NOTE

The paradox of diatom-copepod interactions[*]

Syuhei Ban[1], Carolyn Burns[2], Jacques Castel[3], Yannick Chaudron[4], Epaminondas Christou[5],
Ruben Escribano[6], Serena Fonda Umani[7], Stephane Gasparini[3], Francisco Guerrero Ruiz[8],
Monica Hoffmeyer[9], Adrianna Ianora[10], Hyung-Ku Kang[11], Mohamed Laabir[4], Arnaud Lacoste[4],
Antonio Miralto[10], Xiuren Ning[12], Serge Poulet[4,**], Valeriano Rodriguez[13], Jeffrey Runge[14],
Junxian Shi[12], Michel Starr[14], Shin-ichi Uye[15,***], Yijun Wang[12]

[1]Plankton Laboratory, Faculty of Fisheries, Hokkaido University, Hokkaido, Japan
[2]Department of Zoology, University of Otago, Dunedin, New Zealand
[3]Centre d'Océanographie et de Biologie Marine, Arcachon, France
[4]Station Biologique, CNRS, BP 74, F-29682 Roscoff, France
[5]National Centre for Marine Research, Institute of Oceanography, Hellinikon, Athens, Greece
[6]Universidad de Antofagasta, Facultad de Recursos del Mar, Instituto de Investigaciones Oceonologicas, Antofagasta, Chile
[7]Laboratorio di Biologia Marina, University of Trieste, via E. Weiss 1, I-34127 Trieste, Italy
[8]Departamento de Biologia Animal Vegetal y Ecologia, Facultad de Ciencias Experimentales, Jaen, Spain
[9]Instituto Argentino de Oceanografia, Av. Alem 53, 8000 Bahia Blanca, Argentina
[10]Stazione Zoologica, Villa comunale 1, I-80121 Napoli, Italy
[11]Korea Iter-University Institute of Ocean Science, National Fisheries University of Pusan, Pusan, South Korea
[12]Second Institute of Oceanography, State Oceanic Administration, 310012 Hangzhou, Peoples Republic of China
[13]Departamento de Geologia y Ecologia, Faculdad de Ciencias, Malaga, Spain
[14]Institut Maurice-Lamontagne, Pêches et Océans Canada, BP 1000, Mont-Joli, Québec, Canada G5H 3Z4
[15]College of Oceanic & Atmospheric Sciences, Oregon University, Corvallis, Oregon, USA

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

---

[*]Authors given in alphabetic order.
[**]Addressee for correspondence. E-mail: poulet@sb-roscoff.fr
[***]Present address: Faculty of Applied Biological Science, Hiroshima University, Higashi-Hiroshima, Japan

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 µm 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 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 (Ianora 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 intra-specific differences in their impact (e.g. *Skeletonema costatum*, *Phaeodactylum tricornutum*), 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 ml^{-1} (Fig. 2). In temperate waters, cell
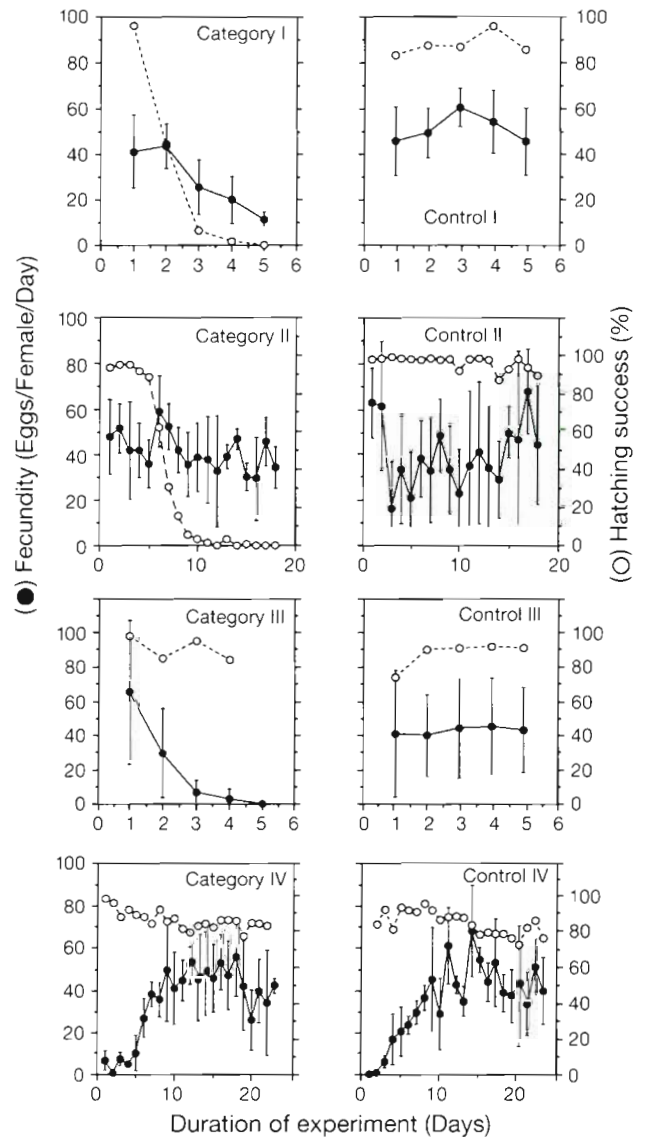

Fig. 1 Variations of egg production and hatching rates induced by diatoms ingested by copepod females maintained for several days in dense food cultures (range of concentrations in diets: 10^3 to 10^5 cells ml^{-1}). Selected combinations of copepod + diatom and non-diatom species, representative of 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 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 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)

Category	Diatom effect	Fecundity (eggs female⁻¹ d⁻¹) Start	End	Hatching success (%) Start	End	Duration of incubation (d)	No. of cases observed in each category	Copepod + diatom combination	No.	Location and type of environment
I	Reduced both fecundity and hatching	12	8	75	38	10	18	Acartia clausi + Skeletonema costatum	1	Greece, Aegean Sea (C)
		1.5	0.7	95	17	9		Acartia clausi + Phaeodactylum tricornutum	2	France, English Channel (C)
		15	10	60	25	20		Acartia clausi + Thalassiosira rotula	3	Italy, Bay of Naples (C)
		54	25	88	55	5		Acartia grani + Chaetoceros gracilis	4	Spain, Alboran Sea (C)
		22	3	88	50	12		Acartia steueri + Thalassiosira weissflogii	5	South Korea, East Japan Sea (E)
		201	1	40	0	4		Acartia tonsa + Chaetoceros debilis	6	Argentina, Bahia Blanca Estuary (E)
		46	3	100	4	12		Boeckella triarticulata + Cyclotella sp.	7	New Zealand, Quarry Pond (F)
		15	2	50	0	23		Calanus finmarchicus + Navicula sp.	8	Canada, St. Lawrence Estuary (E)
		35	5	90	15	12		Calanus helgolandicus + Phaeodactylum tricornutum	9	France, English Channel (C)
		58	11	79	13	10		Centropages hamatus + Thalassiosira weissflogii	10	France, English Channel (C)
		100	22	92	0	8		Centropages typicus + Phaeodactylum tricornutum	11	France, English Channel (C)
		60	5	80	0	10		Centropages typicus + Phaeodactylum tricornutum	12	Italy, Bay of Naples (C)
		100	5	90	0	10		Centropages typicus + Thalassiosira rotula	13	Italy, Bay of Naples (C)
		35	0	98	0	10		Eurytemora affinis + Melosira granulata	14	Japan, Ohnuma Lake (F)
		19	9	88	6	10		Temora longicornis + Thalassiosira weissflogii	15	France, English Channel (C)
		18	1	94	43	10		Temora longicornis + Phaeodactylum tricornutum	16	France, English Channel (C)
		39	19	99	10	13		Temora stylifera + Chaetoceros curvisetum	17	Italy, Bay of Naples (C)
		38	2	100	0	15		Temora stylifera + Phaeodactylum tricornutum	18	Italy, Bay of Naples (C)
II	Reduced hatching but not fecundity	60	60	90	66	6	11	Calanus chilensis + Navicula cryptocephala	19	Chile, South Pacific (C)
		2	40	95	12	23		Calanus finmarchicus + Thalassiosira nordenskioldii	20	Canada, St. Lawrence Estuary (E)
		18	20	90	20	7		Calanus helgolandicus + Thalassiosira rotula	21	France, English Channel (C)
		2	15	90	20	17		Calanus helgolandicus + Thalassiosira weissflogii	22	France, English Channel (C)
		39	48	94	1	17		Calanus pacificus + Chaetoceros difficilis	23	USA, North Pacific (C)
		64	68	90	38	17		Calanus pacificus + Thalassiosira weissflogii	24	USA, North Pacific (C)
		48	34	94	0	17		Calanus pacificus + Ditylum brightwellii	25	USA, North Pacific (C)
		41	38	60	8	11		Eucyclops mucruroides + Nitzschia palea	26	P. R. China, West Lake (F)
		30	30	60	9	11		Eucyclops mucruroides + Synedra acus	27	P. R. China, West Lake (F)
		25	20	45	9	10		Paracyclops affinis + Nitzschia palea	28	P. R. China, West Lake (F)
		40	38	74	12	20		Temora stylifera + Thalassiosira rotula	29	Italy, Bay of Naples (C)
III	Reduced fecundity but not hatching	6	2	63	60	10	7	Acartia clausi + Cylindrotheca closterium	30	Italy, Adriatic Sea (C)
		10	2	90	88	23		Calanus finmarchicus + Chaetoceros debilis	31	Canada, St. Lawrence Estuary (E)
		20	5	80	90	40		Calanus helgolandicus + Cylindrotheca closterium	32	France, English Channel (C)
		25	2	80	80	30		Calanus helgolandicus + Skeletonema costatum	33	France, English Channel (C)
		2	0.6	97	90	10		Eurytemora affinis + Cylindrotheca closterium	34	France, Gironde Estuary (E)
		2	0.6	97	70	10		Eurytemora affinis + Phaeodactylum tricornutum	35	France, Gironde Estuary (E)
		65	3	98	84	4		Temora stylifera + Skeletonema costatum	36	Italy, Bay of Naples (C)
IV	No negative effect	7	46	85	70	15	1	Calanus finmarchicus + Skeletonema costatum	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, ≥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^{-1} d^{-1})		Hatching success (%)	
		Start	End	Start	End
Acartia clausi + N.A.	1	10	10	100	100
Acartia clausi + N.A.	2	1 5	–	95	–
Acartia clausi + *Prorocentrum minimum*	3	20	15	80	70
Acartia grani + *Amphidinium* sp.	4	23	4	82	76
Acartia steueri + *Isochrysis galbana*	5	8	3	95	100
Acartia tonsa + U.F.	6	201	–	40	–
Boeckella triarticulata + *Cryptomonas* sp.	7	47	37	100	31
Calanus finmarchicus + *Prorocentrum micans*	8	0	40	85	88
Calanus helgolandicus + *Prorocentrum micans* and *P. minimum*	9	15	15	95	95
Centropages hamatus + N.A.	10	60	–	100	–
Centropages typicus + N.A.	11	100	–	92	–
Centropages typicus + *Prorocentrum minimum*	12	20	20	80	80
Centropages typicus + *Prorocentrum minimum*	13	20	20	80	80
Eurytemora affinis + *Cryptomonas tetraperynoidosa*	14	45	45	80	80
Temora longicornis + N.A.	15	90	–	90	–
Temora longicornis + N.A.	16	18	–	94	–
Temora stylifera + *Prorocentrum minimum*	17	32	40	98	99
Temora stylifera + *Prorocentrum minimum*	18	32	40	98	99
Calanus chilensis + N.A.	19	60	70	90	100
Calanus finmarchicus + *Prorocentrum micans*	20	0	40	88	85
Calanus helgolandicus + *Prorocentrum minimum* and *P. micans*	21	15	15	95	95
Calanus helgolandicus + *Prorocentrum minimum* and *P. micans*	22	15	15	95	95
Calanus pacificus + *Prorocentrum minimum*	23	63	68	98	94
Calanus pacificus + *Prorocentrum minimum*	24	63	68	98	94
Calanus pacificus + *Prorocentrum minimum*	25	63	68	98	94
Eucyclops mucruroides + N.A.	26	40	39	61	61
Eucyclops mucruroides + N.A.	27	40	39	61	61
Paracyclops affinis + N.A.	28	40	39	45	45
Temora stylifera + *Prorocentrum minimum*	29	40	40	90	90
Acartia clausi + *Prorocentrum minimum*	30	6	2	70	62
Calanus finmarchicus + *Prorocentrum micans*	31	0	40	88	85
Calanus helgolandicus + *Prorocentrum minimum* and *P. micans*	32	15	15	95	95
Calanus helgolandicus + *Prorocentrum minimum* and *P. micans*	33	15	15	95	95
Eurytemora affinis + *Dunaliella tertiolecta*	34	7	14	71	100
Eurytemora affinis + *Dunaliella tertiolecta*	35	7	14	71	100
Temora stylifera + *Prorocentrum minimum*	36	40	40	90	90
Calanus finmarchicus + *Prorocentrum micans*	37	0	40	86	85
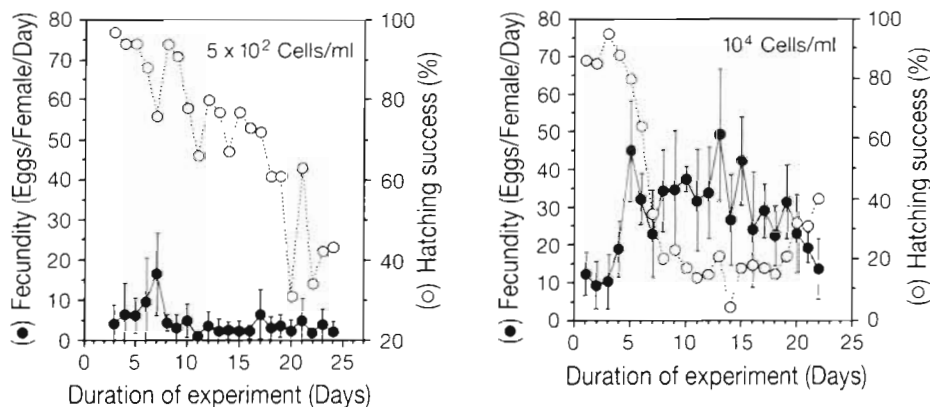
Fig. 2. *Calanus finmarchicus* + *Thalassiosira nordenskioldii*. Mean daily fecundity with standard deviations and hatching success of eggs spawned by females fed with a diatom diet at 2 different concentrations similar to blooms of *T nordenskioldii* naturally occurring in the St. Lawrence Estuary. Results are means of 4 replicate experiments

A

B

Hatching success (%)

100
80
60
40
20
0

PRO ISO PAV PHA CON-1

100
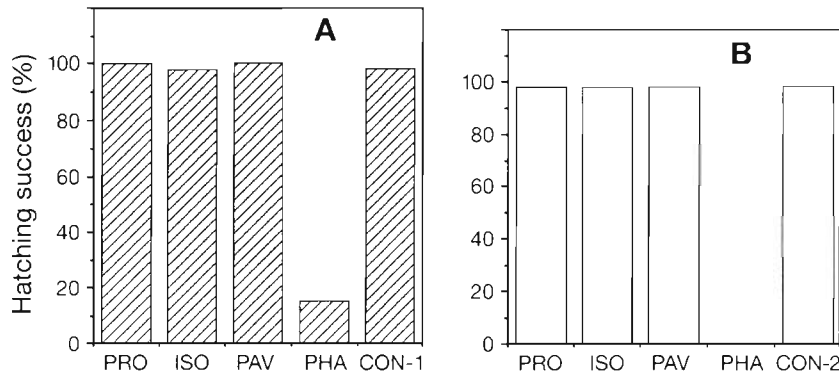80
60
40
20
0

PRO ISO PAV PHA CON-2

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 tricornutum*) at the same concentration (10^5 cells 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°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 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°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 ≤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 tricornutum* (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, Kjørsvik et al. 1990, Jónasdóttir 1994, Jónasdóttir & Kiørboe 1996), PHA lacks the essential PUFAs 18:5ω3 and 22:1ω11, which are also lacking in the other diets (22:1ω11 is missing in PRO, ISO and PAV, while 18:5ω3 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.

LITERATURE CITED

Ackman RG, Tocher CS, Mclachlan J (1968) Marine phytoplankter fatty acids. J Fish Res Bd Can 25:1603–1620

Chaudron Y, Poulet SA, Laabir M, Ianora A, Miralto A (1996) Is hatching success of copepod eggs diatom density-dependent? Mar Ecol Prog Ser 144:185–193

Cushing DH (1989) A difference in structure between eco-systems in strongly stratified waters and those that are only weakly stratified. J Plankton Res 11:1–13

Guillard RRL, Ryther JH (1962) Studies of marine planktonic diatoms. 1. *Cyclotella nana* Hustedt and *Detonula confervacea* (Cleve) Gran. Can J Microbiol 8:229–239

Hitchcock GL (1982) A comparative study of the size-dependent organic composition of marine diatoms and dinoflagellates. J Plankton Res 4:363–377

Ianora A, Mazzochi MG, Grottoli R (1992) Seasonal fluctuations in fecundity and hatching success in the planktonic copepod *Centropages typicus*. J Plankton Res 14:1483–1494

Ianora A, Poulet SA (1993) Egg viability in the copepod *Temora stylifera*. Limnol Oceanogr 38:1615–1626

Ianora A, Poulet SA, Miralto A, Grottoli R (1996) The diatom *Thalassiosira rotula* affects reproductive success in the copepod *Acartia clausi*. Mar Biol 125:279–286

Jónasdóttir SH (1994) Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. Mar Biol 121:67–81

Jónasdóttir SH, Kiørboe T (1996) Copepod recruitment and food composition: do diatoms affect hatching success? Mar Biol 125:743–750

Jones DA, Kanazawa A, Ono K (1979) Studies on the nutritional requirements of larval stages of *Penaeus japonicus* using microencapsulated diets. Mar Biol 54:261–267

Keller MD, Selvin RC, Clauss W, Guillard RRL (1967) Media for the culture of oceanic ultraplankton. J Phycol 23:633–638

Kjørsvik E, Mangor-Jensen A, Holmefjord I (1990) Egg quality in fishes. Adv Mar Biol 26:71–113

Kleppel GS (1993) On the diets of calanoid copepods. Mar Ecol Prog Ser 99:183–195

Kleppel GS, Holliday DV, Pieper RE (1991) Trophic interactions between copepods and microplankton: a question about the role of diatoms. Limnol Oceanogr 36:172–178

Laabir M, Poulet SA, Ianora A, Miralto A, Cueff A (1995) Reproductive response of *Calanus helgolandicus*. II. *In situ* inhibition of embryonic development. Mar Ecol Prog Ser 129:97–105

Lebour MV (1922) The food of plankton organisms. J Mar Biol Assoc UK 12:644–677

Legendre L (1990) The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in oceans. J Plankton Res 12:681–699

Levasseur M, Fortier L, Therriault JC, Harrison PJ (1994) Phytoplankton dynamics in a coastal jet frontal region. Mar Ecol Prog Ser 86:283–295

Levasseur M, Therriault JC, Legendre L (1984) Hierarchical control of phytoplankton succession by physical factors. Mar Ecol Prog Ser 19:211–222

Mann KH (1993) Physical oceanography, food chains, and fish stocks: a review. ICES J Mar Sci 50:105–119

Marshall SM, Orr AP (1955) The biology of a marine copepod, *Calanus finmarchicus* (Gunnerus). Oliver and Boyd, London

Nichols PD, Jones GJ, De Leeuw JW, Johns RB (1984) The fatty acid and sterol composition of two marine dino-flagellates. Phytochemistry 23:1043–1047

Ohman MD, Runge JA (1994) Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. Limnol Oceanogr 39:21–36

Pond D, Harris RG, Head R, Harbour D (1996) Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. Mar Ecol Prog Ser 143:45–63

Poulet SA, Ianora A, Miralto A, Meijer L (1994) Do diatoms arrest embryonic development in copepods? Mar Ecol Prog Ser 111:79–86

Poulet SA, Laabir M, Ianora A, Miralto A (1995) Reproductive response of *Calanus helgolandicus*. I. Abnormal embryonic and naupliar development. Mar Ecol Prog Ser 129: 85–95

Runge JA (1988) Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia 167/168:61–71

Runge JA, de Lafontaine Y (1996) Characterization of the pelagic ecosystem in surface waters of the northern Gulf of St. Lawrence in early summer: the larval redfish-*Calanus*-microplankton interaction. Fish Oceanogr 5:21–37

Sanders RW, Wickham SA (1993) Planktonic protozoa and metazoa: predation, food quality and population control. Mar Microb Food Webs 7:197–223

Turner JT (1984) The feeding ecology of some zooplankters that are important prey items of larval fish. NOAA Technical Reports NMFS 7, Washington, DC, p 1–28

Urban JL, McKenzie CH, Deibel D (1992) Seasonal differences in the content of *Oikopleura vanhoeffeni* and *Calanus finmarchicus* faecal pellets—illustration of zooplankton food web shifts in coastal Newfoundland waters. Mar Ecol Prog Ser 84:255–264

Uye S (1996) Induction of reproductive failure in the planktonic copepod *Calanus pacificus* by diatoms. Mar Ecol Prog Ser 133:89–97

Vidal J (1980) Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus*. Mar Biol 56:134–146

Volkman JK, Jeffrey SW, Nichols PD, Rogers GI, Garland CD (1989) Fatty acid composition of 10 species of microalgae used in mariculture. J Exp Mar Biol Ecol 128:219–240