

NOTE

Fragilidium* cf. *mexicanum*, a thecate mixotrophic dinoflagellate which is prey for and a predator on co-occurring thecate heterotrophic dinoflagellate *Protooperidinium* cf. *divergens

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ABSTRACT: The thecate heterotrophic dinoflagellate *Protooperidinium* cf. *divergens* and the thecate mixotrophic dinoflagellate *Fragilidium* cf. *mexicanum* feed on each other. In general, *F. cf. mexicanum* is the predominant predator in this reciprocal predation. At initial concentration ratios ≤ 0.4 (*F. cf. mexicanum*:*P. cf. divergens*), both species fed on each other, but did not seriously affect the other's population. At ratios ≥ 0.8 , *P. cf. divergens* was drastically reduced to very low concentrations, and active predation by *F. cf. mexicanum* on *P. cf. divergens* was observed. This reciprocal predation may affect our view of energy and cycling of carbon in the planktonic community.

KEY WORDS: Dinoflagellate · Food web · Heterotrophy · Mixotrophy · Protist · Reciprocal predation

Interest in mixotrophic and heterotrophic dinoflagellates has recently increased because of their diverse roles in marine food webs (Hansen 1992, Bockstahler & Coats 1993, Jeong 1994a, b, Jeong & Latz 1994). Several dinoflagellates previously thought to be autotrophic have been found to be heterotrophic or mixotrophic (Gaines & Taylor 1984, Bockstahler & Coats 1993, Jacobson & Anderson 1996, Li et al. 1996).

Species in the genus *Fragilidium* have been reported in the coastal waters of many areas (Balech & Ferrando 1964, Eppley & Harrison 1975, Steidinger & Tangen 1996). *Fragilidium* has chloroplasts and some species have been known to be phagotrophic as well (Balech & Ferrando 1964, Steidinger & Tangen 1996). *Fragilidium* may have a strong prey preference; *F. subglobosum* fed exclusively on *Ceratium* spp. when offered diverse dinoflagellate and diatom prey (Skovgaard 1996), and *F. heterolobum* was observed to feed on *Gonyaulax polyedra* (Balech & Ferrando 1964). However, no studies have considered *Fragilidium* feeding

on heterotrophic organisms or the predators on *Fragilidium*.

Species in the genus *Protooperidinium* are heterotrophic dinoflagellates ubiquitous in the world's oceans (Lessard 1984, Hansen 1991b, Stoecker et al. 1993). They are often particularly abundant during red tides of dinoflagellates (Allen 1949, Legovic et al. 1991, Jeong 1995), or during diatom blooms (Jacobson 1987). Several studies (Allen 1949, Paasche & Kristiansen 1982, Dale & Dahl 1987, Jacobson 1987) reported abundances ≥ 20 *Protooperidinium* ml⁻¹.

Protooperidinium play diverse roles in marine food webs; they are predators of diatoms (Hansen 1992, Jacobson & Anderson 1993, Buskey et al. 1994) and red-tide dinoflagellates (Jacobson & Anderson 1986, Hansen 1991b, Jeong & Latz 1994). They are not only important prey for copepods, but also predators on copepod eggs and early naupliar stages (Jeong 1994a, b). Jeong & Latz (1994) showed that some species of *Protooperidinium* grew well on some southern Californian red-tide dinoflagellates in laboratory cultures, and suggested that *Protooperidinium* might have a considerable grazing impact on prey populations.

We have observed *Protooperidinium* cf. *divergens* (Ehrenberg) Balech predation on a *Fragilidium* cf. *mexicanum* Balech cell, while other *F. cf. mexicanum* in the culture fed on other *Protooperidinium* cells. Therefore, *F. cf. mexicanum* is prey for and a predator on *Protooperidinium*. The present study provides a basis for understanding interactions between *P. cf. divergens* (a thecate heterotrophic dinoflagellate) and co-occurring *F. cf. mexicanum* (a thecate mixotrophic dinoflagellate), and relevant trophodynamics.

Materials and methods. Isolation and culture of dinoflagellates: Plankton samples were taken at the end of the Scripps pier (La Jolla, California, USA) during May 1996 using a 35 cm diameter, 25 μ m mesh

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plankton net, and then screened gently through 101 μm Nitex mesh, placed in 150 ml plastic bottles, and sent to Korea. These samples were transferred to 270 ml polycarbonate (PC) bottles. *Gonyaulax polyedra* Stein was added along with 50 ml of BWM medium (Brand 1986). Bottles were placed on wheels rotating at 0.9 rpm under a 12:12 h light-dark cycle with 50 $\mu\text{E m}^{-2} \text{s}^{-1}$ of cool white fluorescent light at $22 \pm 1^\circ\text{C}$. Every 2 or 3 d, aliquots of the enriched water were transferred to new PC bottles containing freshly filtered seawater and *G. polyedra* to increase the populations of grazers. *Protoperidinium cf. divergens* and *Fragilidium cf. mexicanum* became abundant.

Taxonomic authorities used to identify *Fragilidium cf. mexicanum* were Balech (1959, 1988, 1990) and von Stosch (1969). For identification, its plate patterns and thecate forms were examined with a Jeol JSM5410 scanning electron microscope (Fig 1). The closest species is *F. mexicanum*. Plate 1'' has 4 angles, a slot, and a pore (sometimes not completely perforated, but deeply dented), which are clearly different from *F. heterolobum* and *F. fissile*. Plate 1''' is a narrow trapezoid with a length-to-width ratio of 2.2. Plate 7''' is trapezoidal, wider behind, and obviously different from that of *F. subglobosum*.

Individual *Fragilidium cf. mexicanum* from the enriched water were transferred to wells of a 24-well plate (1 cell per well) containing BWM medium, freshly filtered seawater, and *Gonyaulax polyedra* which was found to support rapid growth of *F. cf. mexicanum* (Jeong unpubl. data). The multi-well plate was placed on a shelf under continuous illumination with 50 $\mu\text{E m}^{-2} \text{s}^{-1}$ of cool white fluorescent light at $22 \pm 1^\circ\text{C}$, and observed daily under a dissecting microscope to examine the condition of *F. cf. mexicanum*. When 1 cell grew to approximately 30 cells in a well, these were distributed into wells of new 24-well plates containing BWM media, freshly filtered seawater, and *G. polyedra*. Two healthy strains of *F. cf. mexicanum* have been established, and one of them was used for these experiments. Once dense cultures of *F. cf. mexicanum* were obtained, they were transferred to bottles of fresh prey every 2 d. To accomplish this, cultures were sieved through 80 μm mesh to remove detritus and then screened through 45 μm mesh to retain the large cells. Large cells were then transferred to 500 or 1000 ml PC bottles containing freshly filtered seawater and *G. polyedra*. Most *F. cf. mexicanum* recovered their normal swimming ability within 1 h of being sieved. When a large volume of *F. cf. mexicanum* culture was available, experiments were conducted.

Details of culturing *Protoperidinium cf. divergens* are described by Jeong & Latz (1994).

Feeding process: To observe the feeding process, dense cultures of *Protoperidinium cf. divergens* and

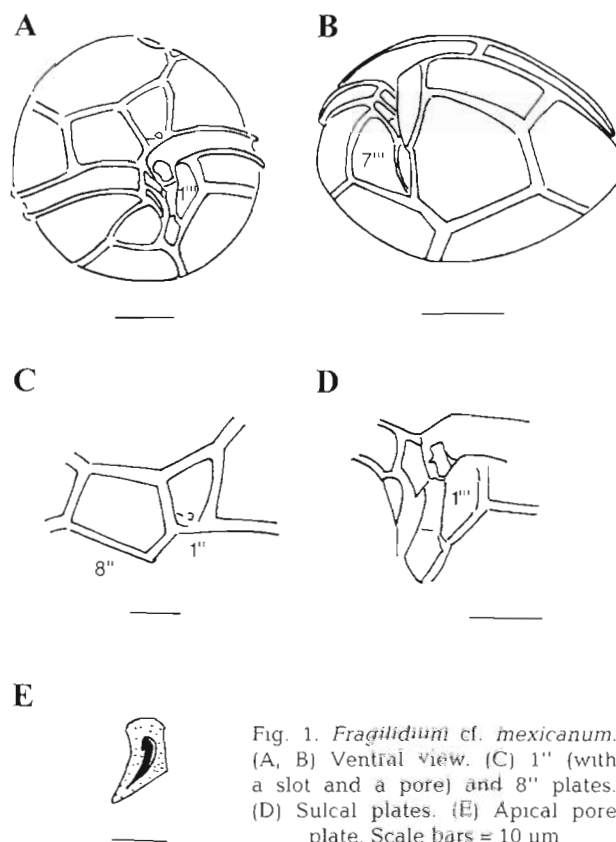


Fig. 1. *Fragilidium cf. mexicanum*. (A, B) Ventral view. (C) 1'' (with a slot and a pore) and 8'' plates. (D) Sulcal plates. (E) Apical pore plate. Scale bars = 10 μm

Fragilidium cf. mexicanum were transferred to 85 ml PC bottles. Bottles were placed on rotating wheels at 0.9 rpm under dim light at 22°C for 1 to 8 h. Contents were then gently transferred to 6-well plates. *P. cf. divergens* cells with a pallium containing several stages of the feeding process and *F. cf. mexicanum* cells containing 1 or more *P. cf. divergens* cells were very carefully transferred by a Pasteur micropipette into Sedgwick-Rafter counting chambers, and then pictures were taken using an Olympus camera on a compound microscope at a magnification of 40 to 400 \times .

The feeding process of *Fragilidium cf. mexicanum* on *Protoperidinium cf. divergens* was also recorded with a video camera system on an Olympus compound microscope and dissecting microscope at a magnification of 10 to 100 \times .

Effects of reciprocal predation: Two experiments were designed to investigate the effects of the reciprocal predation when *Fragilidium cf. mexicanum* and *Protoperidinium cf. divergens* were mixed. The initial concentrations (cells ml^{-1}) of *F. cf. mexicanum* and *P. cf. divergens* (and corresponding ratios of *F. cf. mexicanum* to *P. cf. divergens*) were 5.9:65 (0.09), 11.4:63.4 (0.18), 27.6:65.3 (0.42), 54.2:62 (0.87), and 112:63.5 (1.76) in Expt 1 and 36:39 (0.92) in Expt 2.

More than 2 wk before these experiments were set up, cultures of *Fragilidium cf. mexicanum* or *Protoperidinium cf. divergens* were transferred every 2 d into new bottles containing freshly filtered seawater and *Gonyaulax polyedra*. Dense populations of both grazers actively fed on and eliminated most *G. polyedra* within 2 d and appeared very healthy. When *G. polyedra* concentrations became low, dense cultures were sieved through 45 μm mesh; the retained large cells of each species were transferred to 1000 ml PC bottles. The bottles containing very dense populations of *F. cf. mexicanum* or *P. cf. divergens* with low concentrations of large *G. polyedra* cells were filled to capacity with filtered seawater and placed on rotating wheels at 0.9 rpm under very dim light ($1 \mu\text{E m}^{-2} \text{s}^{-1}$) at 22°C to acclimate for approximately 11 and 7 h in Expts 1 and 2, respectively. Bottles taken from the rotating wheel at intervals were observed under a dissecting microscope to examine the conditions of *F. cf. mexicanum* and *P. cf. divergens* and the presence of *G. polyedra* and then placed back onto the rotating wheels. Most *F. cf. mexicanum* and *P. cf. divergens* cells which had been sieved recovered their normal swimming ability within 1 h. *G. polyedra* completely disappeared within approximately 6 and 4 h in Expts 1 and 2, respectively. Three 1 ml aliquots of *F. cf. mexicanum* or *P. cf. divergens* from the bottles were counted to determine their concentrations under a compound microscope.

In Expts 1 and 2, the initial concentrations of *Fragilidium cf. mexicanum* or *Protoperidinium cf. divergens* were established using an autopipette to deliver known cell concentrations to the bottles. Triplicate 270 ml experiment bottles (mixtures of both species) were set up at all concentration combinations. One set of triplicate control bottles contained only *P. cf. divergens*. The other set of triplicate control bottles containing only *F. cf. mexicanum* were initially set up at all *F. cf. mexicanum* concentrations. Experimental and control bottles were placed on rotating wheels at 0.9 rpm under continuous dim light ($1 \mu\text{E m}^{-2} \text{s}^{-1}$) at 22°C for 64 and 52 h in Expts 1 and 2, respectively. We incubated bottles under dim light to prevent the possible phototrophic growth of *F. cf. mexicanum*. The maximum growth rate of *F. cf. mexicanum* without added prey under continuous illumination ($130 \mu\text{E m}^{-2} \text{s}^{-1}$) at 22°C was approximately 0.3 d^{-1} (Jeong unpubl. data). Ten ml aliquots, taken from all bottles at intervals, were fixed with acidic Lugol's solution. In Expt 1, at 18, 37, and 63 h, and in Expt 2, at 6 h, the contents inside all experimental bottles and 1 control bottle at each concentration were carefully observed (looking through the surface of the bottles without removing the cap) under a dissecting microscope to examine the interactions and condition of *F. cf. mexicanum* and/or *P. cf. divergens*. After subsamples were taken, bottles

were filled again to capacity with freshly filtered seawater using a micropipette and placed back on rotating wheels. The concentrations of *F. cf. mexicanum* or *P. cf. divergens* were determined by counting all cells in five 1 ml Sedgwick-Rafter counting chambers under a compound microscope.

Results. Feeding process: *Fragilidium cf. mexicanum* can engulf *Protoperidinium cf. divergens* cells of similar cell size (Fig. 2A). Within 2 h *F. cf. mexicanum* digested more than one-third of a *P. cf. divergens* cell and engulfed a new *P. cf. divergens* cell (Fig. 2B, C, D). This can be easily detected because the cell surface of *F. cf. mexicanum* is almost transparent. The shape of *F. cf. mexicanum* containing 1 or more *P. cf. divergens* cells was diverse; round, oval, quadrilateral, and sometimes amorphous (Fig. 2A, B, C, D). Their sizes were usually $>70 \mu\text{m}$ and sometimes reached $100 \mu\text{m}$. This large size and shape allowed quick and unambiguous detection of *F. cf. mexicanum* cells containing *P. cf. divergens* at a glance under a dissecting microscope.

Protoperidinium cf. divergens fed on *Fragilidium cf. mexicanum* by means of a pallium (Fig. 2E, F). Sometimes more than 6 *P. cf. divergens* cells could be seen simultaneously attacking a *F. cf. mexicanum* cell, as has been observed when feeding on a copepod egg and nauplius (Jeong 1994b). The pallium containing the fecal aggregations was conspicuous because it was large (similar to the cell size of *P. cf. divergens*) and did not shrink for some time.

Effects of reciprocal predation: In Expt 1, both species fed on each other at low ratios of the initial concentrations (*Fragilidium cf. mexicanum*:*Protoperidinium cf. divergens* ≤ 0.4), but the presence of the reciprocal predators did not markedly affect the other's population (Fig. 3A, B, C). However, at higher ratios (≥ 0.8), the concentrations of *P. cf. divergens* in experimental bottles was markedly lower than those in control bottles (Fig. 3D, E). At the ratio of 1.8, *P. cf. divergens* concentrations in experimental bottles drastically decreased to 3 cells ml^{-1} (5% of the initial concentration) at 64 h. Similar rapid decrease in *P. cf. divergens* concentrations was also found in Expt 2 (ratio of 0.9; Fig. 4). However, the feeding by *F. cf. mexicanum* on *P. cf. divergens* did not support the growth of *F. cf. mexicanum*. In Expt 2 *F. cf. mexicanum* in experimental bottles maintained its population constant from 29 to 52 h after the *P. cf. divergens* concentration drastically declined from 0 to 29 h, while the *F. cf. mexicanum* concentration in control bottles continuously decreased. Energy gained from the predation on *P. cf. divergens* from 0 to 29 h might have enabled *F. cf. mexicanum* to maintain a constant population.

It was observed under a dissecting microscope that the feeding by *Protoperidinium cf. divergens* on *Fragi-*

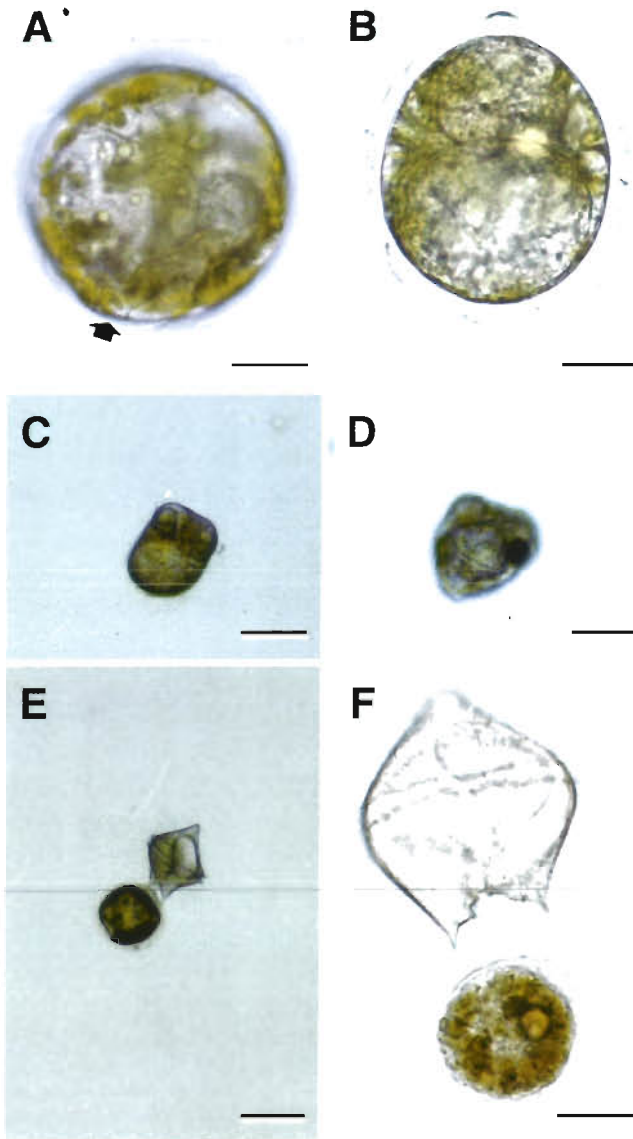


Fig. 2. *Fragilidium cf. mexicanum*. Shape when feeding on *Protoperidinium cf. divergens* (and numbers of prey inside the protoplasm of the predator). (A) Round (1 *P. cf. divergens* cell; antapical horns, arrowhead). (B) Oval (1 cell semi-digested and 1 newly ingested). (C) Quadrilateral (2 almost digested and 1 newly ingested cells). (D) Amorphorous (3 almost digested and 1 newly ingested cells). *P. cf. divergens* feeding on an *F. cf. mexicanum* cell. (E) Attached pallium containing an *F. cf. mexicanum* cell. (F) Detached pallium after feeding was interrupted. *F. cf. mexicanum* and *P. cf. divergens* cells were not the same ones as in A to F. Scale bar = 20 μm in A, B, and F and 60 μm in C, D, and E

lidium cf. mexicanum occurred at all ratios, but especially at the ratios of 0.2, 0.4, and 0.8. The feeding by *F. cf. mexicanum* on *P. cf. divergens* was observed at all ratios except 0.09, but was most marked at ratios of 0.8 and 1.8 in Expt 1. Many large *F. cf. mexicanum*

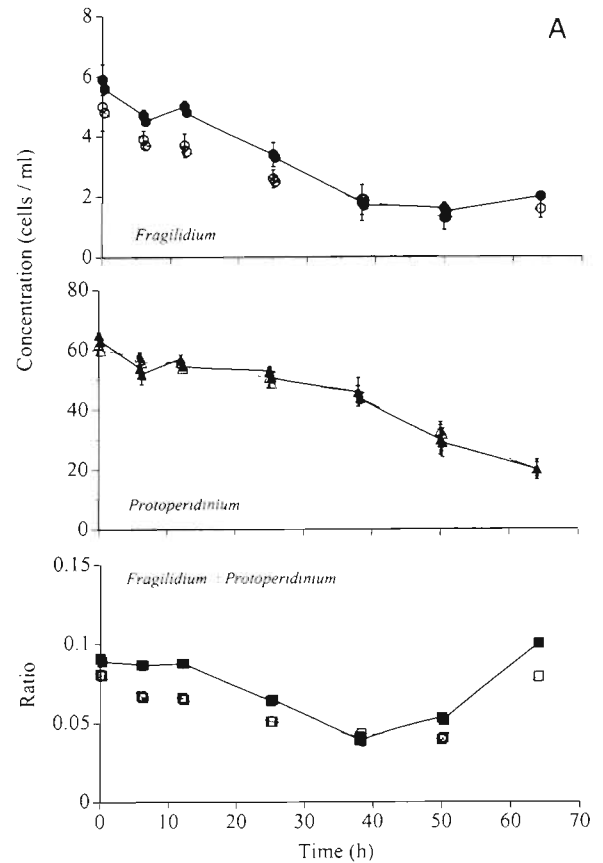
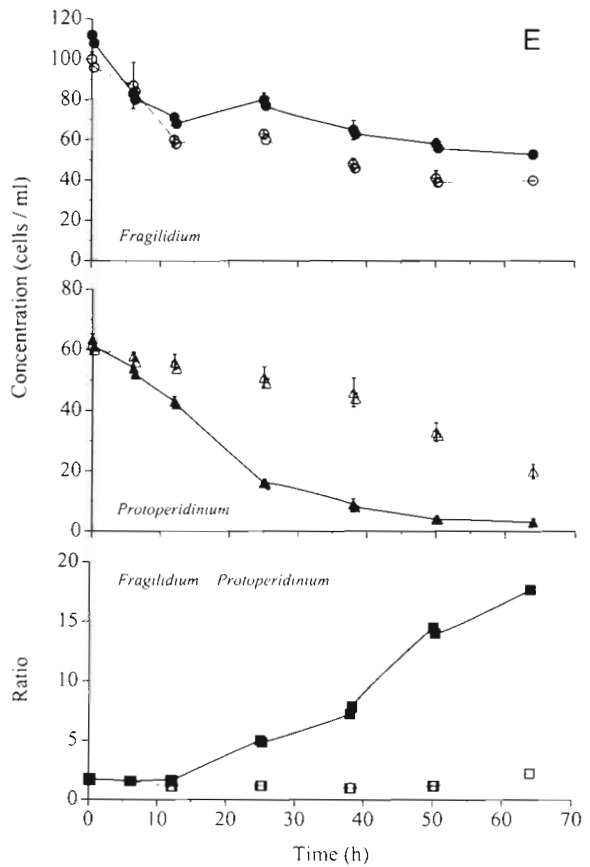
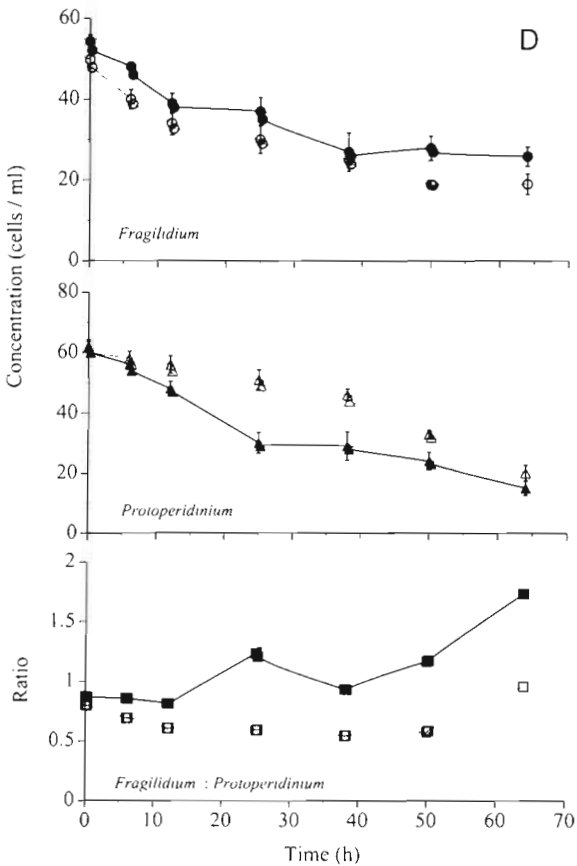
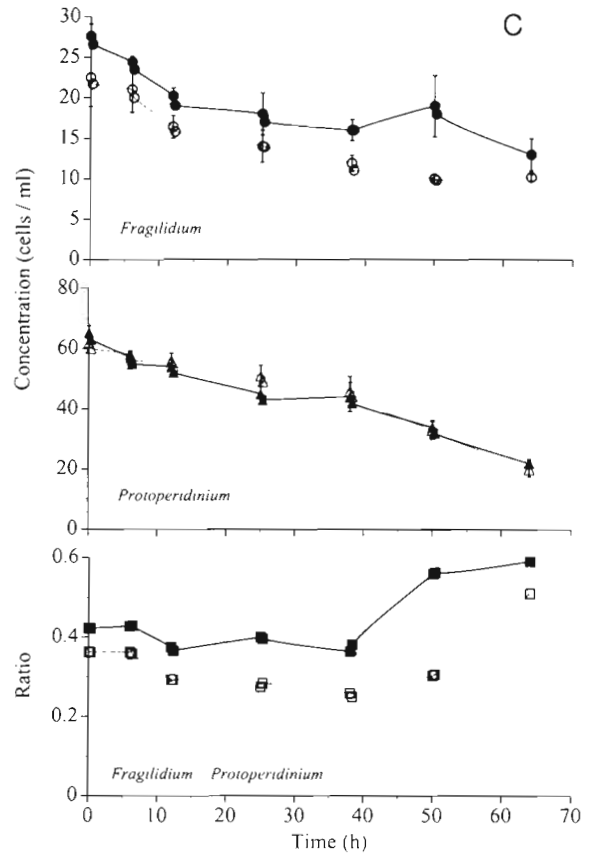
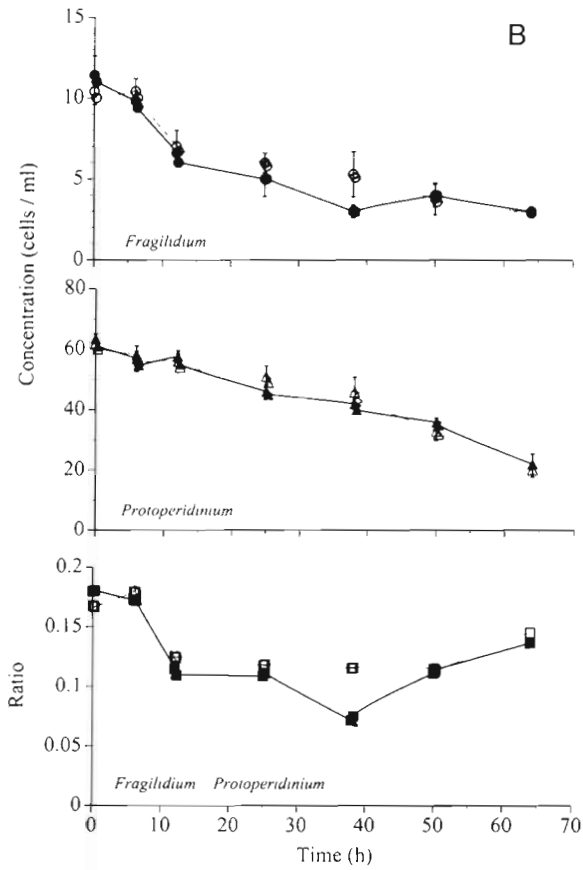


Fig. 3. *Fragilidium cf. mexicanum* and *Protoperidinium cf. divergens*. Concentrations and ratios (*F. cf. mexicanum* : *P. cf. divergens*) as a function of incubation time (Expt 1). Initial concentrations (cells ml^{-1}) of *F. cf. mexicanum* and *P. cf. divergens* (and corresponding ratios of *F. cf. mexicanum* to *P. cf. divergens*) are (A) 5.9:65 (0.09), (B) 11.4:63.4 (0.18), (C) 27.6:65.3 (0.42), (D) 54.2:62 (0.87), (E) 112:63.5 (1.76). Symbols represent treatment means ± 1 SE. (●) Experimental bottles containing *F. cf. mexicanum* and (▲) *P. cf. divergens* and (■) their ratios. (○) Control bottles containing only *F. cf. mexicanum* or (△) only *P. cf. divergens* and (□) their ratios

cells were observed to contain a *P. cf. divergens* cell at 6 h in Expt 2.

The evidence from feeding experiments and microscopic examination suggests that *Fragilidium cf. mexicanum* may have a considerable predation impact on the population of *Protoperidinium cf. divergens* when the ratio of the initial concentrations (*F. cf. mexicanum* : *P. cf. divergens*) is greater than 0.8.

Discussion. The present study shows that *Fragilidium cf. mexicanum* and *Protoperidinium cf. divergens* can prey on each other. However, at ratios of the initial concentrations ≥ 0.8 (*F. cf. mexicanum* : *P. cf. divergens*), *F. cf. mexicanum* fed on *P. cf. divergens* more than *P. cf. divergens* fed on *F. cf. mexicanum*, and *F. cf.*



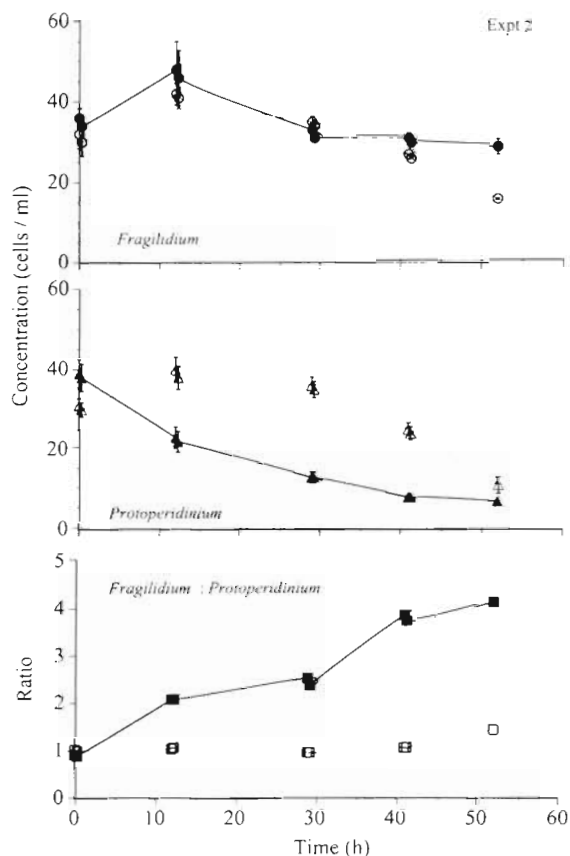


Fig. 4. *Fragilidium cf. mexicanum* and *Protopteridinium cf. divergens*. Concentrations and ratios (*F. cf. mexicanum*:*P. cf. divergens*) as a function of incubation time (Expt 2). Initial concentration (cells ml⁻¹) of *F. cf. mexicanum* and *P. cf. divergens* (and corresponding ratios of *F. cf. mexicanum* to *P. cf. divergens*) was 36:39 (0.92). Symbols represent treatment means \pm 1 SE. Symbols as in Fig. 3

mexicanum had a considerable predation impact on the population of *P. cf. divergens*. This reciprocal predation may be important in planktonic communities in the following ways: (1) *F. cf. mexicanum* can survive at low light intensity and nutrient conditions by feeding on *P. cf. divergens*, and possibly other heterotrophic protists. (2) Carbon would be quickly recycled between the populations of *F. cf. mexicanum* and *P. cf. divergens*. (3) The predator-prey relationship can be reversed any time. (4) The grazing impact by *Protopteridinium* populations on preferred red-tide dinoflagellate prey can be reduced if *F. cf. mexicanum* co-occurs.

Reversals of prey-predator relationships have also been observed between *Protopteridinium cf. divergens* and copepods, and between the dinoflagellate genus *Dinophysis* and the ciliate *Tiarina fusus*. *P. cf. divergens*, prey for adult copepods, itself feeds on copepod eggs and early naupliar stages (Jeong 1994b). *T. fusus*

is a predator of autotrophic *Dinophysis* spp., but prey for heterotrophic *Dinophysis* spp. (Hansen 1991a). However, there have been few reports of direct reversal of the prey-predator relationship in marine planktonic communities.

Toxicity of *Fragilidium cf. mexicanum* has not been studied, but it is unlikely that there were toxic effects of *F. cf. mexicanum* on *Protopteridinium cf. divergens*. When the ratios of *F. cf. mexicanum* to *P. cf. divergens* were similar (0.87 in Fig. 3D and 0.92 in Fig. 4), the reduction in the population of *P. cf. divergens* (difference in reductions between experimental and control bottles: 53.2% – 25.8% = 27.4%) at the higher concentration of *F. cf. mexicanum* (54.2 cells ml⁻¹; Fig. 3D) for the first 40 h was rather smaller than that (79.5% – 19.4% = 60.1%) at the lower concentration (36 cells ml⁻¹; Fig. 4).

To understand further the interactions between *Protopteridinium* and *Fragilidium* populations, it would be worthwhile to explore the distributions and population dynamics of *Protopteridinium* and *Fragilidium*, and effects of the presence of alternative prey during and/or after red tides dominated by common prey (e.g. *Gonyaulax polyedra*, and possibly *Alexandrium tamarense*, *Scrippsiella trochoidea* etc.) when both groups are abundant.

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