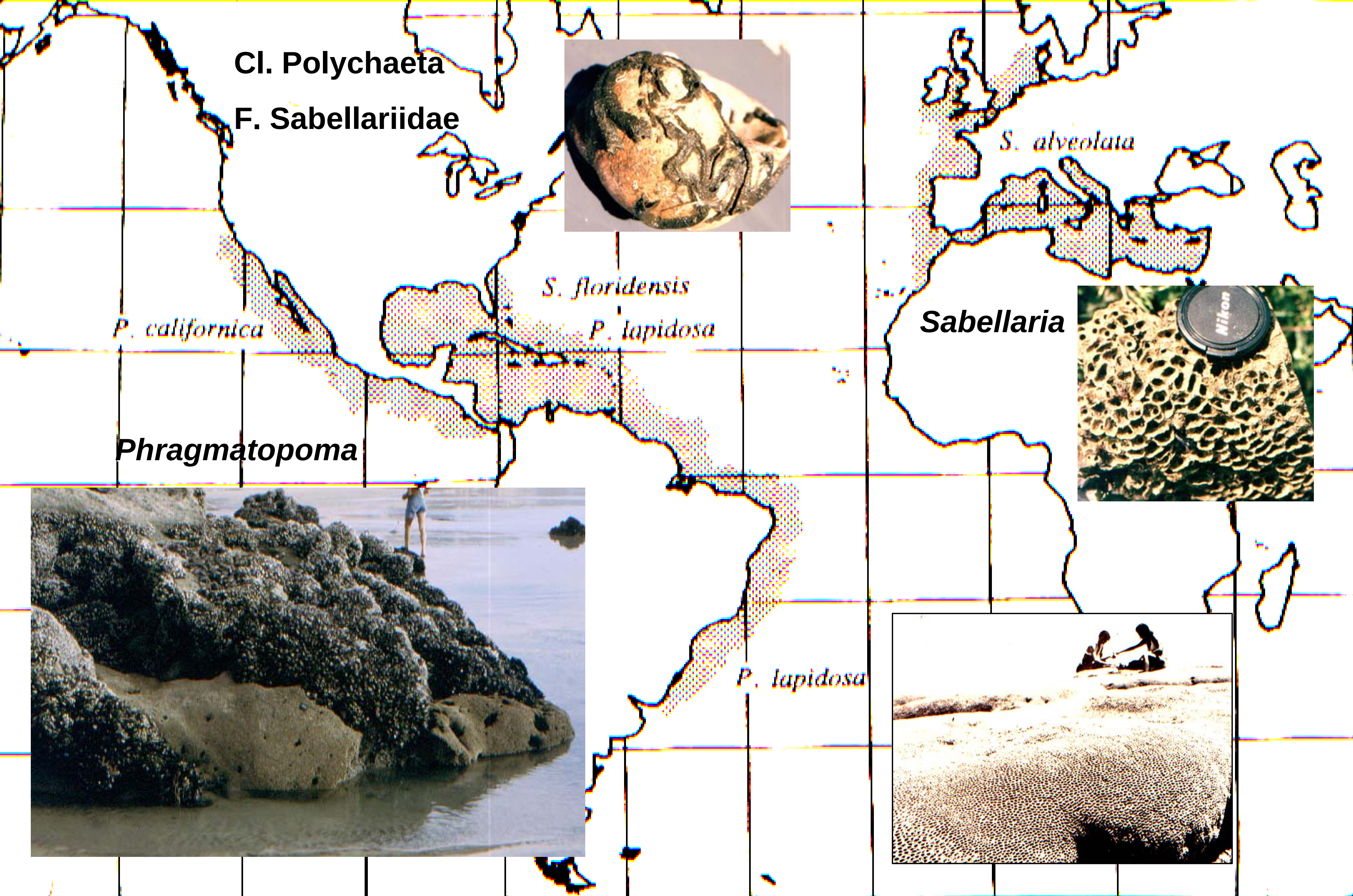
CHEMICAL ECOLOGY OF MARINE INVERTEBRATE LARVAL SETTLEMENT: Part II

"A tale of two worms"



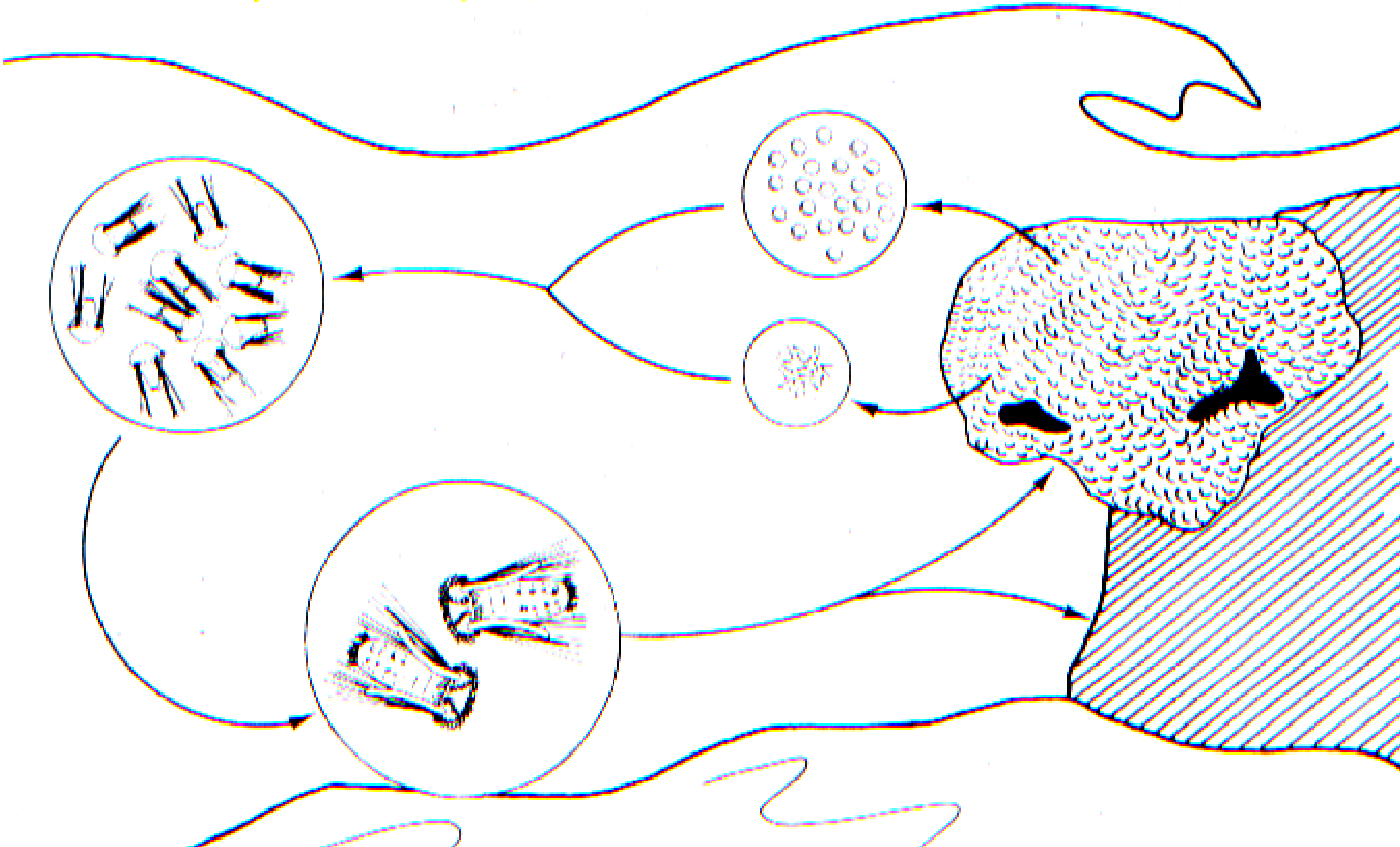
Phragmatopoma californica

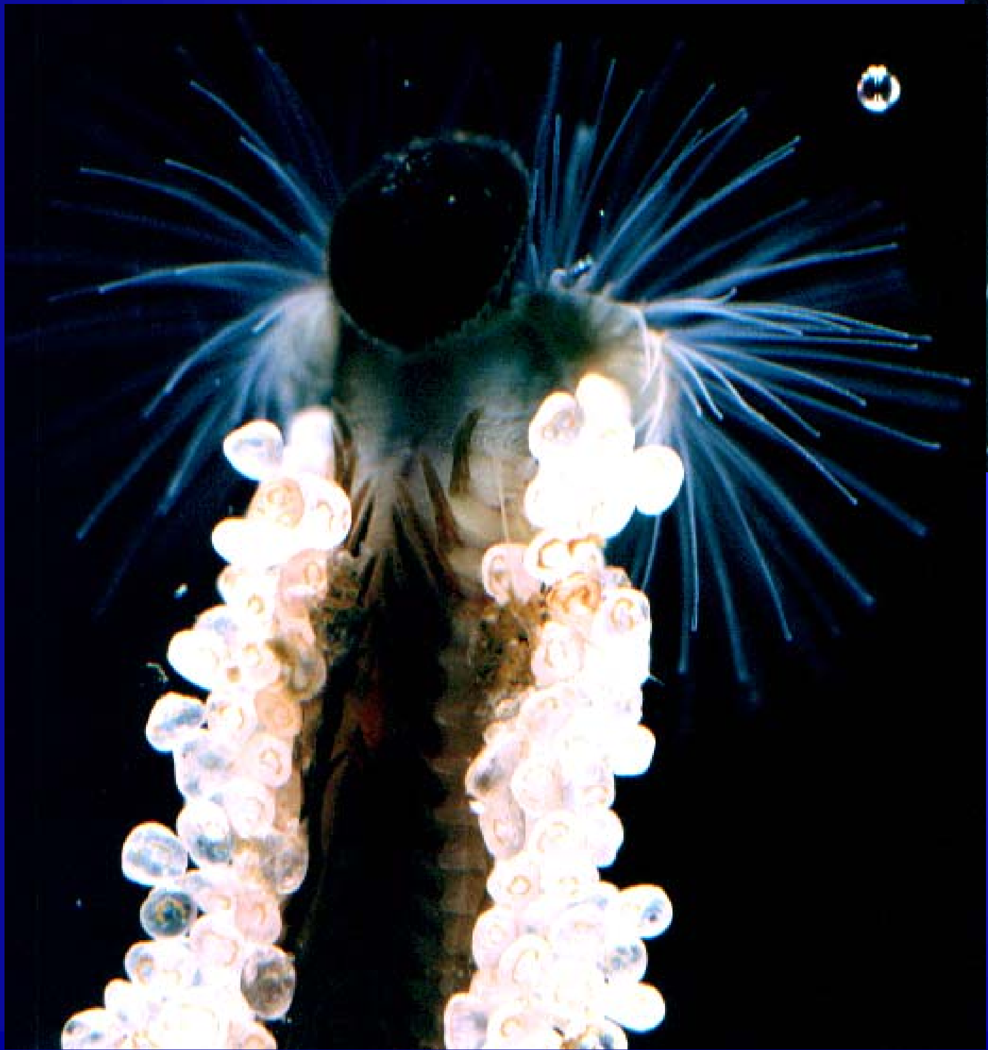
Hydroides dianthus

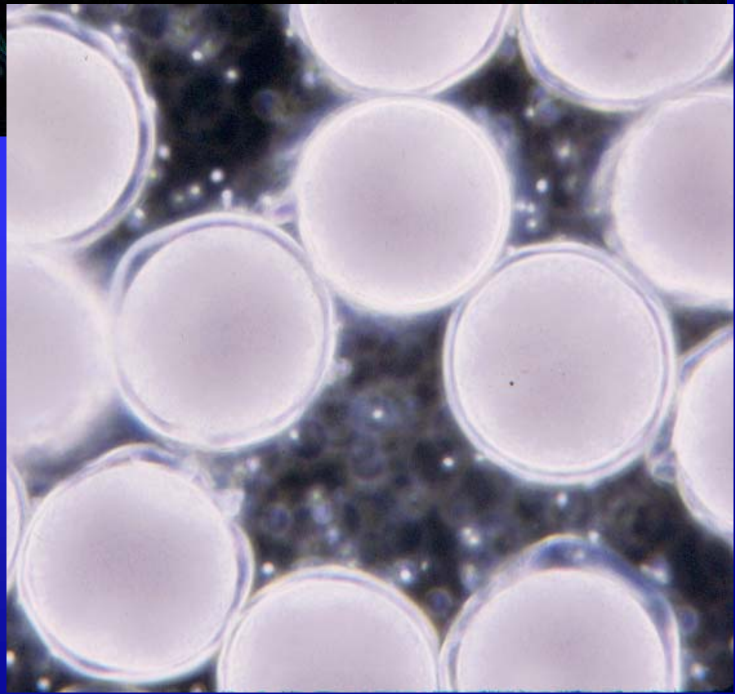


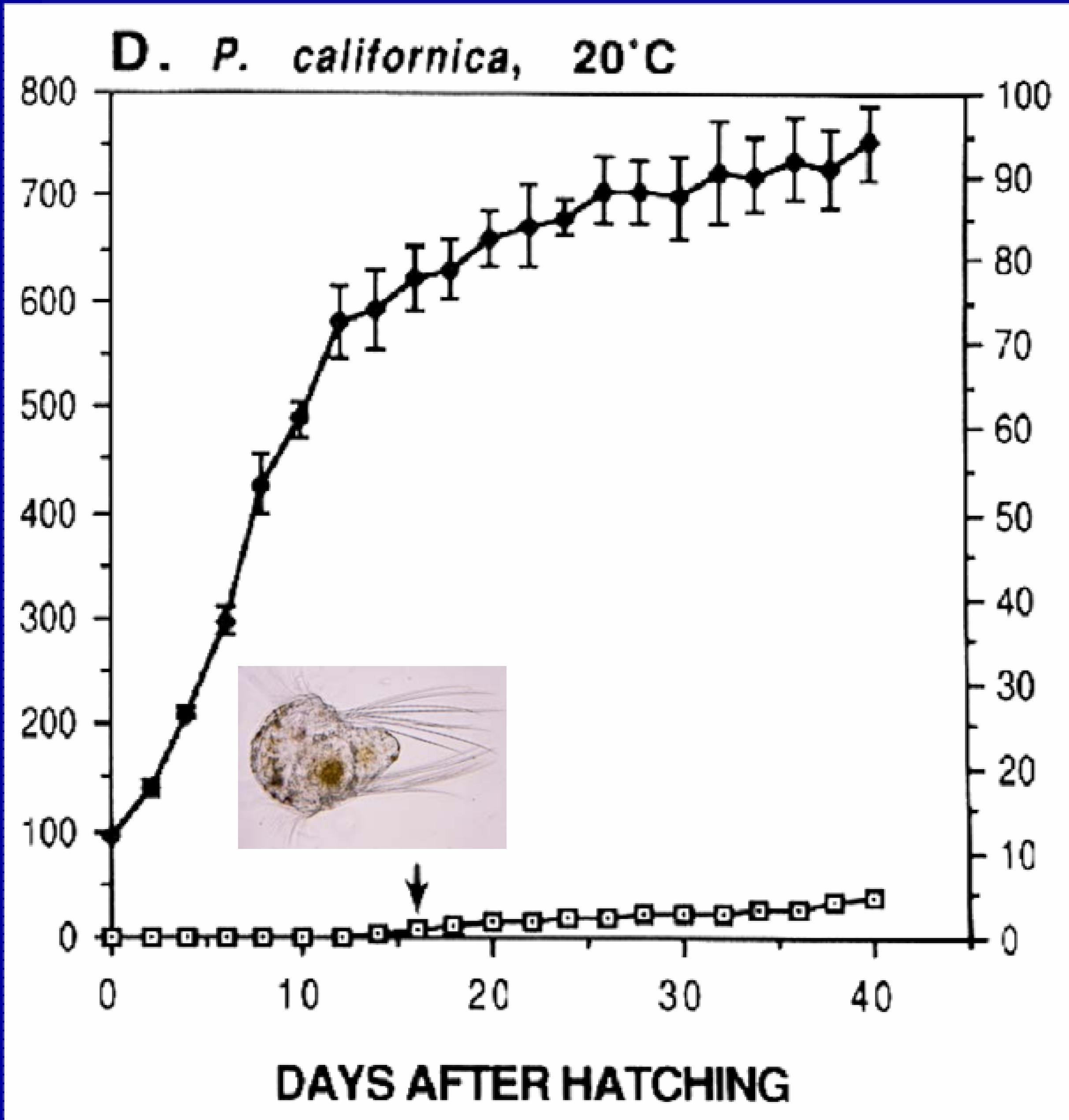
Cl. Polychaeta
F. Sabellariidae
S. alveolata
S. floridensis
P. lapidosa
P. californica
Sabellaria
Phragmatopoma
Nikon
P. lapidosa

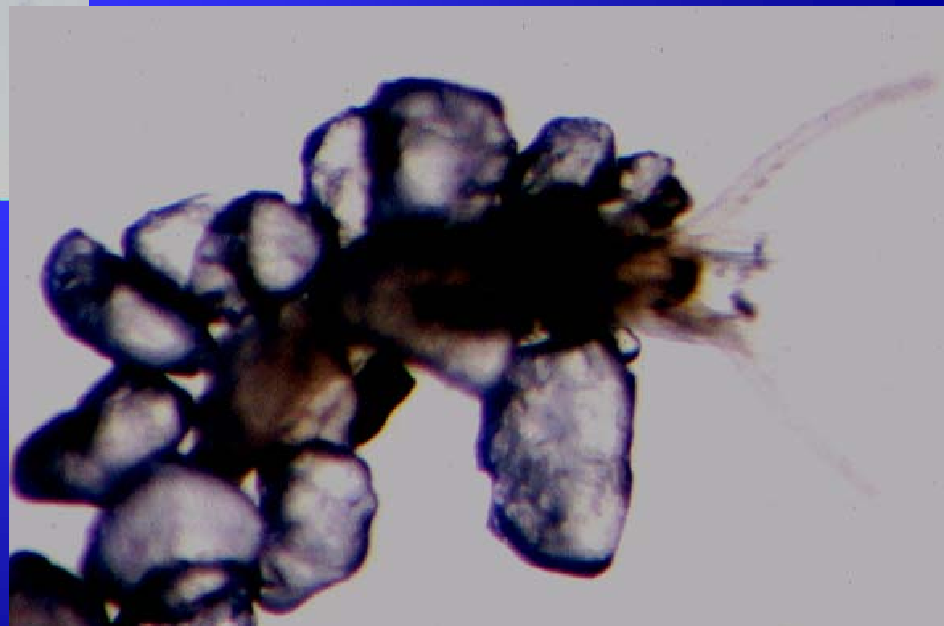
Life cycle of a gregarious sabellariid polychaete

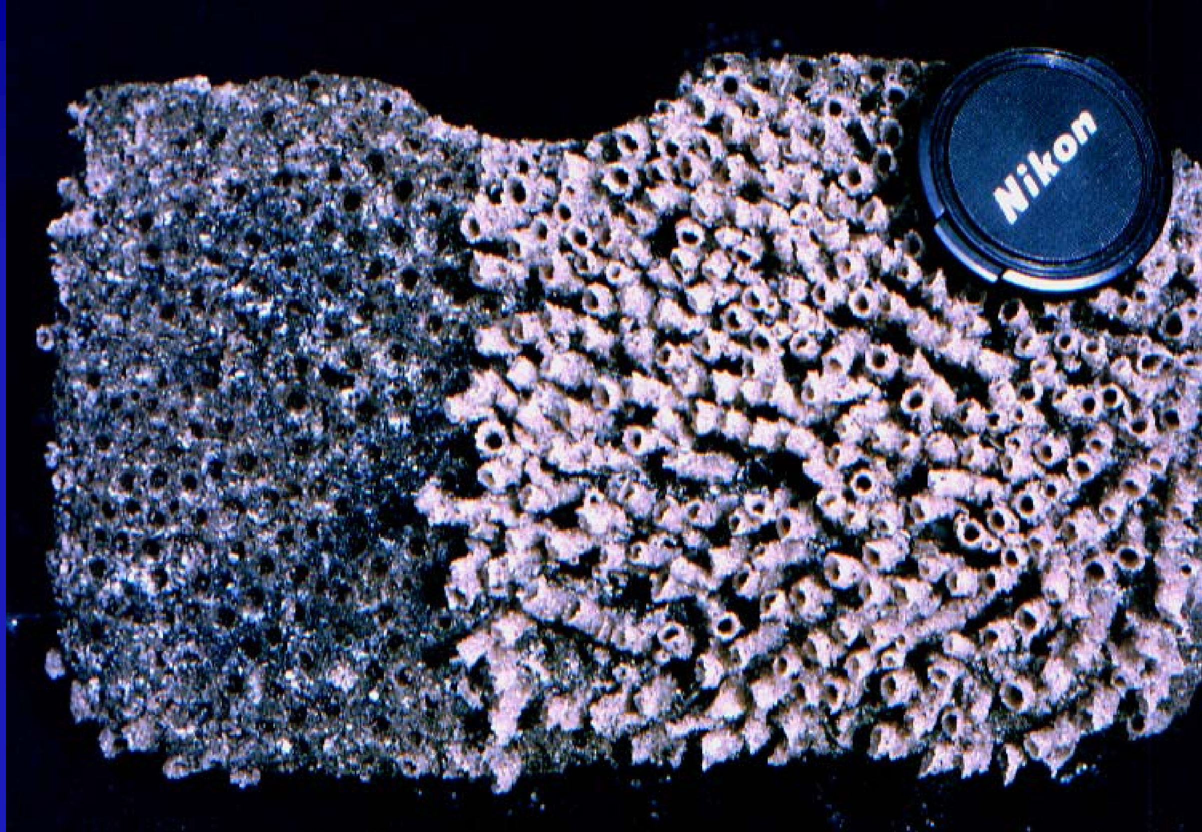


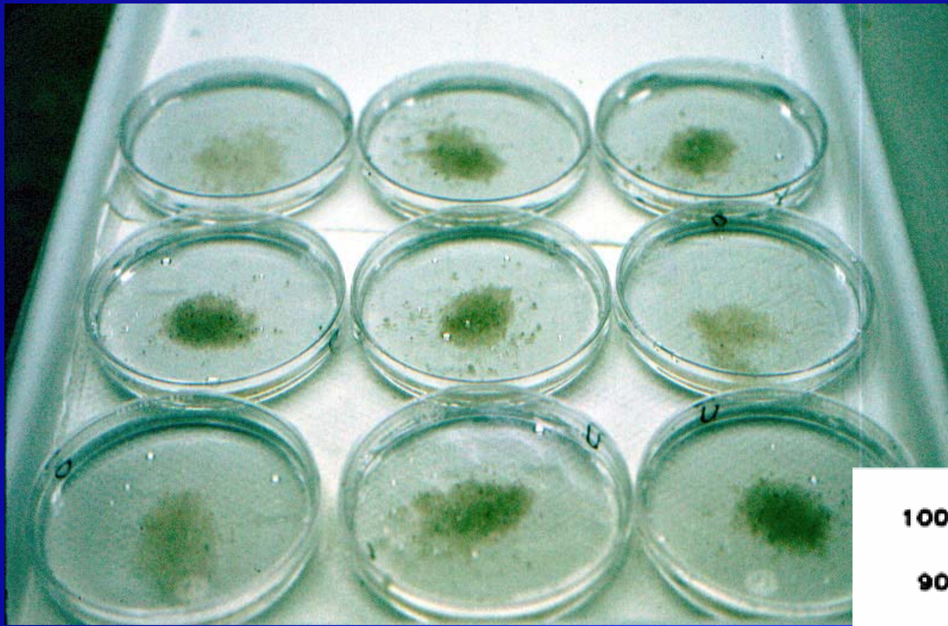



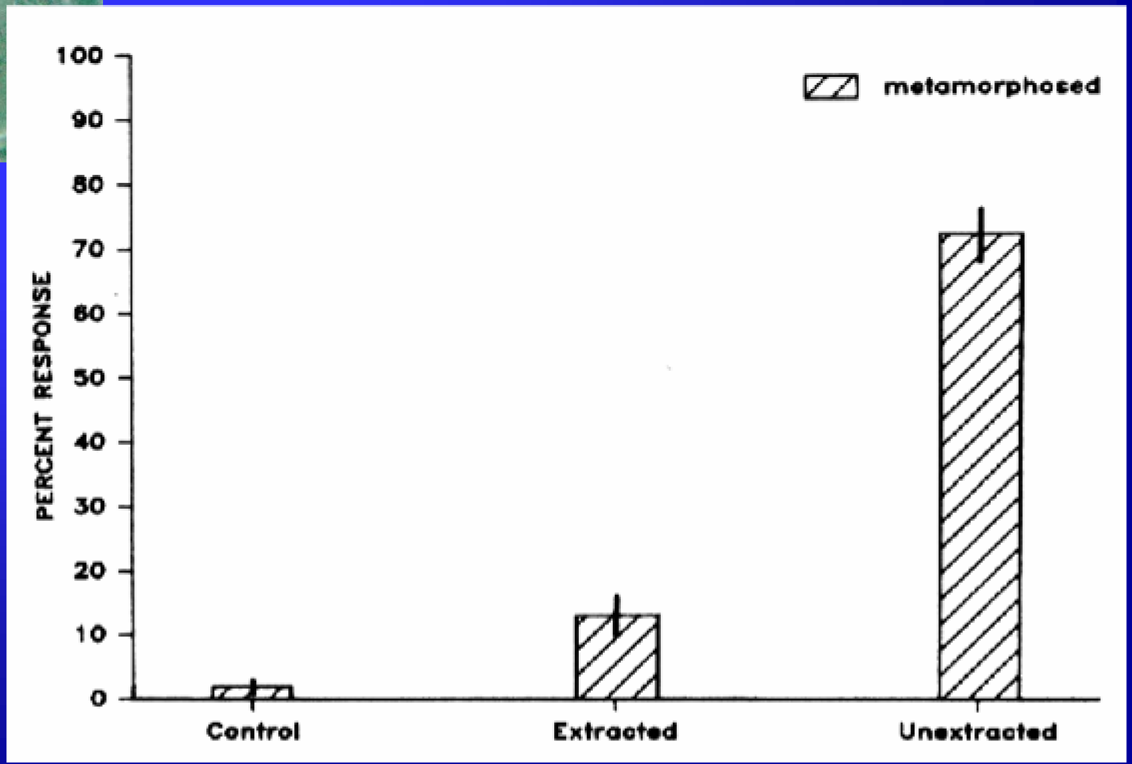



D. P. californica, 20°C
800
700
600
500
400
300
200
100
0
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
DAYS AFTER HATCHING

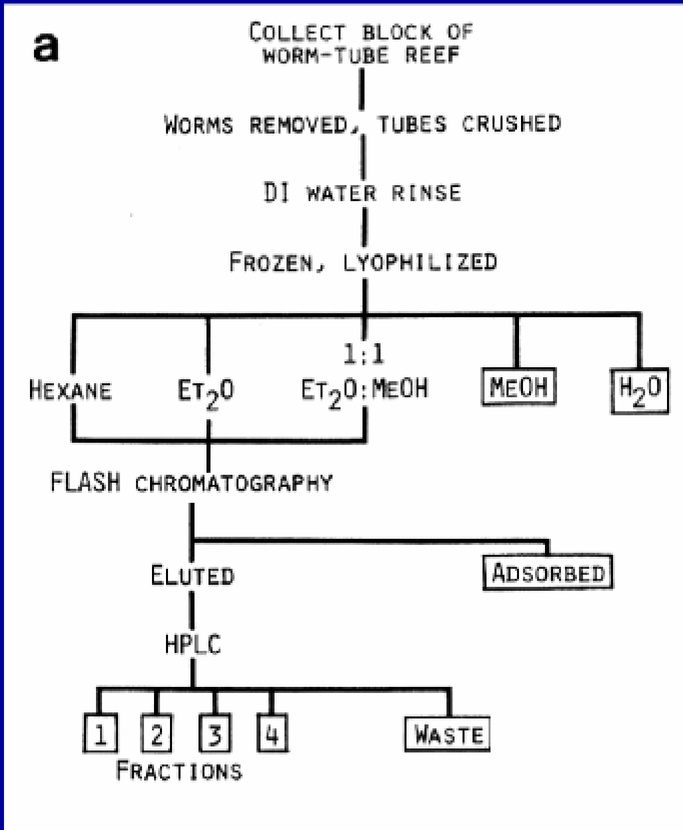



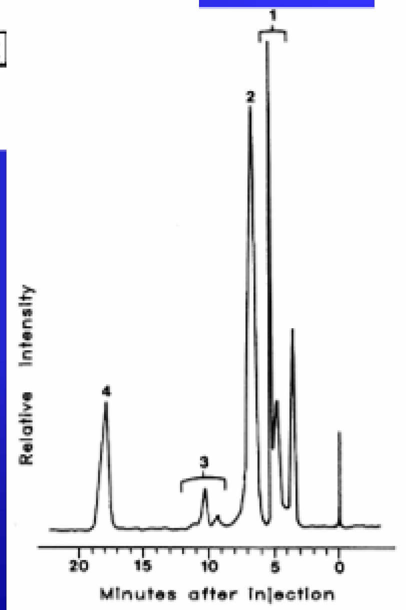

Nikon

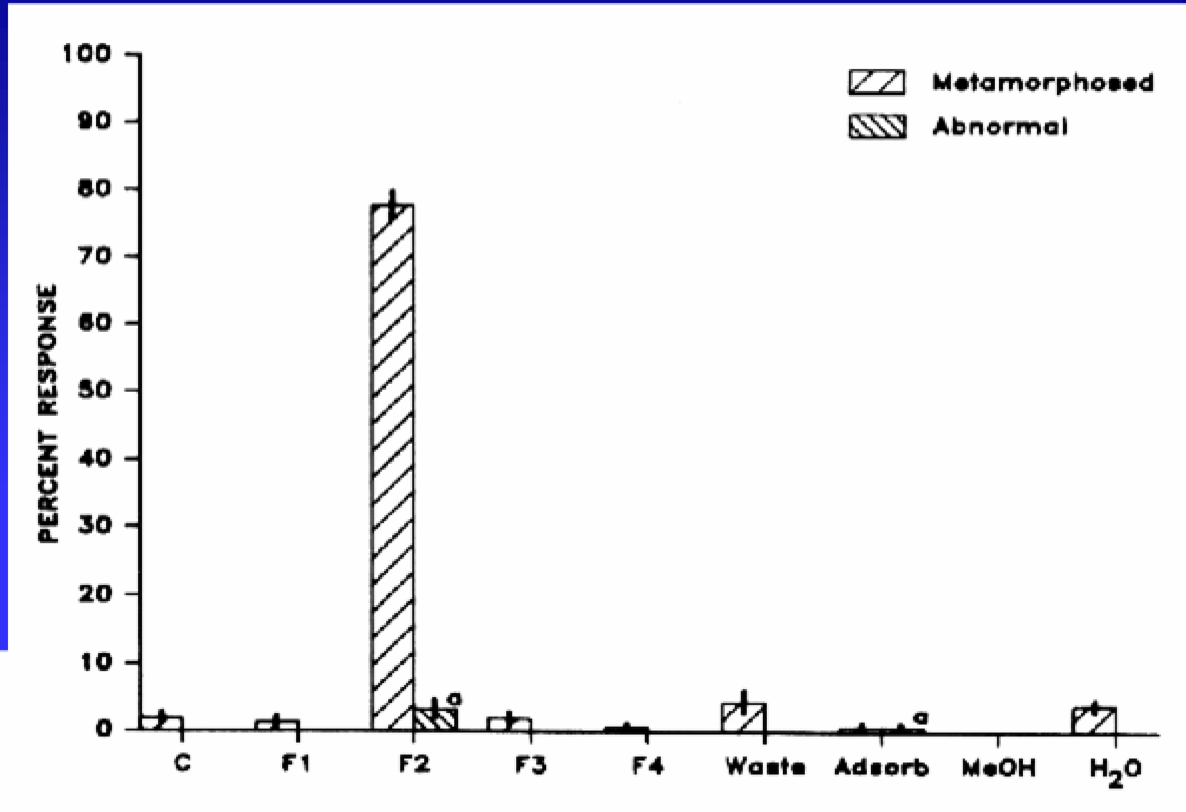




metamorphosed
PERCENT RESPONSE
100
90
80
70
60
50
40
30
20
10
0
Control
Extracted
Unextracted







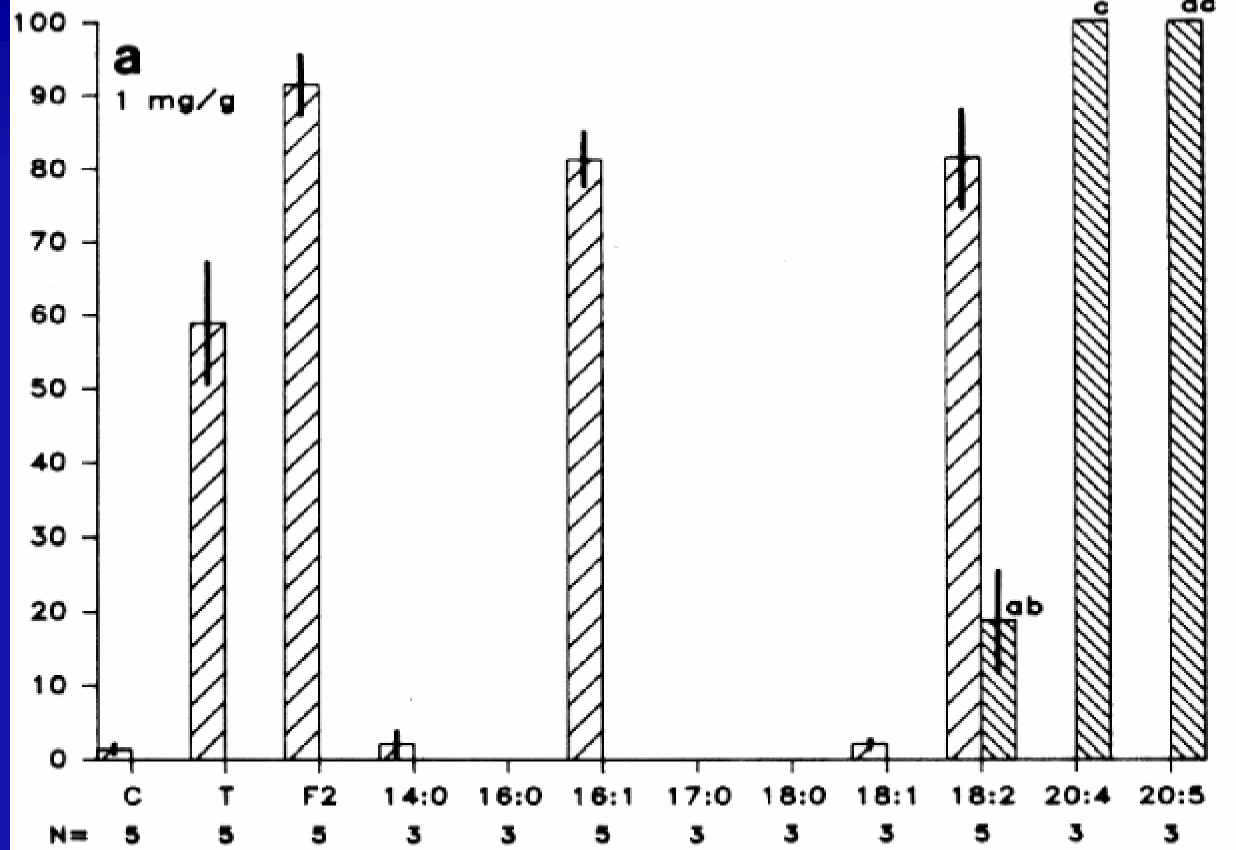
Marine Biology 91, 59–68 (1986)

Table 1. *Phragmatopoma californica.* Percentage composition of HPLC-Fraction 2. For free fatty acids (FFAs), the number of carbon atoms in the molecule precedes the colon, the number of double bonds follows (br = branch- and straight-chain FFAs present). Data from a total of five separate extraction and isolation procedures. GC-MS: One run by Finnigan gas chromatography-mass spectrometry; HP-GC: normalized averages of four runs by gas chromatography alone

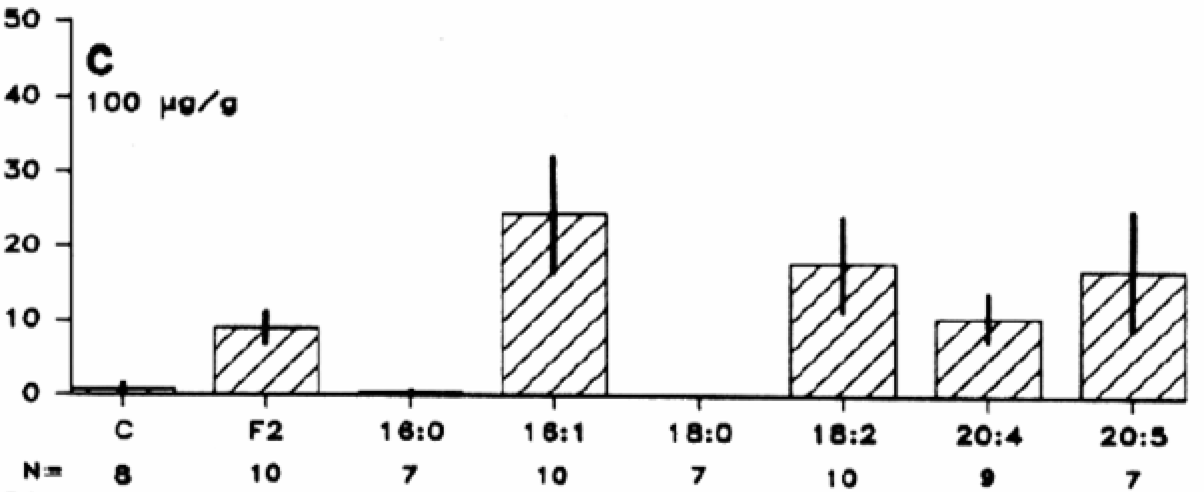
Detected compounds	GC-MS	HP-GC
FFAs		
14:0[a]	2.1	4.9
15:0 br	1.8	2.0
16:2	0.2	15.6 (16:2 + 16:1)
16:1[a]	10.4	
16:0[a]	12.0	16.6
17:0 br	4.9	3.0
18:3	1.8	
18:2[a]	3.1	12.1 (18:3 + 18:2 + 18:1)
18:1[a]	9.5	
18:0[a]	4.7	6.4
20:5[a]	19.2	23.5
20:4[a]	4.9	
20:3	1.7	4.7 (20:4 – 20:1)
20:2	0.8	
20:1	2.0	
22:4	2.5	
22:3	1.3	6.4 (22:4 – 22:2)
22:2	2.9	
Phthalates	12.0	4.9

[a] FFA constituting more than 3% of the sample in either column

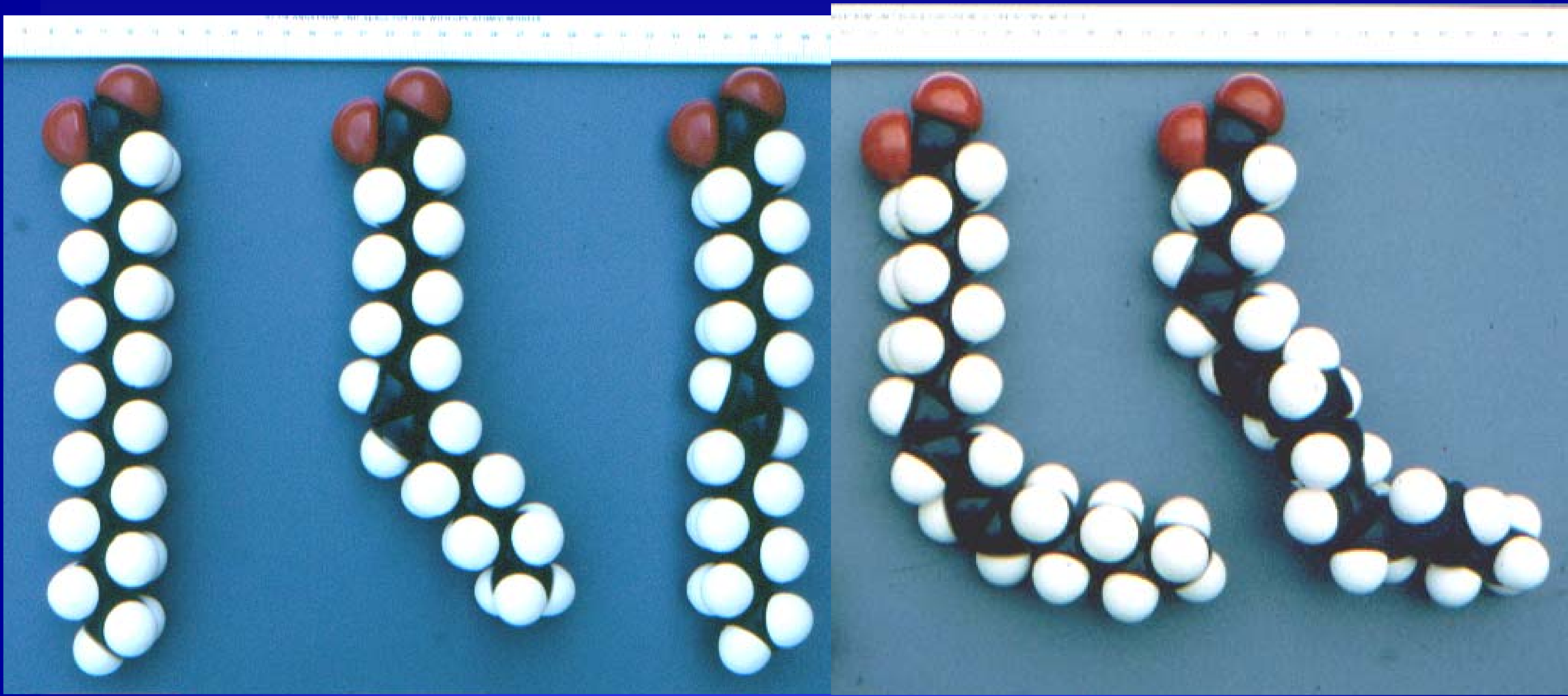
Marine Biology 91, 59–68 (1986)



a
1 mg/g
100
90
80
70
60
50
40
30
20
10
0
ab
c
C
T
F2
14:0
16:0
16:1
17:0
18:0
18:1
18:2
20:4
20:5
N=
5
5
5
3
3
5
3
3
3
5
3
3



c
100 μg/g
50
40
30
20
10
0
C
F2
16:0
16:1
18:0
18:2
20:4
20:5
N=
8
10
7
10
7
10
9
7



16:0 Palmitic	16:1 cis 9 Palmitoleic	16:1 trans 9 Palmitelaidic	18:2 Linoleic	20:5 Eicosapentaenoic
—	+	—	+	+

Response dependent on size, shape, functionality

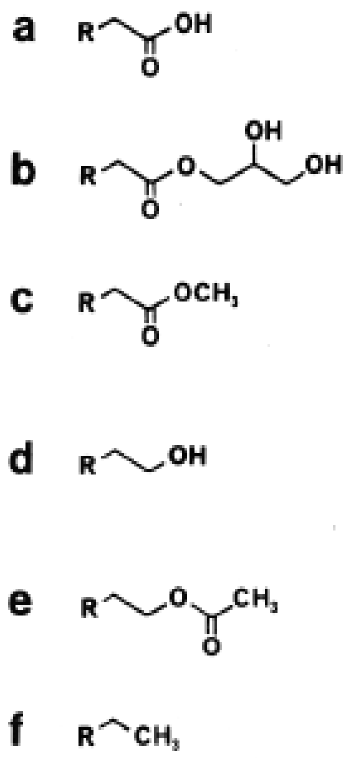


Fig. 2. End-group structures of a FFA (a) and of FFA derivatives (b–f): b: monoglyceride: c: methyl ester; d: alcohol; e: acetate; f: alkene.

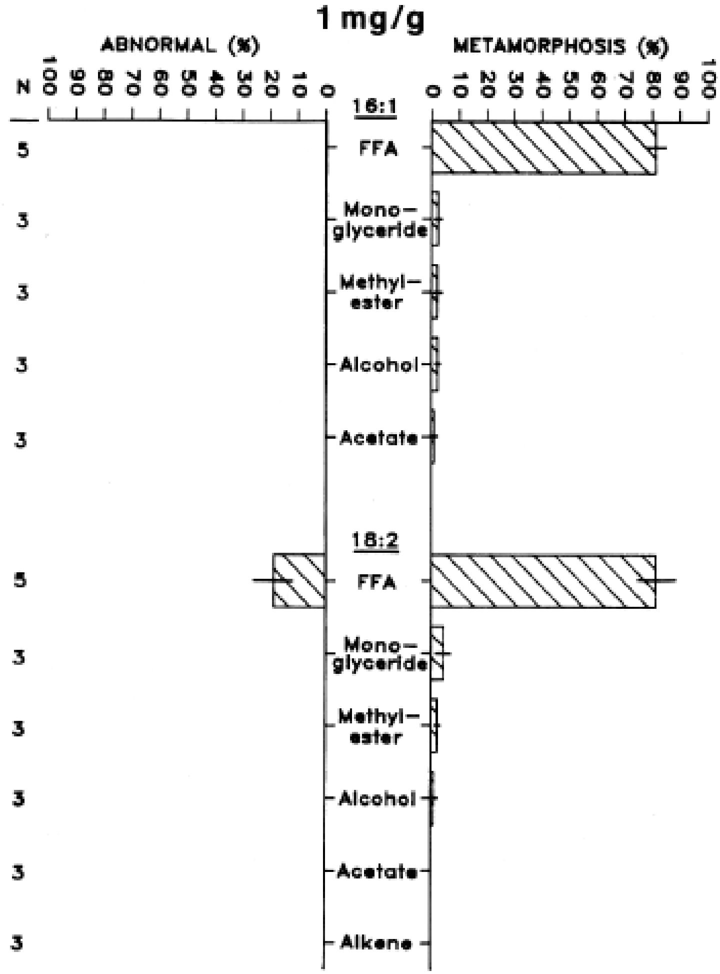
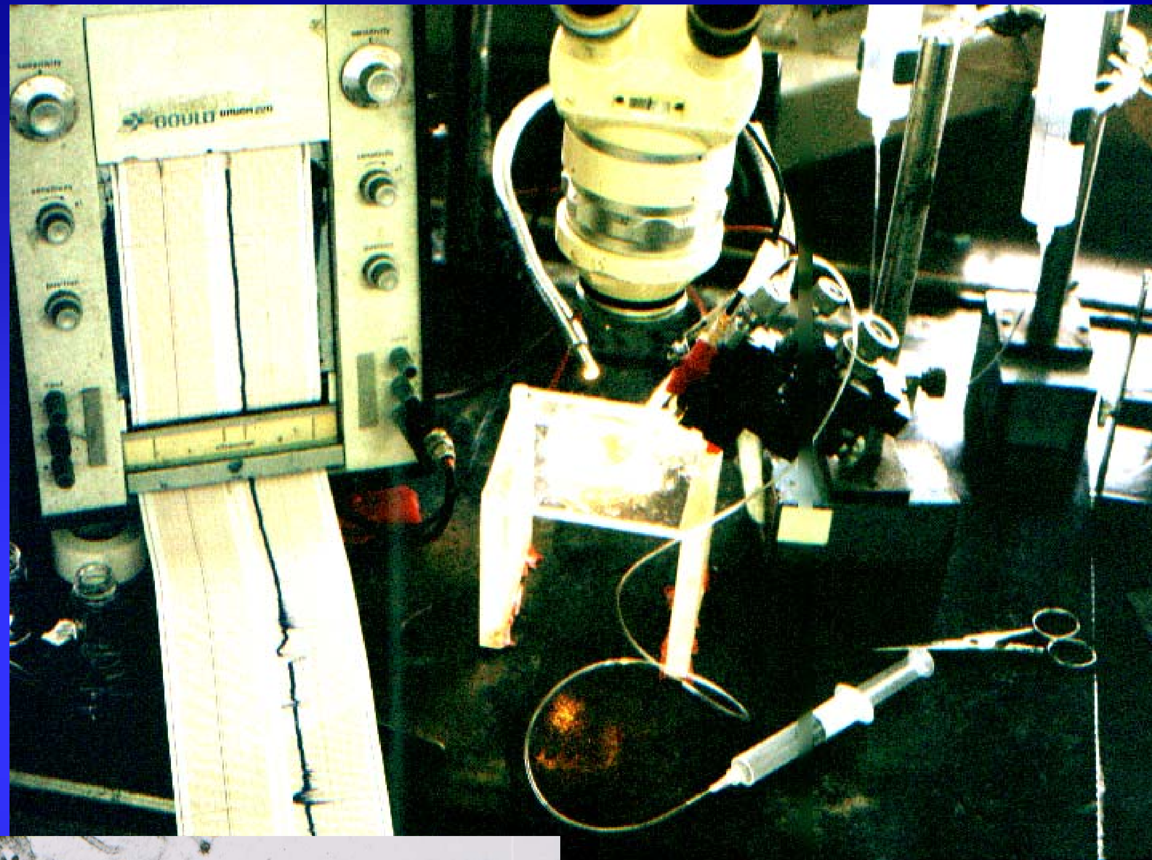
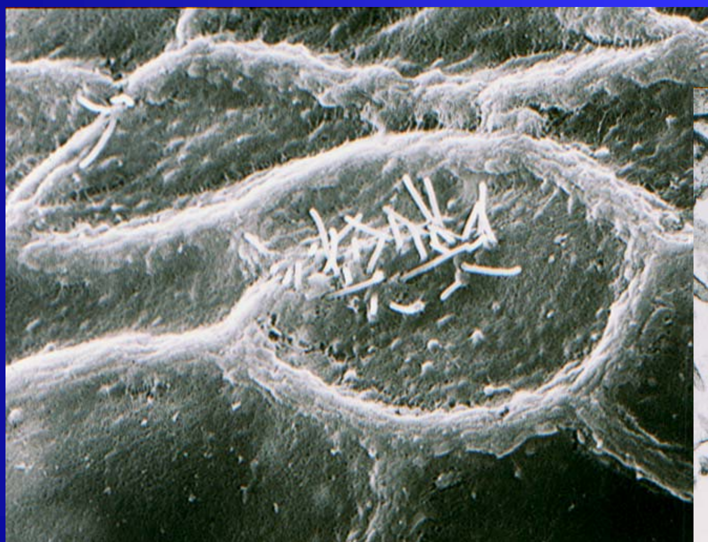


Fig. 3. Mean percentage response ($\pm$ SE) of *Phragmatopoma californica* larvae to sand treated with the FFA, monoglyceride, methyl ester, alcohol and alcohol acetate ester of 16 : 1 and these five plus the *n*-alkene of 18 : 2 at 1 mg/g sand (refer to Fig. 2).

=

?


GOULD



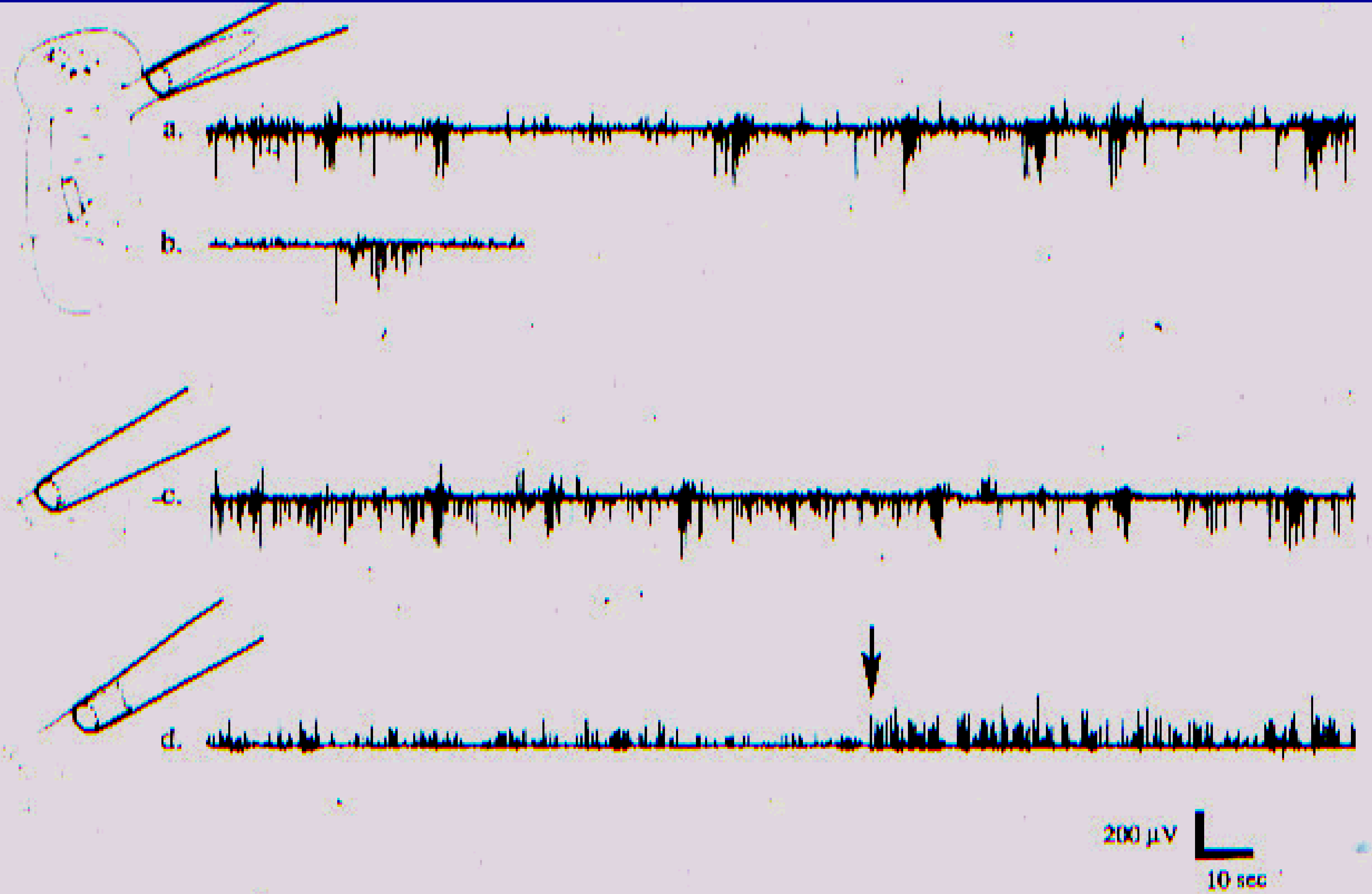
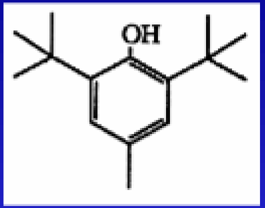
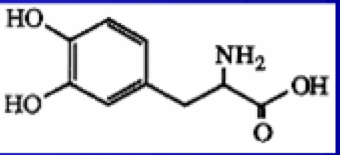


Fig. 1. Electrical activity of the larval tentacles of *Phragmatopoma lapidosa californica*. (a) Suction electrode enclosing tentacle attached to larva. (b) Detail of burst, 5X chart record speed, same conditions as in (a). (c) Activity of tentacle severed from larva, tip in, severed end slightly protruding from electrode tip. (d) Activity of severed tentacle after having been ejected from the electrode and sucked back up with the severed end in and the tip exposed, with 3/4 of the tentacle length enclosed in the electrode. The arrow marks the point at which a suspension of eicosapentaenoic acid (induces larval settlement and metamorphosis) was squirted over the preparation.





DOPA

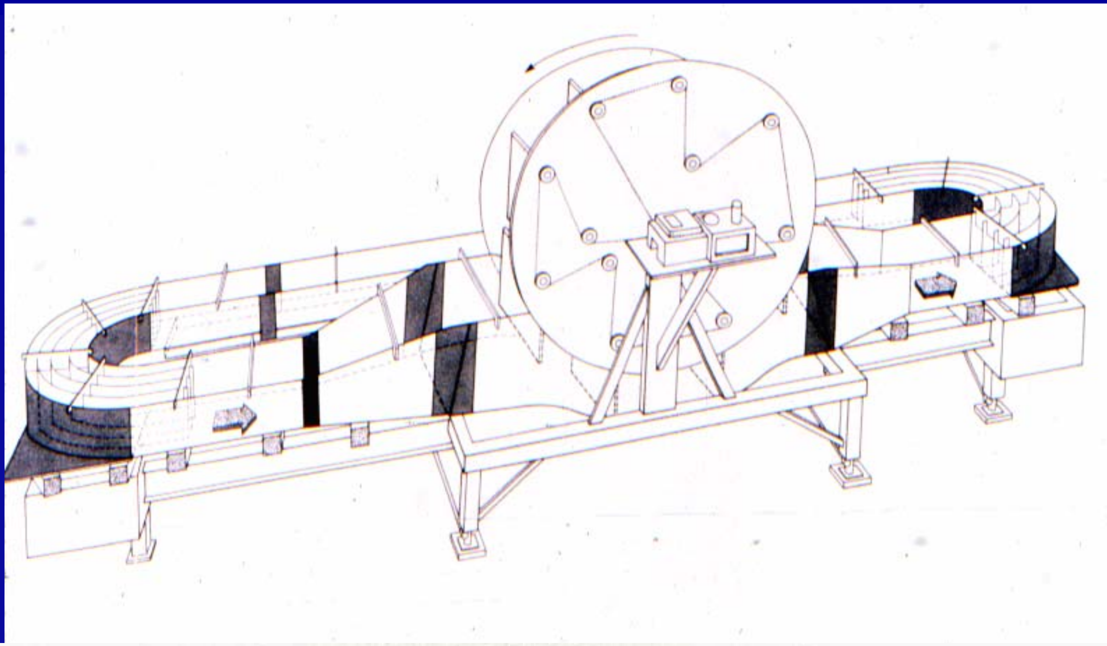
BUT....

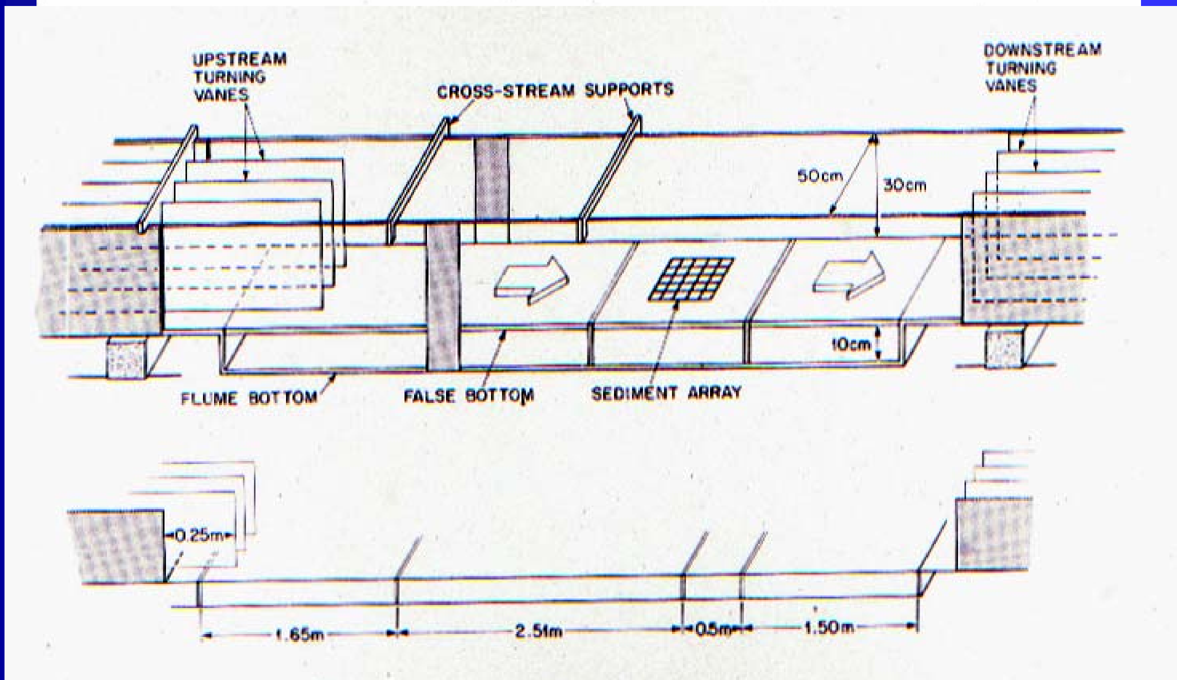
- Morse's group demonstrated activity of BHT
- could not detect FFAs in tube sand samples

SO, is the response of *Phragmatopoma* non-specific???

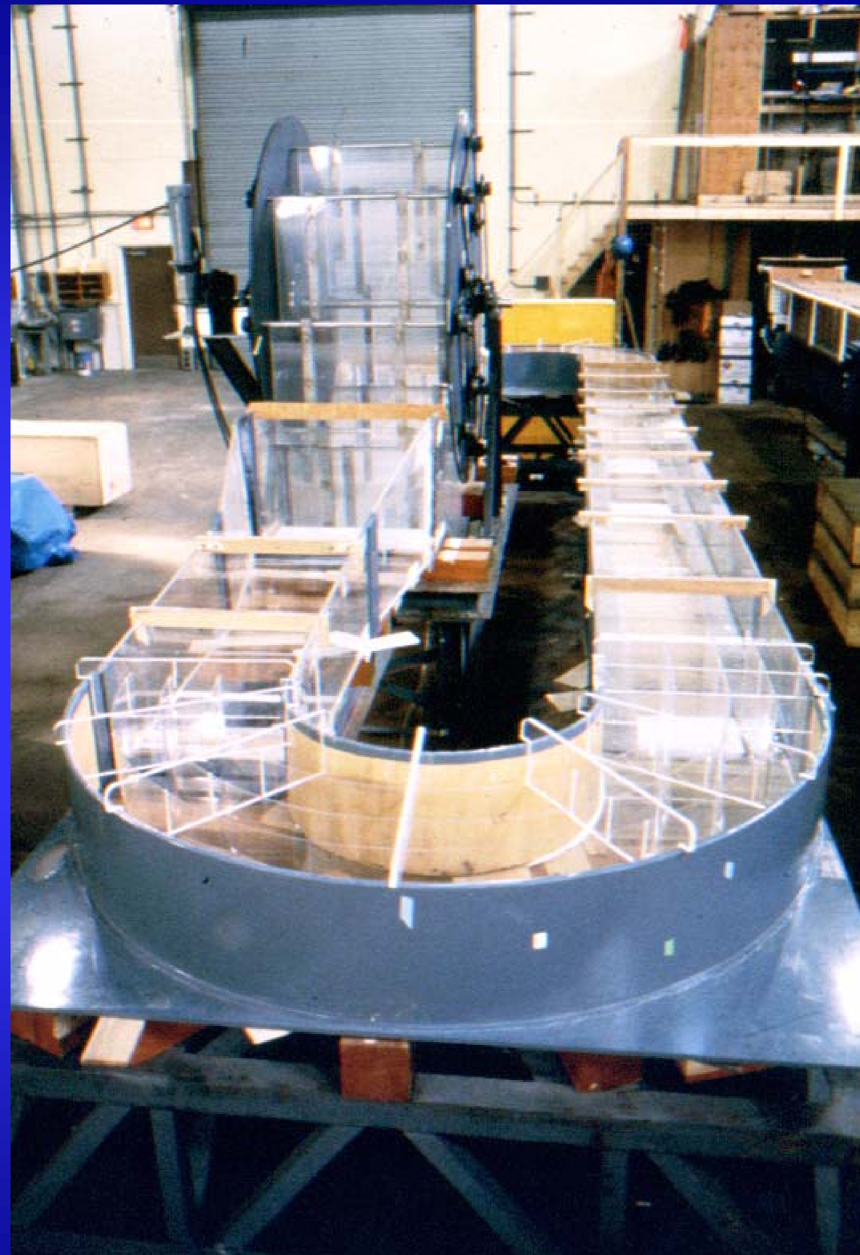
PROBABLY NOT:

1) organic extraction of natural tubes results in loss of activity
2) FFAs are only component in organic extract that induces
3) Larvae of reef-building and non-reef-building species do not respond to FFAs or are deterred from settlement
4) Natural sand tubes of non-responsive, non-reef-building species has 1/10th the concentration of FFAs



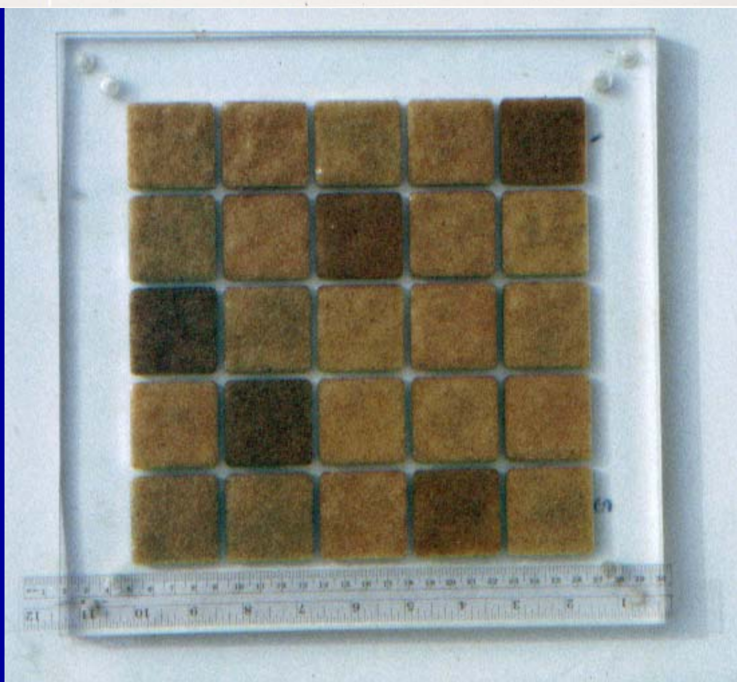


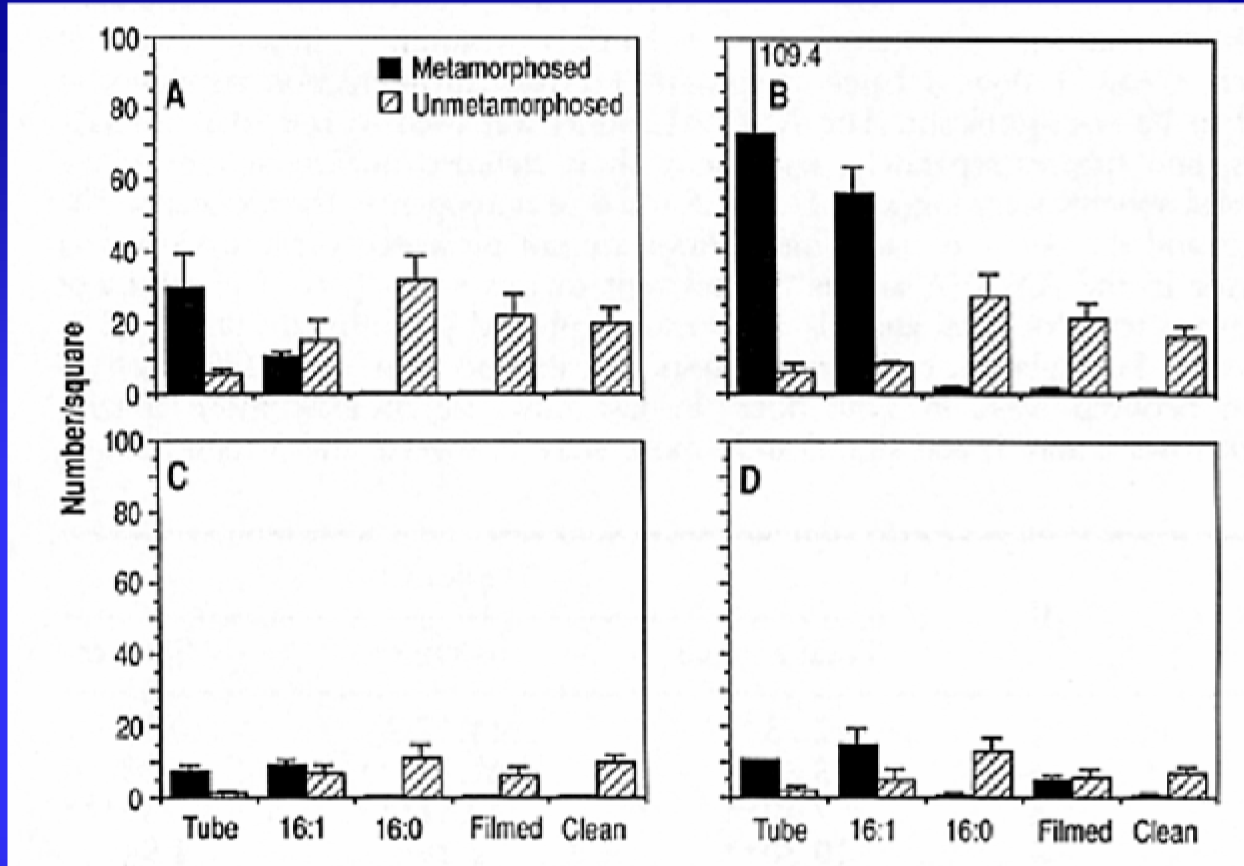
UPSTREAM
TURNING
VANES
CROSS-STREAM SUPPORTS
DOWNSTREAM
TURNING
VANES
50cm
30cm
10cm
FLUME BOTTOM
FALSE BOTTOM
SEDIMENT ARRAY
0.25m
1.65m
2.51m
0.5m
1.50m



SAND TREATMENTS

1. *TUBE - from adult worm tubes
2. FILMED - control for TUBE
3. *16:1 - coated with inductive FFA
4. 16:0 - coated with non-inductive FFA
5. CLEAN - control for treatments 1-4

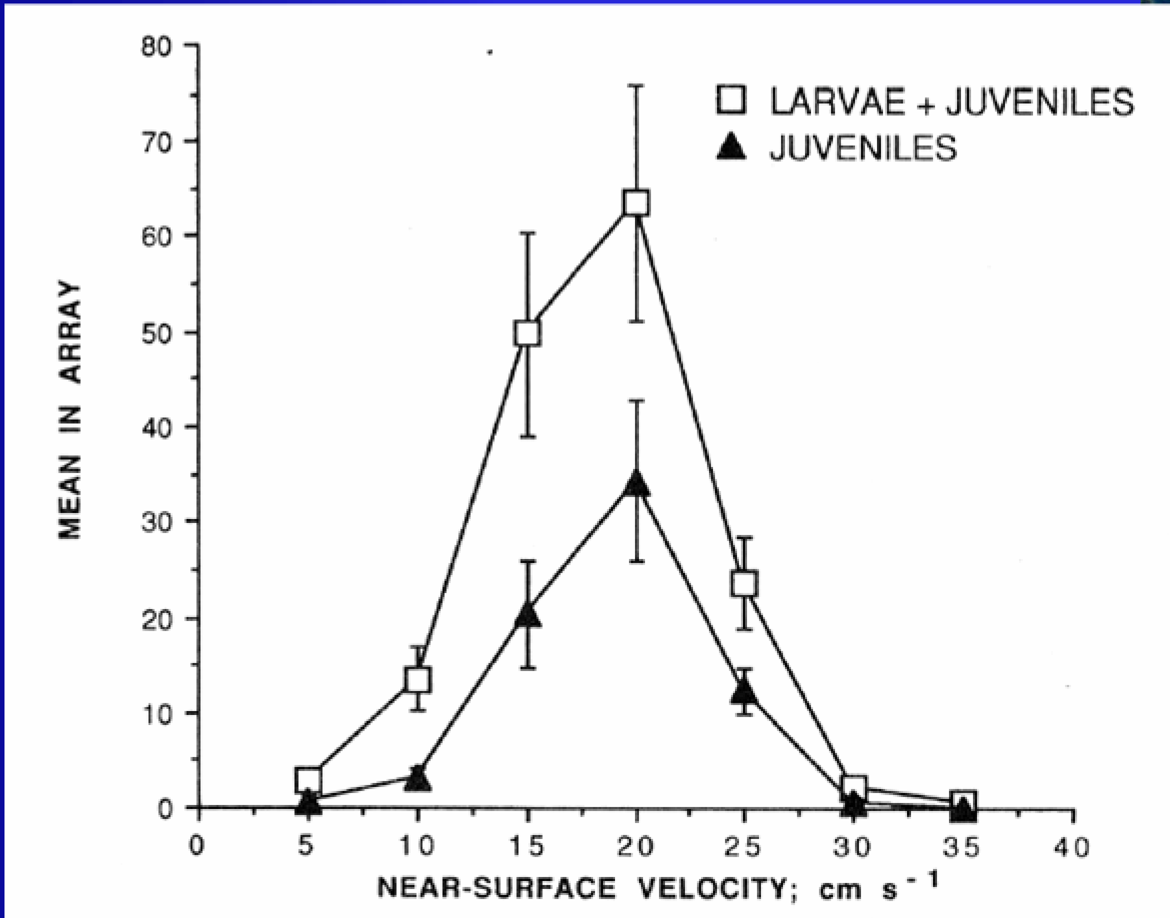




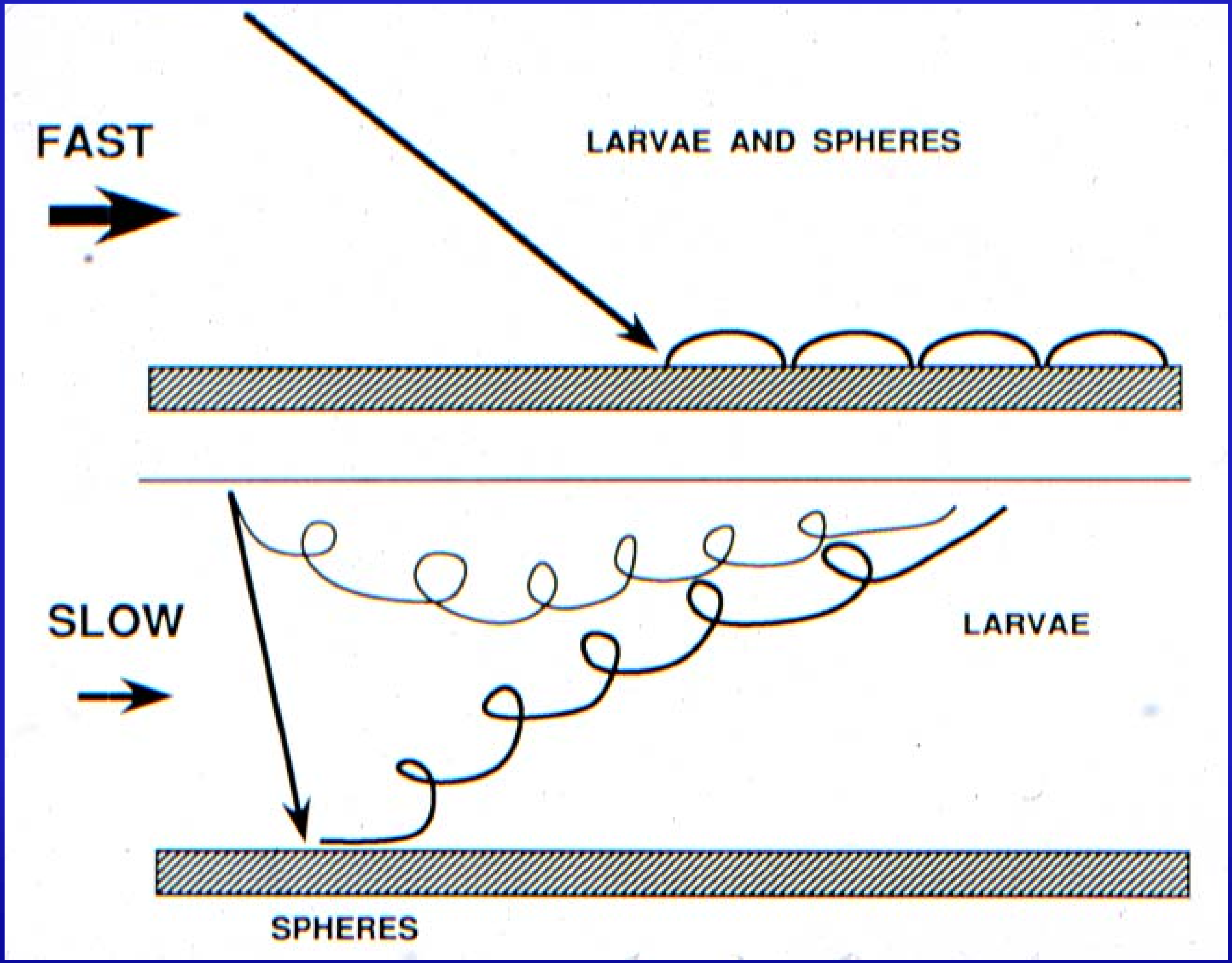
Source of variation	df	*F* values		
		Total animals	Juveniles	Spheres
Flow	1	22.75*	14.17	0.17
Treatment	4	3.39	161.42***	1.33
Row	4	7.40**	19.52***	23.56***
Column	4	10.30**	2.24	1.94
Flow × treatment	4	2.08	7.66**	0.98
Flow × row	4	4.89*	5.74*	26.78***
Flow × column	4	4.96*	0.70	0.66
Flow × batch × treatment	8	2.41*	1.61	1.11
Flow × batch × row	8	3.74***	0.91	0.31
Flow × batch × column	8	0.76	0.95	1.62
Error	72			

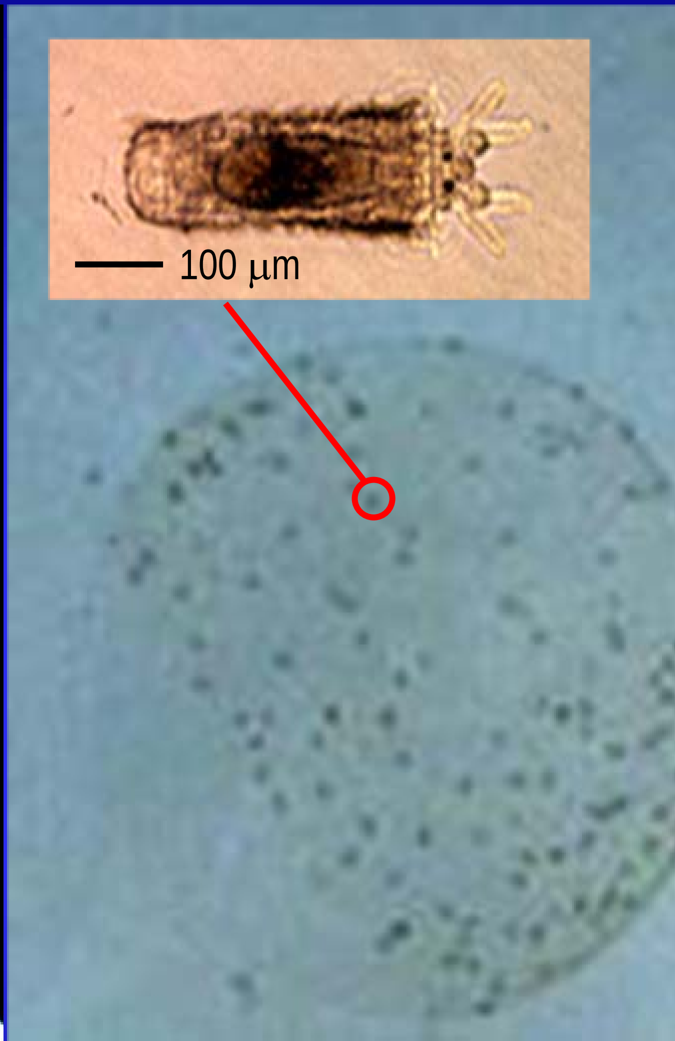
*$P \leq 0.05$. **$P \leq 0.01$. ***$P \leq 0.001$.

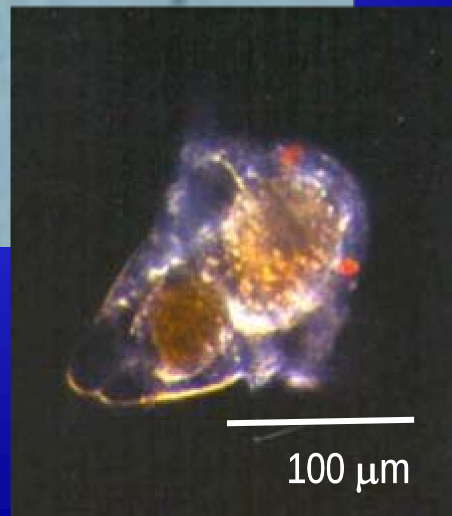
Limnol. Oceanogr., 38(8), 1993, 1730–1740



Larvae are not passive! Behavior is important.




100 µm


100 µm

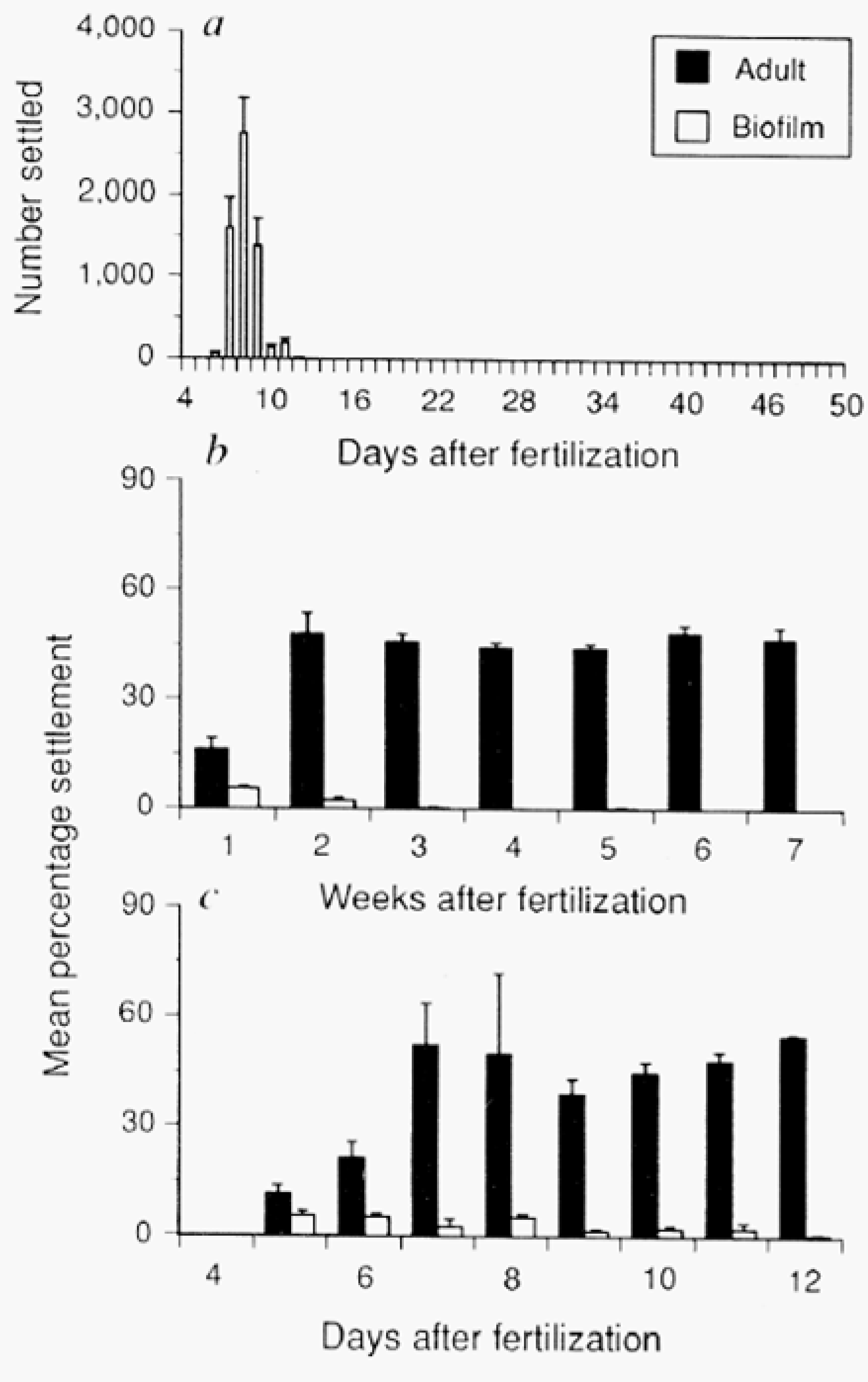


FIG. 2 Settlement of *H. dianthus* when the whole population was exposed to biofilmed slides daily, but only samples were exposed to adult slides. *a*, Number of founding settlers ($n = 3$, + 1 s.e.) from daily whole-population assays of biofilmed slides. *b*, Weekly mean percentage settlement ($n = 12$, + 1 s.e.) in sample assays of biofilmed and adult slides. Sample assays were conducted daily for the first 14 days, and weekly thereafter. *c*, Daily mean percentage settlement for the first week, a weekly mean of which is shown in *b*.

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