

## NOTE

**The paradox of diatom-copepod interactions\***

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**ABSTRACT:** Traditionally, diatoms have been associated with productive pelagic food chains that lead, through suspension-feeding planktonic copepods, to top consumers and important fisheries. Here, 15 laboratories located worldwide in 12 different countries and representing a variety of marine, estuarine and freshwater environments present strong evidence that diatom diets are in fact inferior for copepod reproduction. When fed to females of 16 copepod species, all but 1 of the 17 diatoms examined significantly reduced egg production rates or egg viability compared to non-diatom controls. These effects are hypothesized to influence copepod recruitment patterns and the flow of energy in marine food webs.

**KEY WORDS:** Diatom-copepod interactions · Copepod recruitment · Food webs

The 'classic' pelagic food web refers to the widely held concept of a trophic linkage between outbursts of diatom-rich phytoplankton, copepod production and fish (Runge 1988, Cushing 1989, Legendre 1990). The spring diatom bloom, for example, is considered to

initiate and support the cycle of secondary production and growth of fish larvae that depend predominantly on the egg and naupliar stages of planktonic copepods, the dominant constituents of the zooplankton in most oceanic regions, for food (Turner 1984, Mann 1993). The stratified waters of the oligotrophic or post-bloom temperate ocean, on the other hand, support a flagellate-dominated, microbial production, which has traditionally been considered to be ineffectively transferred to the mesozooplankton and fish (Cushing 1989). It has long been known that many copepod species feed on diatoms in the sea (Lebour 1922, Marshall & Orr 1955). However, the importance of diatoms as a dominant and high quality food source for copepod production has recently been questioned (Kleppel et al. 1991, Kleppel 1993). For example, new studies have reported that some diatom species induce copepod egg mortality by blocking embryogenesis (Poulet et al. 1995, Ianora et al. 1996, Uye 1996). The implications of these results challenge the traditional view of the role of diatoms in the pelagic food web.

Here, we report observations designed to determine whether the inhibitory effects of diatoms on copepod reproduction are indeed a widespread phenomenon. Using the same protocols described in detail in Poulet

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et al. (1995) and Uye (1996), 15 laboratories located worldwide have examined the reproductive response of a number of copepod species to different diatom species, representing a variety of temperate and sub-arctic freshwater, estuarine, and coastal ocean environments (see Table 1). The reproductive response of copepods to various food treatments was quantified by incubating adult females in containers holding 150 to 1000 ml, 0.45  $\mu\text{m}$  filtered seawater enriched with diatom or non-diatom (control, usually a dinoflagellate) diets. Algae were cultured in F/2 (diatoms) and K (non-diatoms) media (Guillard & Ryther 1962, Keller et al. 1967) and were given in excess ( $10^2$  to  $10^5$  cells  $\text{ml}^{-1}$ ) to copepods. Experiments ran for 4 to 40 d, depending on the copepod species and diets. Each day, copepods were transferred to new containers with fresh media and eggs were counted and left undisturbed for 48 to 72 h to determine hatching success. Details of preparation of phytoplankton extracts are given elsewhere (Poulet et al. 1994, Uye 1996). Tests demonstrating that culture media, bacteria in cultures and anoxia did not affect hatching had already been conducted (Ivanora et al. 1996, Uye 1996).

Among the 37 diatom-copepod combinations examined, there were 4 categories of responses (Table 1, Fig. 1). Except for 1 combination (Category IV), where there was no negative effect, diatoms supported either lower copepod fecundity (Category III) or hatching success (Category II) or both (Category I), when compared to non-diatom diets ( $p < 0.01$ ). Thus, while diatoms may provide a source of energy and materials for copepod growth (Vidal 1980), they often reduce fecundity and/or hatching success. These observations constitute the paradox of diatom-copepod interactions in the pelagic food web. How can diatoms support copepod development yet depress their reproductive potential? The results in Table 1 show that diatoms reduced fecundity, on average, by 87% (Categories I and III) and hatching success by 80% (Categories I and II) with time. Non-diatom diets in controls (Table 2) induced negligible changes in both fecundity (+16%) and hatching success (-4%). Among cultured clones, the same diatom species showed considerable intraspecific differences in their impact (e.g. *Skeletonema costatum*, *Phaeodactylum tricornerutum*), reflecting species-specific feeding behaviors or variable intracellular composition of the algae. For example, *S. costatum* reduced fecundity and hatching in *Acartia clausi*, fecundity but not hatching in *Calanus helgolandicus*, and neither of the two in *C. finmarchicus*.

Chaudron et al. (1996) have shown that a decrease in egg viability was significantly correlated to diatom cell concentrations in diets. In the present study, hatching success was affected at even lower diatom concentrations of  $10^2$  cells  $\text{ml}^{-1}$  (Fig. 2). In temperate waters, cell

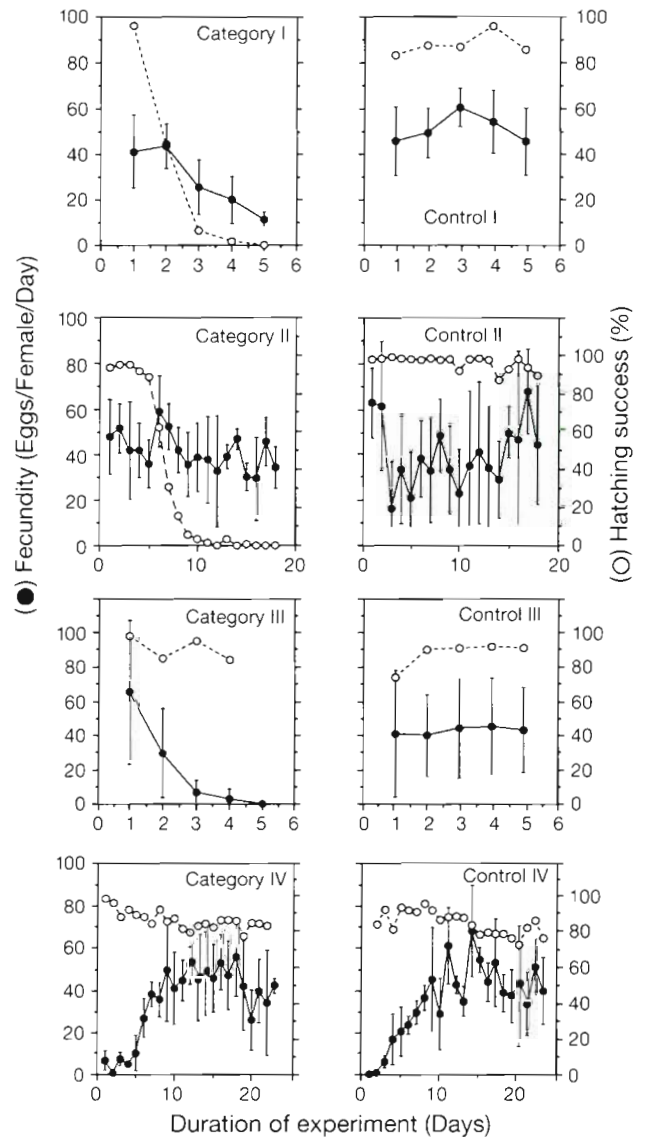


Fig. 1 Variations of egg production and hatching rates induced by diatoms ingested by copepod females maintained for several days in dense food cultures (range of concentrations in diets:  $10^3$  to  $10^5$  cells  $\text{ml}^{-1}$ ). Selected combinations of copepod + diatom and non-diatom species, representative of the data sets in Tables 1 & 2, are: Category I, *Eurytemora affinis* + *Melosira granulata*; Category II, *Calanus pacificus* + *Ditylum brightwellii*; Category III, *Temora stylifera* + *Skeletonema costatum*; and Category IV, *Calanus finmarchicus* + *Skeletonema costatum*. Control diets in these experiments were: I, the flagellate *Cryptomonas tetrapyrenoidosa*; and II, III and IV, the dinoflagellate *Prorocentrum minimum*. With these non-diatom diets in concentrations of  $10^4$  to  $10^5$  cells  $\text{ml}^{-1}$ , both fecundity and hatching were normal. Results are means of 5 to 20 replicate tests, vertical bars are standard deviations

densities during diatom blooms generally range from  $10^2$  to  $10^4$  cells  $\text{ml}^{-1}$ . For example, in the St. Lawrence Estuary, the diatom *Thalassiosira nordenskioldii* is

Table 1. Synopsis of feeding/reproduction experiments: A total of 17 diatom and 16 copepod species, representative of a variety of worldwide temperate and subarctic freshwater (F), estuarine (E) and coastal ocean (C) environments, were screened. Data for fecundity and hatching success are average values measured at the start and end of the incubations in a minimum of 3 replicate batches, showing the variation in time of the effects of diatoms on copepod reproduction. Level of significance of the diatom effect between treatments and controls (e.g. non-diatom diets) in categories I to III was  $p < 0.01$ . No., rank (for comparison with Table 2)

Cate- gory	Diatom effect	Fecundity (eggs female <sup>-1</sup> d <sup>-1</sup> )		Hatching success (%)		Duration of incubation (d)	No. of cases observed in each category	Copepod + diatom combination	No.	Location and type of environment
		Start	End	Start	End					
I	Reduced both fecundity and hatching	12	8	75	38	10	18	<i>Acartia clausi</i> + <i>Skeletonema costatum</i>	1	Greece, Aegean Sea (C)
		1.5	0.7	95	17	9		<i>Acartia clausi</i> + <i>Phaeodactylum tricornutum</i>	2	France, English Channel (C)
		15	10	60	25	20		<i>Acartia clausi</i> + <i>Thalassiosira rotula</i>	3	Italy, Bay of Naples (C)
		54	25	88	55	5		<i>Acartia grani</i> + <i>Chaetoceros gracilis</i>	4	Spain, Alboran Sea (C)
		22	3	88	50	12		<i>Acartia steueri</i> + <i>Thalassiosira weissflogii</i>	5	South Korea, East Japan Sea (E)
		201	1	40	0	4		<i>Acartia tonsa</i> + <i>Chaetoceros debilis</i>	6	Argentina, Bahía Blanca Estuary (E)
		46	3	100	4	12		<i>Boeckella triarticulata</i> + <i>Cyclotella</i> sp.	7	New Zealand, Quarry Pond (F)
		15	2	50	0	23		<i>Calanus finmarchicus</i> + <i>Navicula</i> sp.	8	Canada, St. Lawrence Estuary (E)
		35	5	90	15	12		<i>Calanus helgolandicus</i> + <i>Phaeodactylum tricornutum</i>	9	France, English Channel (C)
		58	11	79	13	10		<i>Centropages hamatus</i> + <i>Thalassiosira weissflogii</i>	10	France, English Channel (C)
		100	22	92	0	8		<i>Centropages typicus</i> + <i>Phaeodactylum tricornutum</i>	11	France, English Channel (C)
		60	5	80	0	10		<i>Centropages typicus</i> + <i>Phaeodactylum tricornutum</i>	12	Italy, Bay of Naples (C)
		100	5	90	0	10		<i>Centropages typicus</i> + <i>Thalassiosira rotula</i>	13	Italy, Bay of Naples (C)
		35	0	98	0	10		<i>Eurytemora affinis</i> + <i>Melosira granulata</i>	14	Japan, Ohnuma Lake (F)
		19	9	88	6	10		<i>Temora longicornis</i> + <i>Thalassiosira weissflogii</i>	15	France, English Channel (C)
		18	1	94	43	10		<i>Temora longicornis</i> + <i>Phaeodactylum tricornutum</i>	16	France, English Channel (C)
		39	19	99	10	13		<i>Temora stylifera</i> + <i>Chaetoceros curvisetum</i>	17	Italy, Bay of Naples (C)
		38	2	100	0	15		<i>Temora stylifera</i> + <i>Phaeodactylum tricornutum</i>	18	Italy, Bay of Naples (C)
II	Reduced hatching but not fecundity	60	60	90	66	6	11	<i>Calanus chilensis</i> + <i>Navicula cryptocephala</i>	19	Chile, South Pacific (C)
		2	40	95	12	23		<i>Calanus finmarchicus</i> + <i>Thalassiosira nordenskioldii</i>	20	Canada, St. Lawrence Estuary (E)
		18	20	90	20	7		<i>Calanus helgolandicus</i> + <i>Thalassiosira rotula</i>	21	France, English Channel (C)
		2	15	90	20	17		<i>Calanus helgolandicus</i> + <i>Thalassiosira weissflogii</i>	22	France, English Channel (C)
		39	48	94	1	17		<i>Calanus pacificus</i> + <i>Chaetoceros difficilis</i>	23	USA, North Pacific (C)
		64	68	90	38	17		<i>Calanus pacificus</i> + <i>Thalassiosira weissflogii</i>	24	USA, North Pacific (C)
		48	34	94	0	17		<i>Calanus pacificus</i> + <i>Ditylum brightwellii</i>	25	USA, North Pacific (C)
		41	38	60	8	11		<i>Eucyclops mucronoides</i> + <i>Nitzschia palea</i>	26	P. R. China, West Lake (F)
		30	30	60	9	11		<i>Eucyclops mucronoides</i> + <i>Synedra acus</i>	27	P. R. China, West Lake (F)
		25	20	45	9	10		<i>Paracyclops affinis</i> + <i>Nitzschia palea</i>	28	P. R. China, West Lake (F)
		40	38	74	12	20		<i>Temora stylifera</i> + <i>Thalassiosira rotula</i>	29	Italy, Bay of Naples (C)
III	Reduced fecundity but not hatching	6	2	63	60	10	7	<i>Acartia clausi</i> + <i>Cylindrotheca closterium</i>	30	Italy, Adriatic Sea (C)
		10	2	90	88	23		<i>Calanus finmarchicus</i> + <i>Chaetoceros debilis</i>	31	Canada, St. Lawrence Estuary (E)
		20	5	80	90	40		<i>Calanus helgolandicus</i> + <i>Cylindrotheca closterium</i>	32	France, English Channel (C)
		25	2	80	80	30		<i>Calanus helgolandicus</i> + <i>Skeletonema costatum</i>	33	France, English Channel (C)
		2	0.6	97	90	10		<i>Eurytemora affinis</i> + <i>Cylindrotheca closterium</i>	34	France, Gironde Estuary (E)
		2	0.6	97	70	10		<i>Eurytemora affinis</i> + <i>Phaeodactylum tricornutum</i>	35	France, Gironde Estuary (E)
		65	3	98	84	4		<i>Temora stylifera</i> + <i>Skeletonema costatum</i>	36	Italy, Bay of Naples (C)
IV	No negative effect	7	46	85	70	15	1	<i>Calanus finmarchicus</i> + <i>Skeletonema costatum</i>	37	Canada, St. Lawrence Estuary (E)

Table 2. Combinations of copepod and non-diatom diets used in controls in concentrations ranging from  $10^4$  to  $10^5$  cells  $ml^{-1}$ . Rank and combination number same as in Table 1. Data for fecundity and hatching success are average values measured at the start and end of the incubations in a minimum of 3 replicate batches. N.A.: natural assemblages of phytoplankton at time of incubation were: for No. 1, 40% diatoms; for Nos. 2, 10, 11, 15 and 16,  $\geq 50\%$  diatoms; for No. 19, unidentified seston; and for Nos. 26, 27 and 28, around 12% diatoms. U.F.: unidentified flagellates

Copepod + non-diatom combination (controls)	No.	Fecundity (eggs female <sup>-1</sup> d <sup>-1</sup> )		Hatching success (%)	
		Start	End	Start	End
<i>Acartia clausi</i> + N.A.	1	10	10	100	100
<i>Acartia clausi</i> + N.A.	2	15	–	95	–
<i>Acartia clausi</i> + <i>Prorocentrum minimum</i>	3	20	15	80	70
<i>Acartia grani</i> + <i>Amphidinium</i> sp.	4	23	4	82	76
<i>Acartia steueri</i> + <i>Isochrysis galbana</i>	5	8	3	95	100
<i>Acartia tonsa</i> + U.F.	6	201	–	40	–
<i>Boeckella triarticulata</i> + <i>Cryptomonas</i> sp.	7	47	37	100	31
<i>Calanus finmarchicus</i> + <i>Prorocentrum micans</i>	8	0	40	85	88
<i>Calanus helgolandicus</i> + <i>Prorocentrum micans</i> and <i>P. minimum</i>	9	15	15	95	95
<i>Centropages hamatus</i> + N.A.	10	60	–	100	–
<i>Centropages typicus</i> + N.A.	11	100	–	92	–
<i>Centropages typicus</i> + <i>Prorocentrum minimum</i>	12	20	20	80	80
<i>Centropages typicus</i> + <i>Prorocentrum minimum</i>	13	20	20	80	80
<i>Eurytemora affinis</i> + <i>Cryptomonas tetraperynoidosa</i>	14	45	45	80	80
<i>Temora longicornis</i> + N.A.	15	90	–	90	–
<i>Temora longicornis</i> + N.A.	16	18	–	94	–
<i>Temora stylifera</i> + <i>Prorocentrum minimum</i>	17	32	40	98	99
<i>Temora stylifera</i> + <i>Prorocentrum minimum</i>	18	32	40	98	99
<i>Calanus chilensis</i> + N.A.	19	60	70	90	100
<i>Calanus finmarchicus</i> + <i>Prorocentrum micans</i>	20	0	40	88	85
<i>Calanus helgolandicus</i> + <i>Prorocentrum minimum</i> and <i>P. micans</i>	21	15	15	95	95
<i>Calanus helgolandicus</i> + <i>Prorocentrum minimum</i> and <i>P. micans</i>	22	15	15	95	95
<i>Calanus pacificus</i> + <i>Prorocentrum minimum</i>	23	63	68	98	94
<i>Calanus pacificus</i> + <i>Prorocentrum minimum</i>	24	63	68	98	94
<i>Calanus pacificus</i> + <i>Prorocentrum minimum</i>	25	63	68	98	94
<i>Eucyclops mucruroides</i> + N.A.	26	40	39	61	61
<i>Eucyclops mucruroides</i> + N.A.	27	40	39	61	61
<i>Paracyclops affinis</i> + N.A.	28	40	39	45	45
<i>Temora stylifera</i> + <i>Prorocentrum minimum</i>	29	40	40	90	90
<i>Acartia clausi</i> + <i>Prorocentrum minimum</i>	30	6	2	70	62
<i>Calanus finmarchicus</i> + <i>Prorocentrum micans</i>	31	0	40	88	85
<i>Calanus helgolandicus</i> + <i>Prorocentrum minimum</i> and <i>P. micans</i>	32	15	15	95	95
<i>Calanus helgolandicus</i> + <i>Prorocentrum minimum</i> and <i>P. micans</i>	33	15	15	95	95
<i>Eurytemora affinis</i> + <i>Dunaliella tertiolecta</i>	34	7	14	71	100
<i>Eurytemora affinis</i> + <i>Dunaliella tertiolecta</i>	35	7	14	71	100
<i>Temora stylifera</i> + <i>Prorocentrum minimum</i>	36	40	40	90	90
<i>Calanus finmarchicus</i> + <i>Prorocentrum micans</i>	37	0	40	86	85

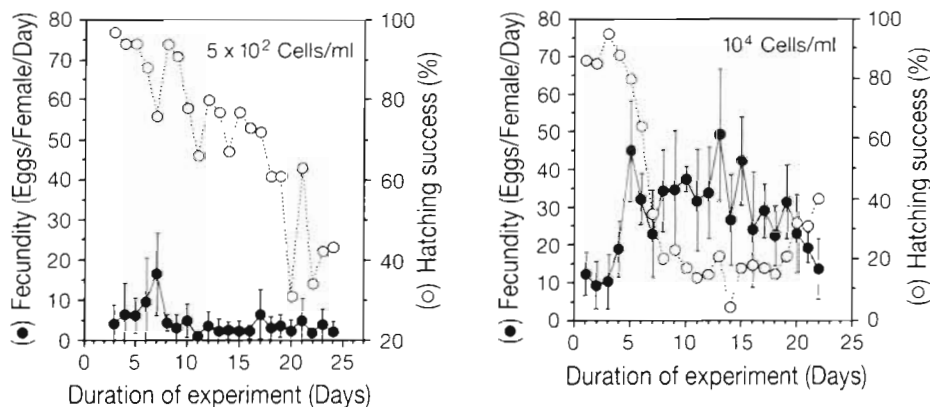


Fig. 2. *Calanus finmarchicus* + *Thalassiosira nordenskioldii*. Mean daily fecundity with standard deviations and hatching success of eggs spawned by females fed with a diatom diet at 2 different concentrations similar to blooms of *T. nordenskioldii* naturally occurring in the St. Lawrence Estuary. Results are means of 4 replicate experiments

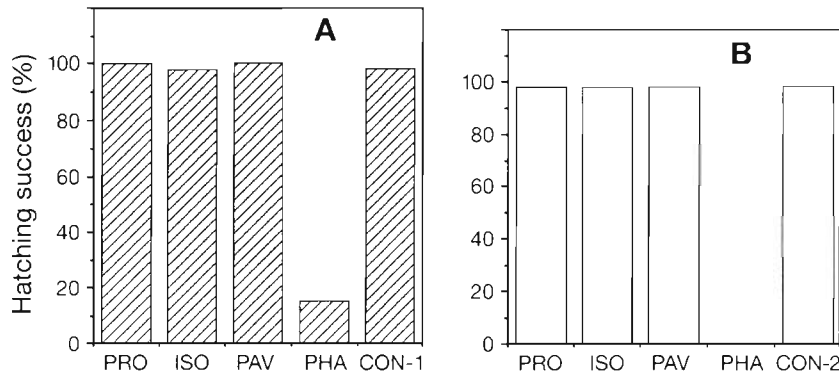


Fig. 3. (A) Comparison between the hatching rates of eggs spawned by *Calanus helgolandicus* fed with non-diatom diets (PRO: *Prorocentrum minimum*; ISO: *Isochrysis galbana*; PAV: *Pavlova lutheri*) and a diatom diet (PHA: *Phaeodactylum tricorutum*) at the same concentration ( $10^5$  cells  $\text{ml}^{-1}$ ). Rates were estimated at the end of an 8 d incubation period. CON-1: controls on Day 4 (starved females in filtered seawater stopped spawning beyond this time). For each treatment, triplicate batches of 5 females each were incubated at  $12^\circ\text{C}$  in 300 ml filtered seawater enriched with algae, renewed every day, under a 12 h:12 h day-night cycle. (B) Comparison between the hatching rates of normal, 5 min old eggs, produced by wild *C. helgolandicus* females, that were incubated in extracts of different algae (PRO, ISO, PAV and PHA; concentrations in extracts equivalent to  $10^7$  cells  $\text{ml}^{-1}$ ). Extracts of dense phytoplankton cultures were prepared as before (see Poulet et al. 1994, Uye 1996 for details). Batches of 40 to 50 eggs were incubated in 1 ml of each algal extract, or filtered seawater (CON-2:controls), at  $12^\circ\text{C}$  for 24 h

very common and regularly dominates the biomass during the phytoplankton blooms (Levasseur et al. 1984, 1994). Natural diatom concentrations (same as given in Fig. 2) during bloom periods may thus be sufficient to induce  $\leq 50\%$  embryonic mortality and demographic failure in 5 d or more, assuming that no compensatory mechanisms, such as feeding avoidance or enzymatic destruction of the inhibitor, occur.

What is it about diatoms that modifies copepod reproduction? Is this effect due to missing essential nutrients (hypothesis 1) or to the presence of inhibitory compounds (hypothesis 2)? Categories I to III may reflect lower nutritional quality of some diatom species (i.e. as a group, diatoms contain less lipids, carbohydrates and proteins per cell volume than dinoflagellates; Hitchcock 1982) even though the 'ad libitum' diets used in these experiments should be able to compensate for any nutrient deficiency. Alternatively, a more insidious possibility, for which there is mounting evidence (Poulet et al. 1995, Uye 1996, M. Starr, J. A. Runge & J. C. Therriault unpubl.), is that the cells of many diatom species contain an as yet unidentified inhibitory compound that blocks copepod embryogenesis when ingested by the females. This 'inhibition' may represent a defense mechanism by diatoms against grazing by copepod offspring, thereby prolonging diatom blooms. The results shown in Fig. 3 allow us to distinguish more clearly between the 2 hypotheses. Among 4 diets tested on *Calanus helgolandicus*, the diatom *Phaeodactylum tricorutum* (PHA) was the only one capable of blocking hatching success after 8 d of incubation at constant food concentrations (Fig. 3A). Taking polyunsaturated fatty acids

(PUFAs) as a reference to qualify one of the possible missing essential nutrients in the diets (i.e. when they are lacking, such deficiencies are known to be detrimental to growth, fecundity and egg development; Jones et al. 1979, Kjörsvik et al. 1990, Jónasdóttir 1994, Jónasdóttir & Kjørboe 1996), PHA lacks the essential PUFAs 18:5 $\omega$ 3 and 22:1 $\omega$ 11, which are also lacking in the other diets (22:1 $\omega$ 11 is missing in PRO, ISO and PAV, while 18:5 $\omega$ 3 is missing in PAV; Ackman et al. 1968, Nichols et al. 1984, Volkman et al. 1989). Notwithstanding this, hatching success was much higher with the non-diatom diets (Fig. 3A). Moreover, if a deficiency in PUFAs was responsible for low hatching rates, starved females (controls: CON-1), as well, should have spawned high proportions of non-viable eggs, assuming that starvation is equivalent to severe PUFA deficiency. Starved females stopped spawning on Day 4 due to food shortage; however, 100% eggs hatched from Day 1 to 4, showing that energy limitation and/or essential nutrient deficiency affected fecundity but not hatching. In order to further distinguish between hypotheses 1 and 2, extracts of the same algal cultures were tested on normal, freshly-spawned eggs, produced by wild *C. helgolandicus* females (Fig. 3B; controls: CON-2). Results showed that hatching of these eggs was blocked only with diatom extracts, suggesting that inhibition of embryonic development was due to factors other than nutrient deficiency.

Measurements of egg viability in the sea have only recently been initiated; the available data indicate that egg hatching success is variable, from 20 to 95%, over the course of the reproductively active season (Ianora

et al. 1992, Ianora & Poulet 1993, Laabir et al. 1995, Pond et al. 1996). Hence, hatching success cannot be ruled out as an important factor determining the timing and duration of copepod recruitment. It would be worth examining whether diatom blooms could actually inhibit population growth even if copepod productivity during the spring bloom is apparently high. This may explain several field observations, both old and new, of the relationship between primary production cycles and copepod reproduction, such as the disappearance of the April 1934 egg cohort recorded in Loch Striven, Scotland (Marshall & Orr 1995). Recent studies show that mesoplankton in temperate oceans are omnivorous, feeding on dinoflagellates and ciliates, especially after the spring diatom bloom is past, and that feeding on dinoflagellates and ciliates can sustain egg production (Kleppel et al. 1991, Sanders & Wickham 1993, Ohman & Runge 1994). A close examination of growth periods in fish larvae indicates that copepod recruitment and prey productivity for fish larvae may at times be more favorable in post-bloom conditions (e.g. when the microbial food web is established) than during diatom blooms, as suggested for *Calanus finmarchicus* (and fish larvae feeding on *C. finmarchicus*) in the Gulf of St. Lawrence (Runge & de Lafontaine 1996).

Although it is well established that copepods feed on mixed diets at sea, it is also known from fecal pellet analysis that diatoms constitute a large fraction of the diet in certain periods of the year (Urban et al. 1992, Laabir et al. 1995). The present results show that a majority of diatoms cannot as the sole food support high egg production and hatching rates. Also, both high and low diatom concentrations can negatively impact copepod reproduction (Fig. 2; Chaudron et al. 1996). This brings into question the relative roles of diatom blooms and the more complex microbial trophic pathways in supplying energy and materials for copepod growth and reproduction. These new data are further evidence for revision of the traditional view of the significance of diatoms in the pelagic ecosystem.

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