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A re-evaluation of toxic dinoflagellate biology and ecology

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1. INTRODUCTION

Dinoflagellates are microscopic algae (Pyrrhophyta) that have two distinct identifying characters at the light microscope level: a prominent, large nucleus with continually condensed chromosomes, and a bi-flagellated, motile stage at some time in their life-cycle. Most dinoflagellates are free-living, although parasitic and other symbiotic species occur. Free-living species can be photosynthetic (auto- or auxo-

trophic) or heterotrophic or both, with varied habitat and nutritional requirements. At the electron microscope level, dinoflagellates are distinguished by: a vesicular cell covering, a nucleus with a persistent nuclear envelope, a 2–3 membrane chloroplast envelope, and chromosomes attached to the nuclear envelope (see Steidinger and Cox 1980). Biochemically, dinoflagellates are also distinct in their photosynthetic pigments; i.e. those that are photosynthetic usually have distinct xanthophylls, e.g. peridinin.

Twenty or so dinoflagellates have been documented to produce non-proteinaceous toxins or poisons (Table 1), which can cause marine animal or bird kills, toxic bivalves (shellfish), or an illness called ciguatera. Those dinoflagellates that cause ciguatera have not been associated with marine mortalities or toxic bivalves as yet, and those that cause toxic shellfish and its resultant shellfish poisoning in humans or other animals rarely cause direct, extensive marine mortalities with the exception of two unrelated species: *Pyrodinium bahamense* var. *compressa* and *Ptychodiscus brevis*. Since there are 1,000–1,500 extant dinoflagellate species, this translates to <2% that are poisonous or present human health or environmental hazards.

Toxic species belong to widely divergent genera, i.e. *Prorocentrum, Dinophysis, Amphidinium, Gymnodinium, Ptychodiscus, Protogonyaulax, Gonyaulax(?), Ostreopsis, Gambierdiscus,* and *Pyrodinium,* and there is no obvious relationship to explain why these few species produce such potent neurotoxins and hemolytic agents while over a thousand dinoflagellates do not elaborate such secondary metabolites. All toxic species do have at least two common denominators. They are all photosynthetic and they synthesize long-chained (C_{14}, C_{16}, C_{18}, C_{22}), unsaturated fatty acids as food reserves; but, so do most free-living dinoflagellates. If elaboration of a metabolic product provides an inter-specific competitive advantage that enhances species' survival, then why don't all species capable of producing monospecific blooms synthesize such toxins? Or, is it that the toxin is chemically functional in some other aspect more basic to survival and that all bloom species produce such functional byproducts of different structure and activity? Is toxicity an adaption to survival as it is in some terrestrial plant-animal and animal-animal relationships, particularly in highly diverse tropical or warm temperate areas? Is it a specific adaptation, or is it another chance event involving in infestations and resultant viral or bacterial recombinant DNA? There are no definitive answers to the preceding questions, although limited phycological and other research suggest that both explanations are plausible.

This review is intended to present an update on toxic dinoflagellate research as it relates to systematics of the causative organisms, their life histories, toxin structure, activity, and impacts, and selected aspects of ecology that address the mechanisms involved in biotic and abiotic interactions. At the same time, the

Table 1.

List of toxic dinoflagellates and selected parameters.

	Species	Toxic lab/field	Water or organic solvent soluble	Fish kills or ichthyotoxic in lab tests or hemolytic	Ciguatera NSP, PSP or DSP	Sexual cycle known	References	Figure
1.	**Amphidinium carterae* Hulburt, 1957	L	O	I/H	–	+	Nakajima et al. 1981; Ikawa and Sasner 1975; Ikawa and Taylor 1973.	–
2.	**A. klebsii* Kofoid & Swezy emend. D. Taylor, 1971	L	O	I/H	–	ND	Nakajima et al. 1981; McLaughlin and Provasoli 1957	–
3.	*A. rhychocheplum* Anissimowa, 1926	L	O	I	–	ND	McLaughlin and Provasoli 1957	–
4.	*Dinophysis fortii* Pavillard, 1923	F	O	ND	DSP	ND	Yasumoto et al. 1980b; Murata et al. 1982	–
5.	**Gambierdiscus toxicus* Adachi & Fukuyo, 1979	L	O/W	H	Ciguatera	+	Adachi and Fukuyo 1979; Nakajima et al. 1981	15
6.	*Gonyaulax monilata* Howell, 1953	L	W	FK/I	PSP	+	Sievers 1969; Walker and Seidinger 1979	12,13
7.	*G. polyedra* Stein, 1883	L(?)	W?		–	ND	Schradie and Bliss 1962	–
8.	*Gymnodinium catenatum* Graham, 1943	L/F	W		PSP	?	Morey-Gaines 1982	1
9.	*G. veneficum* Ballantine, 1956	L	O	I	ND	ND	Ballantine 1956; Abbott and Ballantine 1957	8
10.	**Ostreopsis ovata* Fukuyo, 1981	L	O	H	–	ND	Nakajima et al. 1981	–
11.	**O. siamensis* Schmidt, 1901	L	W	H	–	ND	Nakajima et al. 1981	–
12.	*Prorocentrum balticum* (Lohmann) Loeblich, 1970	?	O	FK		ND		–
13.	**P. concavum* Fukuyo, 1981	L	O	I/H	Ciguatera	ND	Fukuyo 1981; Nakajima et al. 1981	17

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Table 1. *(Contd.)*

	Species	Toxic lab/field	Water or organic solvent soluble	Fish kills or ichthyotoxic in lab tests or hemolytic	Ciguatera NSP, PSP or DSP	Sexual cycle known	References	Figure
14.	**P. lima* (Ehrenberg) Dodge, 1975	L	O/W	H	Ciguatera?	ND	Dodge 1975; Fukuyo 1981; Nakajima et al. 1981; Murakami et al. 1982	16
15.	*P. minimum* [incl. *P. minimum* var. *marie-lebourae*]	?				ND	Nakajima 1965	20
16.	**P. mexicanum* Tafall [=*P. rhyathymum* Loeblich, Sairley & Schmidt, 1979]	L	O	H	Ciguatera?	ND	Loeblich et al. 1979; Steidinger and Dodge 1982; Nakajima et al. 1981	19
17.	*Pretogonyaulax acatenella* (Whedon & Kofoid) Taylor, 1979	L	W	–	PSP	ND	Taylor 1979a	–
18.	*P. catenella* (Whedon & Kofoid) Taylor, 1979	L/F	W	–	PSP	+	Taylor 1979a; Yoshimatsu 1981	9
19.	*P. tamarensis* (Lebour) Taylor, 1979 [incl. var. *excavata* & *P. phoneus* (Woloszynska & Conrad) Taylor, 1979]	L/F	W	FK**	PSP	+	Taylor 1979a; Loeblich and Loeblich 1979; Turpin et al. 1978; Anderson and Wall 1978; White 1981, 1982a	10,11
20.	*Ptychodiscus brevis* (Davis) Steidinger, 1979	L/F	O	FK/I/H	NSP	+(in part)	Steidinger 1979; Walker 1982; Baden 1983	2,3,4,7
21.	*Pyrodinium bahamense* var. *compressa* (Böhm) Steidinger, Tester & Taylor, 1980	L/F	W	FK/I	PSP	ND	Maclean 1977; Worth et al. 1975; Steidinger et al. 1980; Harada et al. 1982	14

*Benthic species. **Fish kills via food chain. ND = no data.

presentation will detail avenues for future investigations and raise questions that lead to more questions and inquiry.

2. SYSTEMATICS AND LIFE HISTORIES

2.1. Gymnodinium/Ptychodiscus

To date, six unarmored dinoflagellates (those without cell walls divided into valves or plates) are known to produce poisons or toxins. Three of these are gymnodinoid in gross appearance: *Gymnodinium veneficum* Ballantine, 1956; *G. catenatum* Graham, 1943; and *Ptychodiscus brevis* (Davis) Steidinger, 1979 (= *Gymnodinium breve* Davis 1948) (see Figs 1–8). Of these, the most recent work has centered around *P. brevis* and *G. catenatum,* and other species they resemble morphologically. All are free-living, photosynthetic, <50 μm in diameter, and planktonic in the vegetative stage. However, *P. brevis* and *G. veneficum* produce ichthyotoxins while *G. catenatum* produces paralytic shellfish poisoning (PSP); *P. brevis* and *G. veneficum* are of North Atlantic distribution, while *G. catenatum* is Pacific; *G. catenatum* is a chain former while the other two are principally solitary; *P. brevis* lacks evidence of a thecal membrane or structural polysaccharides in its thecal vesicles, while *G. catenatum* may have such a membrane. The only possibly true species of toxic *Gymnodinium* is *G. veneficum* and this may be open to question once this genus and *Balechina, Ptychodiscus,* and *Gymnodinium* are completely redescribed at the SEM, TEM, and biochemical levels. The type species of *Gymnodinium* is the freshwater species, *G. fuscum,* which has structural remnants in its thecal vesicles (Dodge and 1969) and probably contains the xanthophyll peridinin.

Gymnodinium catenatum is morphologically identical to *Protogonyaulax catenella* (Whedon & Kofoid) Taylor, 1979, except that it lacks a cell wall divided into plates. It even has an analagous apical pore plate at the apex; this structure is characteristic of the *Gonyaulax "Catenella"* group or *"tamarensis* complex" as described by Steidinger (1971), Taylor (1975), and Dodge and Hermes (1981). The associated anterior attachment pore is also characteristic of armored chain-forming species such as *P. catenella* and *Gonyaulax monilata;* but this is a transitory character associated with chain formation and disappears when single cells are produced in culture. Even though a posterior attachment pore was not described by Morey-Gaines (1982), his Figure 5 and the presence of an anterior attachment pore imply that one exists. Further TEM and SEM on *G. catenatum* material using EM fixes should clarify its thecal organization and whether or not it is truly unarmored. Since the species produces PSP, another characteristic of *P. catenella* and some related armored dinoflagellates, and since it is morphologically identical to *P. catenella* except that it may lack thecal plates, and since its distribution is a latitudinal extention of *P. catenella,* this form must have been derived from *P.*

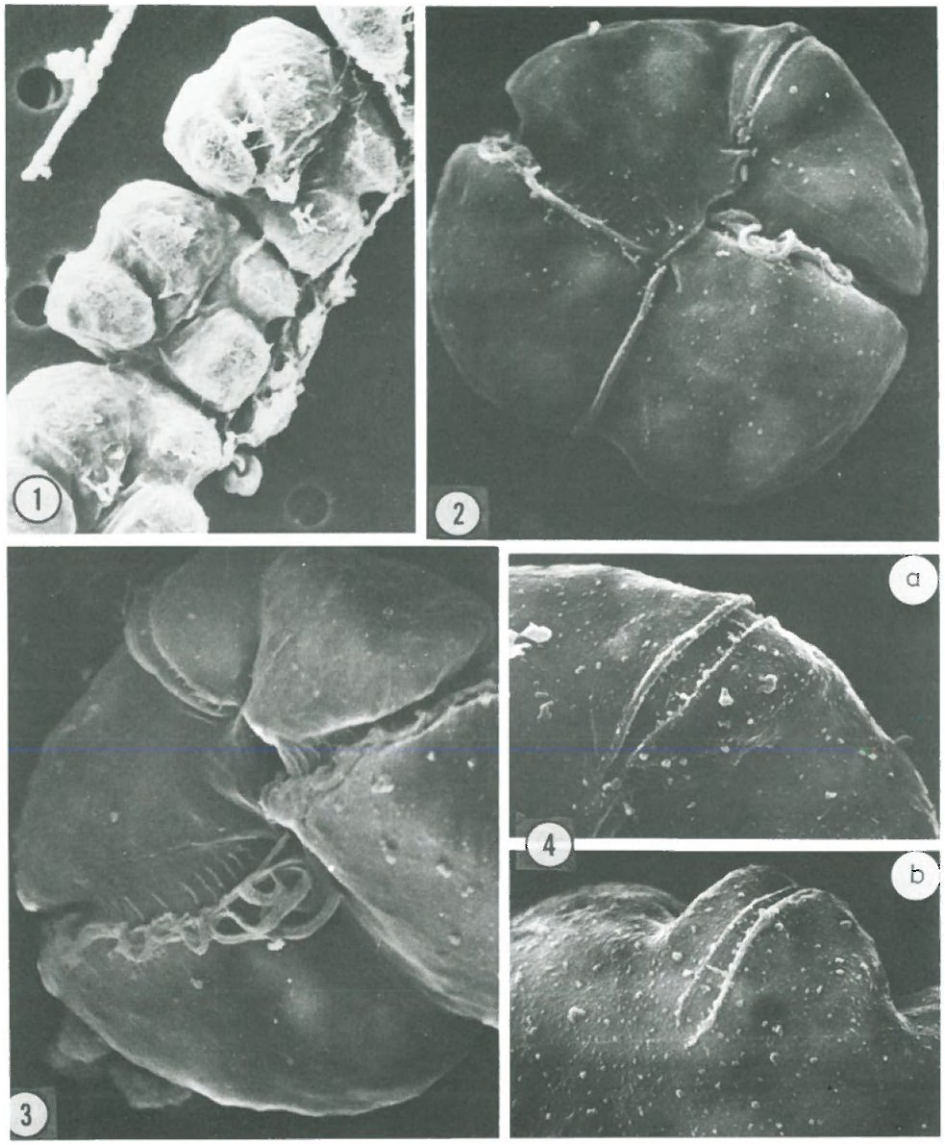


Fig. 1. *Gymnodinium catenatum;* from Morey-Gaines 1982 (SEM).

Fig. 2. *Ptychodiscus brevis;* ventral view (SEM).

Fig. 3. *Ptychodiscus brevis;* thecal ridges in cingulum and pronounced carina (SEM).

Fig. 4. *Ptychodiscus brevis;* a) ventral view of groove in carina; b) dorsal view.

catenella as speculated by Morey-Gaines, rather than evolving along separate lines. Is this then a new species in the biological or evolutionary sense of "species" (see Grant 1971) only because of a possible single allelic mutation. Or, should such

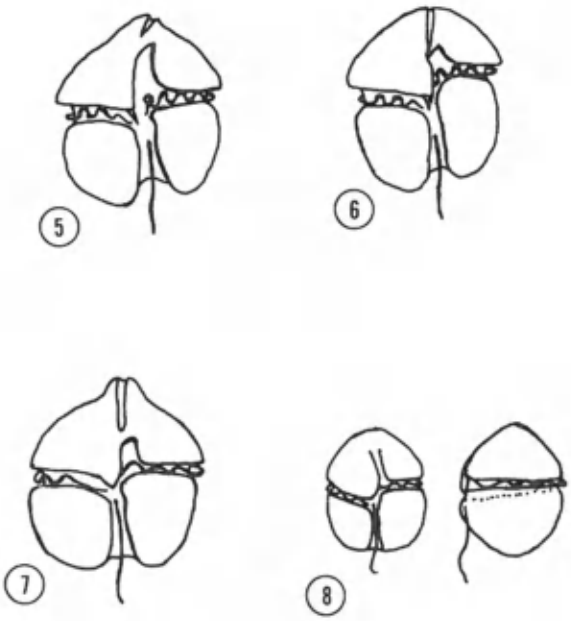


Fig. 5. *Gymnodinium breve*-like species from Japan; adapted from Takayama (1981). Note sulcal configuration and intrusion on epitheca. Compare to Figs 6 and 7.

Fig. 6. *Gymnodinium nagaski;* adapted from Takayama 1981.

Fig. 7. *Ptychodiscus brevis;* note pronounced carina and cingulum-sulcus junction.

Fig. 8. *Gymnodinium veneficum;* after Ballantine 1956.

mutants, or other mutants such as apochloric forms or polyploids, be named varieties? Obviously, a discussion of what is a species or perhaps a species complex is not the purpose of this particular chapter, yet such concepts will necessarily affect all aspects of research. For example, since the heterothallic sexual life cycle of *P. catenella* has recently been described (Yoshimatsu 1981), it seems a logical extension to try clonal crosses of *P. catenella* and *G. catenatum,* once *G. catenatum* is cultured. Although *G. catenatum* does not have a documented sexual life cycle, with the end product being a hypnozygote, Morey-Gaines (1982) suggested the existence of such a benthic stage in his Figure 14, which was a photomicrograph of a dinoflagellate cyst found in sediments after the *G. catenatum* bloom. Since the species is probably derived from *P. catenella,* which does produce hypnozygotes, a sexual life history involving benthic stages capable of constituting seed beds for future blooms is plausible.

In 1948, *Ptychodiscus brevis* was originally described as a *Gymnodinium* based on light microscopy (LM). It was a unique bloom species characterized by dorsoventral compression, dorsal convexity, ventral concavity, prominent apical process directed ventrally, sulcus on the epitheca (epicone), and a large, posterior nucleus.

In addition, the species has been observed to contract laterally, probably through the activity of thecal microtubules. Later, Steidinger et al. (1978) and Steidinger (1979a) better characterized the species with LM and TEM and described cells as having highly vesiculated cytoplasm; lobed, peripheral chloroplasts with multistalked pyrenoids; ultrastructural differences between field and culture specimens; and thecal ridges in the cingulum (= girdle). Steidinger (1979b) then transferred this species to *Ptychodiscus* based on the cingular thecal ridges (TEM and SEM) and the presence of a distinct apical carina (= apical process; Fig. 3). The species is also distinct from most dinoflagellates in lacking the xanthophyll peridinin (Jeffrey et al. 1975). In addition, the species has a median apical groove that extends the length of the carina, both dorsally and ventrally (Fig. 4). The groove has a thick, rolled right edge. This groove is not a diagnostic character of *Ptychodiscus* although such a groove was described for *P. carinatus* (Kofoid 1907) and Boalch (1969) synonymized *P. carinatus* with *P. noctiluca* Von Stein, 1883, the type species. Although this groove may be considered analogous to an acrobase (see Biecheler 1952) by some researchers, species such as *G. splendens* have an encircling acrobase revealed by silver staining (Biecheler 1952) but not SEM, therefore, I question whether the structures are analogous.

Taylor (1976) differentiated *Ptychodiscus* from *Gymnodinium* and *Balechina* by the presence of one ventral flagellar pore. The best described species, *P. carinatus,* was originally described with a single, large ventral flagellar pore; however, descriptions of other *Ptychodiscus* including the type species do not document whether one or two flagellar pores occurred (Von Stein 1883; Pavillard 1916; Gaarder 1954) and most descriptions were based on preserved material. *Ptychodiscus brevis* has two flagellar pores ventrally and one large dorsal pore in the cingulum of unknown function. The two ventral pores are not clearly discernible at the LM level because of a concave sulcal area. This species also has a flange obscuring the transverse flagellar pore and a rounded indentation at the proximal end of the transverse flagellum.

Dragovich (1967) described a number of morphological forms of *P. brevis* including the "butterfly" type which can reach 90 μm in width and is typically encountered in very low numbers further offshore than the common form described by Steidinger and Joyce (1973). W.B. Wilson (personal communication, 1967) always thought that this form was a nutrient starved cell type awaiting the right conditions to undergo mitosis. However, in all probability, particularly in relation to recent descriptions of *P. brevis*-like organisms from Japan (Iizuka 1975; Takayama 1981) and reports from Spain (S. Fraga, personal communication, 1982), this probably represents a new cosmopolitan species with similar morphology and cytology but with a less prominent apical process. Cingular displacement and sulcal characters in this form have always been difficult to elucidate and only SEM can clarify its affinities.

In 1975, Iizuka described and illustrated (LM) a species of obvious affinities to

P. brevis but with a less pronounced carina and more heavily pigmented chloroplasts; he also reported the "butterfly" (?) type. The species occurred in low concentrations and was not associated with fish kills. Later, Takayama (1981) was able to isolate and culture this species from the same locality, Omura Bay, Nagasaki Prefecture, Japan, and conduct SEM analyses (Fig. 5). Although similar to *P. brevis* (e.g. presence of a reduced apical process and an apical groove, thecal ridges in the cingulum, a dorsal cingular pore, sulcal intrusion on the epitheca and cingulum displacement), the Japanese species is very distinct in the latter two characters. Takayama's species has a distally upturned cingulum that joins a broad anterior end of the sulcus and the sulcus penetrates further on the epitheca. The sulcal extension and the direction of the apical groove of Takayama's *Gymnodinium* sp. (Type '65) cf. *G. nagasaki* are more like *P. brevis* than his "*Gymnodinium breve*-like species" (compare Figs 5–7). Additionally, the Japanese species has a deeply excavated, broad sulcus on the hypotheca and the apical groove is shorter and at a distinct angle. I believe pigment analyses will show that the Japanese species has peridinin and that it does not elaborate an ichthyotoxin(s). In addition to needed biochemical analyses, chromosome spreads or squashes should be attempted to elucidate the haploid number; *P. brevis* has 121 ± chromosomes. On morphology alone, it should be classified as a distinct species. This may be the same species as encountered by Fraga in Riá de Vigo, Spain.

Scanning electron microscopy is an exceptional tool for taxonomic studies, and as fixation techniques are refined for unarmored dinoflagellates (e.g. the use of a combined GTA-OsO_4 fixative iso-osmotic with media; see Figs 2–4), the genera *Gymnodinium, Gyrodinium, Balechina, Ptychodiscus* and others will be modified, split, and redescribed. Such fixation techniques even for armored dinoflagellates are leading to continual taxonomic revisions. Although this is progress and may better clarify evolutionary affinities and trends, such reclassification of toxic species (which can be considered species of "economic importance") creates problems in technical and public reports, as well as public awareness and acceptance. Recently, a recommendation was put before the Botanical Nomenclatural Committee for conservation of specific names of economically important species. If this article passes, then it could be suggested that all toxic microphytoflagellate species that elaborate poisons have their original names conserved, e.g. *Gymnodinium breve, Gonyaulax catenella,* etc. Or, perhaps common names could be assigned to species as is done for higher plants and animals of importance or interest.

Like many other unarmored dinoflagellates, *P. brevis* divides obliquely in mitosis with division rates usually between 0.3–0.5/day. Sexually, it is a heterothallic species with isogamous gametes that fuse to produce a planozygote morphologically similar to the vegetative cell, but slightly larger (Walker 1982). Although hypnozygotes have not been induced and planozygotes have died in culture, possible *P. brevis* cysts have been observed during a bloom (see Walker 1982; Fig. 7). The existence of hypnozygotes for this species is essential to the concept of seed beds and bloom initiation (see Section 4 on Ecology).

2.2. *Protogonyaulax/Gonyaulax/Pyrodinium*

All toxic species (Table 1) in these closely related genera have the plate formula: Ap, Cp, 4′, Oa, 6″, 6c, 6–8s, 6″, 1p, and 1‴ if an extended Kofoidian plate nomenclature is used. However, if Balech's (1980) new concept of antapicals (those plates that touch sulcal plates but not cingulars), or Loeblich and Loeblich's (1979) use of plate overlap, or Taylor's (1979a) use of plate homologies is applied to plate tabulation, then the posterior intercalary (1p) becomes an antapical, making a total of 2‴.

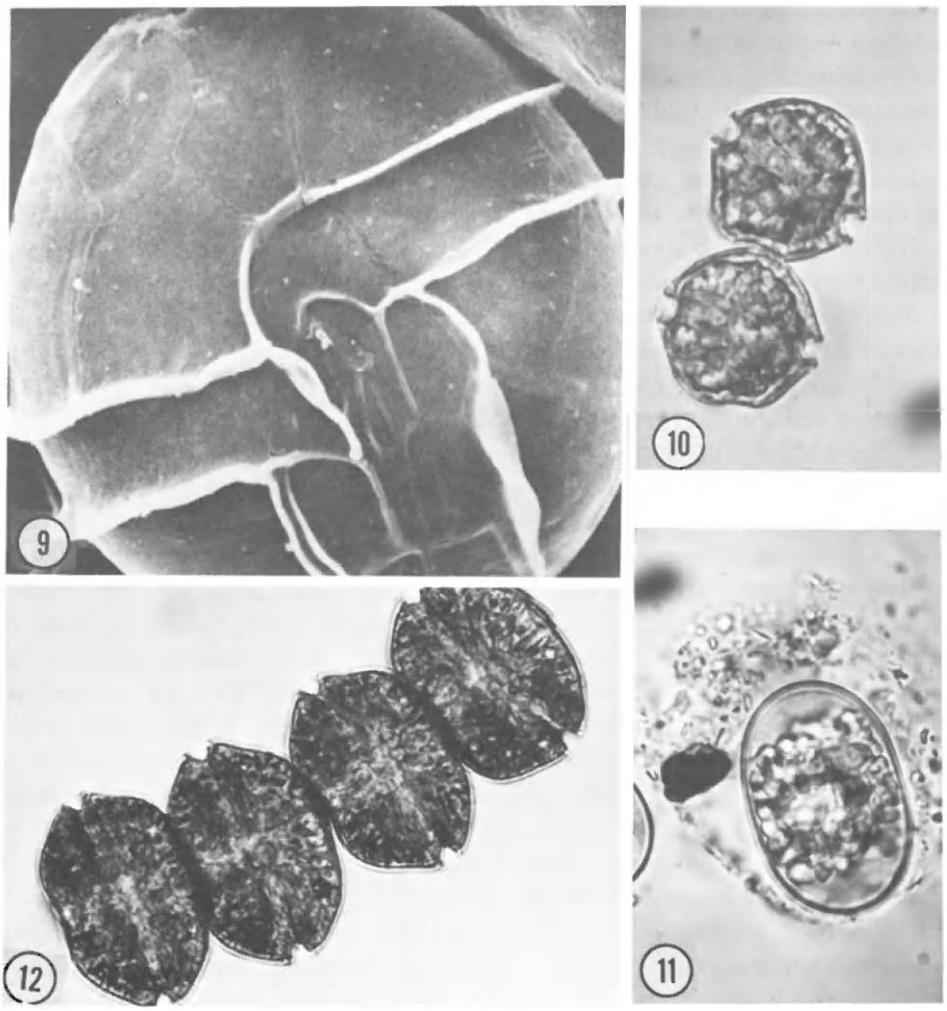


Fig. 9. *Protogonyaulax catenella;* from Postek and Cox 1976 (SEM).

Fig. 10. *Protogonyaulax tamarensis;* courtesy of David Wall (LM).

Fig. 11. *Protogonyaulax tamarensis;* courtesy of David Wall, hypnozygote (LM).

Fig. 12. *Gonyaulax monilata;* chain of cells (LM).

Steidinger (1971) was the first to point out that the *"Catenella* group" of *Gonyaulax* was distinct and probably should be separated out as a new genus and that this group's affinities were with *Alexandrium, Heteraulacus,* and *Pyrodinium.* The *"Catenella* group," or what Taylor (1975) termed the *"tamarensis"* complex, originally included: *Gonyaulax catenella* (Fig. 9), *G. tamarensis* and its varieties (Figs 10 and 11), *G. acatenella, G. fractercula, G. cohorticula, G. dimorpha, G. monilata* (Figs 12 and 13), *G. balechii,* and others. Taylor (1979a) transferred the first six of these plus *G. peruviana* to the new genus *Protogonyaulax* but left *G. monilata* and *G. balechii* as *Gonyaulax* pointing out their affinities with *Alexandrium* and *Pyrodinium* because of a displaced first apical plate. At the same time, Loeblich and Loeblich (1979) transferred all of the eight listed species to *Gessnerium* Halim, a genus erroneously based on an already described species, *Gonyaulax monilata* Howell, 1953. Also at the same meeting, Schmidt and Loeblich (1979a) reassessed *G. tamarensis* and *G. excavata* and relegated them back to varieties, i.e. *G. tamarensis* var. *tamarensis* (with a ventral pore on 1') and *G. tamarensis* var. *excavata* (without a ventral pore) and even speculated that *G. acatenella, G. catenella,* and *G. excavata* belonged to the first described species in this complex – *G. tamarensis* Lebour, 1925. Schmidt and Loeblich (1979b), using mouse bioassays, determined that some strains of both *tamarensis* varieties are toxic. These authors also demonstrated that of 23 dinoflagellates tested, PSP was only identified in members of the *Catenella* Section. To date, the only other dinoflagellates in different genera known to produce PSP are *Gymnodinium catenatum* (probably a derivative of *Protogonyaulax catenella*) and *Pyrodinium bahamense* var. *compressa* (Fig. 14), a species related to the *Catenella* Section.

The *Catenella* Section is indeed separable both morphologically and biochemically and therefore should not remain in the genus *Gonyaulax* with the type species *G. spinifera* (Claparède & Lachmann) Diesing, 1866 – a species of differing plate tabulation, thecal structure, cingular displacement, apical pore structure, nuclear shape, and resting cyst morphology. In all probability, all the *Catenella* Section species should be in *Alexandrium* which is the oldest available name, even though no Latin diagnosis was provided, the iconotype was misrepresented, and the species has a displaced 1' plate. Balech (personal communication) is currently reassessing and redescribing this group along with *A. minutum* Halim, 1960 based on type locality material and other geographical isolates. Until his work is completed, three synonyms are available for each of the species in the *Catenella* Section and it becomes a matter of personal preference as to which is used. In this chapter, *Protogonyaulax tamarensis, P. catenella, P. acatenella,* and *Gonyaulax monilata* will be used because recent literature incorporates these specific synonyms most frequently. The above taxonomic discussion lends further suppport for conservation of species names for toxic dinoflagellates or for assigning common names to avoid confusion in popular and medical literature.

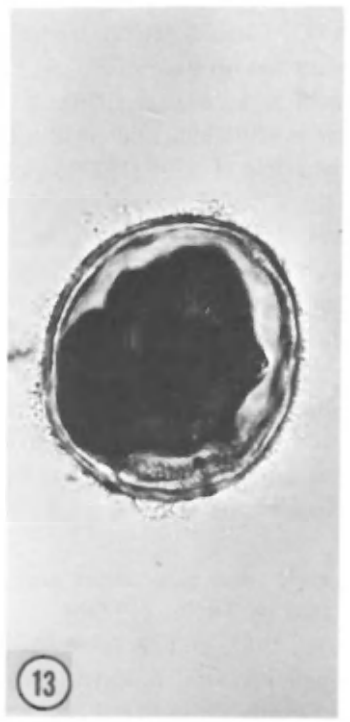
Toxigenic gonyaulacoid dinoflagellates have been known to produce benthic

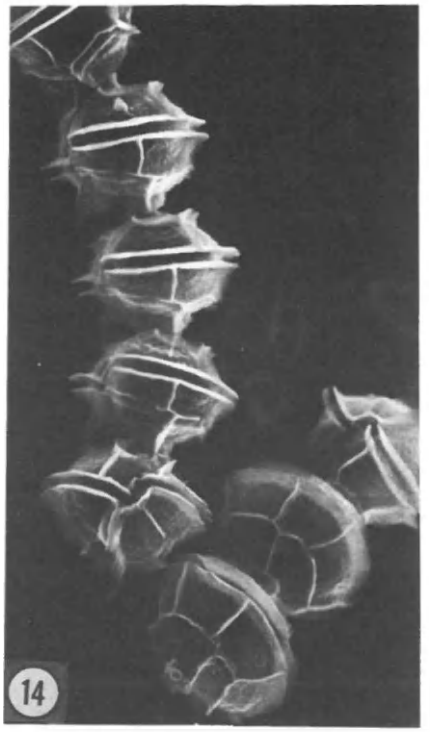
dinocysts since Prakash (1967); however, only in the last 4 years have smooth, thick-walled, round to ovoid cysts been characterized and identified as hypnozygotes. The sexual life histories of *Protogonyaulax tamarensis* (Anderson and Wall 1978; Turpin et al. 1978; Anderson 1980), *P. catenella* (Yoshimatsu 1981), and *Gonyaulax monilata* (Walker and Steidinger 1979) have been elucidated from gamete fusion through planozygote, hypnozygote formation, maturation of hypnozygotes, and finally, release of meiospores. These species are probably all heterothallic, although heterothallism is only confirmed for *P. catenella.* Induction of isogamete production was under nitrogen limitation for two of these species and gamete production usually involves <10% of the culture population. The entire process from gametes to early stage hypnozygotes can take several weeks and hypnozygote obligate dormancy can be 1–4 months depending on changes in ambient conditions. In all species, naturally occurring hypnozygotes have been "excysted" to produce typical vegetative 1 N cells. Steidinger and Haddad (1981) estimated that 4 hypnozygotes cm^{-2} could seed a 2 km^2 area with a 10 m depth, producing 24,576 cells $liter^{-1}$ if the cell division rate was 0.5 day^{-1} for 14 days and motility success was 50%. Cell densities of 10,000–20,000 $liter^{-1}$ have been speculated to cause toxicity in Alaska butter clams if they are exposed over several months (Schantz et al. 1975). In *P. tamarensis,* hypnozygote excystment has been associated with temperature changes to the point of explaining both spring and fall blooms (Anderson 1980).

Therefore, at least in the *Protogonyaulax* and *Gonyaulax* group of toxic dinoflagellates, hypnozygotes have been shown to constitute "seed beds" and act as an inoculum for water column blooms, thus confirming Prakash's (1967) and Steidinger's (1973, 1975a, 1975b) early hypotheses on initiation of red tides and the significance of life history strategies.

2.3. Gambierdiscus/Ostreopsis/Prorocentrum

Gambierdiscus toxicus Adachi & Fukuyo, 1979 (Fig. 14) has been implicated as the cause of ciguatera in the Pacific because of its distribution, toxicity to mice, fat-soluble toxic fraction, and presence in stomach contents of toxic fish and their diet (Yasumoto et al. 1979, 1980a; Nakajima et al. 1981). Yasumoto et al. (1980a) stated, "A number of toxic animals have been reported to occur in coral reef areas. Some of these animals are known or suspected to obtain their toxins from the diets of yet unidentified nature. Our discovery of *Gambierdiscus toxicus* as the probable cause of ciguatera provided the first example of the implication of a benthic dinoflagellate in the food chain transmittance of toxins in coral reef community." In addition to *G. toxicus, Prorocentrum lima* (Fig. 16), *P. concavum* (Fig. 17), *Ostreopsis siamensis,* and *O. ovata* have also been implicated based on distribution, toxicity to mice and a fat-soluble toxic fraction (Yasumoto et al. 1980a; Nakajima et al. 1981, and others). All of these species also occur in the tropical Caribbean and subtropical North Atlantic; they usually occur together as part of a benthic assemblage. Extracts from *Prorocentrum* species are more potent than from *G. toxicus.*





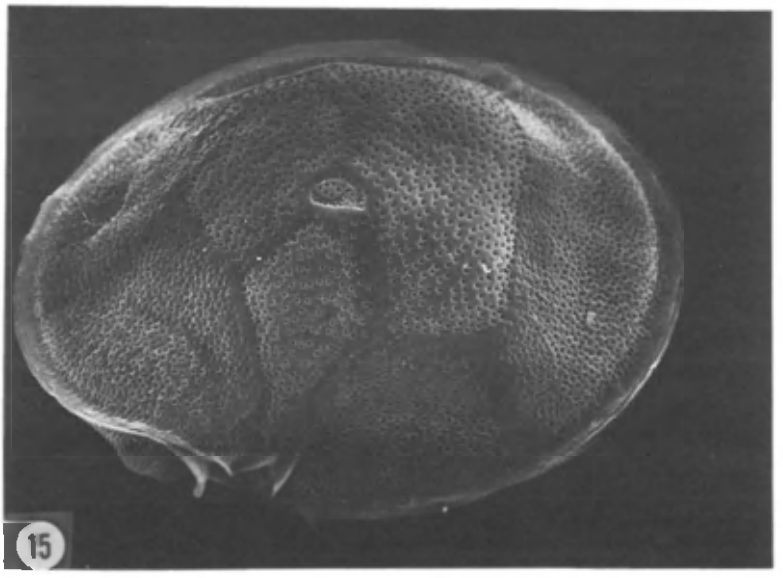


Fig. 13. *Gonyaulax monilata;* hypnozygote (LM).

Fig. 14. *Pyrodinium bahamanse* var. *compressa;* chain of cells (SEM).

Fig. 15. *Gambierdiscus toxicus;* anterior view (SEM).

Gambierdiscus is currently a monotypic genus with *G. toxicus* anterioposteriorly compressed, 42–140 μm wide and 24–60 μm long, and a plate formula of Po, 3′, 7″, 6c, 8c, 6‴, 1p and 1⁗ as originally described (Adachi and Fukuyo 1979). It is epiphytic on red, brown, and green macroalgae, or free in sediments and coral rubble. The plate formula is open to interpretation, for example, Taylor (1979b) gave Po, 3′, 7″, 6c, 4+s, 7‴, and 3⁗. He pointed out that the 7″ could be interpreted as an Sd sulcal plate. Besada et al. (1982) gave a formula of Po, 4′, 6″, 6c(?), 8s(?), 5‴, and 2⁗. Those authors interpreted the 1″ as a displaced 1′. My interpretation would be Ap, Cp(?), 4′ (displaced 1′), 6″, 6c, 8s, 6‴, and 2⁗, using Balech's (1980) new definition for antapicals. In addition to plate formula affinities with gonyaulacoid dinoflagellates, this species has the characteristic apical pore platelet (Ap) with a cresent-shaped pore but it has an ascending cingulum. Most authors place *Gambierdiscus* in the Heteraulaceae, while Besada et al. (1982) moved it to Ostreopsidaceae based on plate tabulations. *Ostreopsis* and *Coolia* both have the apical pore platelet displaced dorsally while *Gambierdiscus* has it displaced ventrally.

Gambierdiscus toxicus probably has a sexual life cycle since isogametes and a planozygote have been partially described and illustrated by Taylor (1979b).

Ostreopsis siamensis Schmidt, 1901, *O. ovata* Fukuyo, 1981, and *O. lenticularis* Fukuyo, 1981 are all rather similar except for body shape and size. Fukuyo (1981) gave a plate formula of Po, 3′, 7″, 5‴, and 1⁗ while Besada listed Po, 4′, 6″, 6c, 8s, 5‴ and 2⁗ for *O. siamensis*. Plate interpretations, definitions, and homologies differ among researchers with most problems centering around apical, antapical and sulcal series. Taxonomy of toxic species would be less confusing if Balech's definition for antapicals, i.e. those plates that contact the sulcus but not the cingulum, was used in conjunction with a new definition for the first apical plate, i.e. the epithecal plate that contacts the anterior margin of the anterior sulcal plate.

The genus *Prorocentrum* is more difficult to discuss and review because essentially it has only two opposing valves and several (5–14) small flagellar pores or periflagellar platelets. In a *Prorocentrum* assemblage collected from Caribbean ciguateric areas around the British Virgin Islands, I have identified *P. lima* (Ehrenberg) Dodge, 1975, *P. concavum* Fukuyo, 1981, *P. emarginatum* Fukuyo, 1981 (Fig. 18), *P. mexicanum* Tafall, 1942 (Fig. 19), and two new species. These species usually occurred in association with *Ostreopsis* and *Gambierdiscus* when they were encountered. Even though *Prorocentrum* species do not have a Kofoidian plate tabulation, they can be separated by the following characters when used together: general shape; shape and excavation of anterior margin of the right valve; an optical edge effect created by peripheral pores or aerolae; arrangement of pores, aerolae, foveolae, reticulae, papillae, spines, granules (as illustrated in Williams et al. 1978: p. 111); convexity or concavity of valves; anterior spines (anterior tooth) and associated wings; and cytological features such as pigmentation, pyrenoids, and location of nucleus.

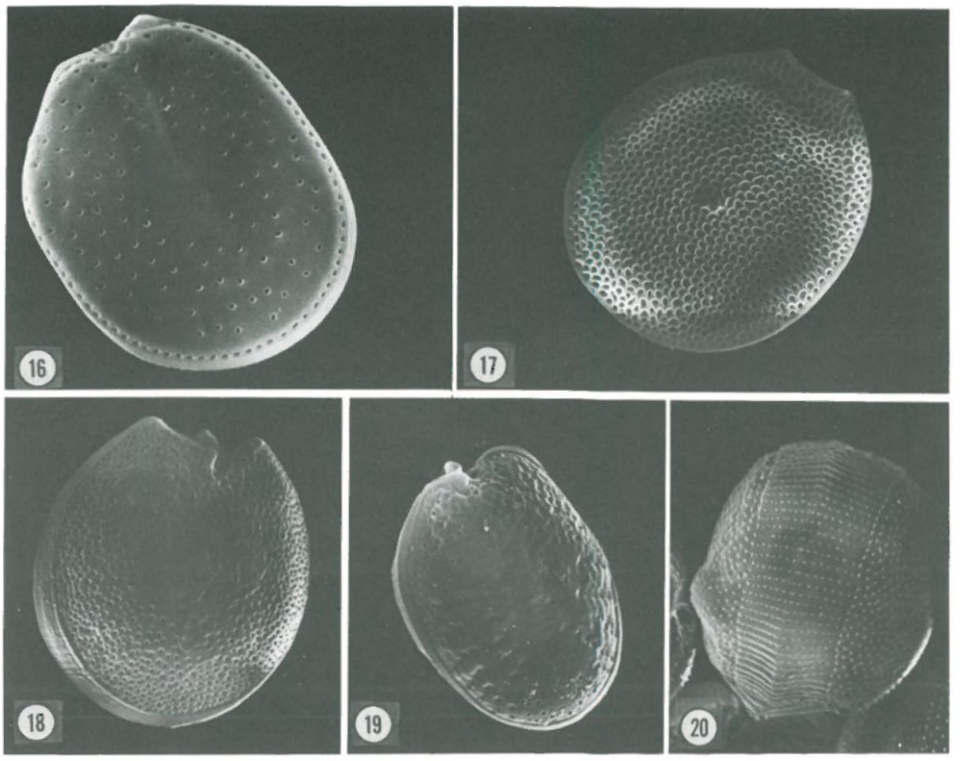


Fig. 16. *Prorocentrum lima;* note pore pattern (SEM).

Fig. 17. *Prorocentrum concavum;* note reticulae (SEM).

Fig. 18. *Prorocentrum emarginatum;* note surface markings and age of cell (SEM).

Fig. 19. *Prorocentrum mexicanum;* note pore structure and pattern (SEM).

Fig. 20. *Prorocentrum minimum* (var. *marie-lebourae*); note spines (SEM).

Prorocentrum lima is distributed world-wide in both cold and warm waters and is the easiest to identify of the group. It is ovoid and has large marginal poroids and smaller valve poroids. The species can range up to 70 μm long. It has 7 or 8 flagellar pore platelets all of which, except one, are attached to the right valve. It can be confused with *P. concavum;* however, *P. concavum* is completely aerolate on both valves which are centrally concave. In addition, *P. concavum* is broader than *P. lima.* These species also can be differentiated by their optical edge effect, i.e. *P. lima* has large marginal pores which produce a valve edge appearance of blunt "teeth," while *P. concavum* has an aerolated margin and the edge effect appears as broad-based spines.

Prorocentrum mexicanum is synonymous with *P. rhathymum* Loeblich, Sherley & Schmidt, 1979 and was properly illustrated by Tafall (1942) except for one character regarding valve markings. The radiating rows of posterior pits that con-

tain trichocyst pores were illustrated by Tafall as spines because of an optical artifact with light microscopy. In fact, the species lacks spines except for a small anterior winged spine on a right valve pore platelet. Recently, Loeblich et al. (1979) have demonstrated that this species and *P. minimum* (Fig. 20) have both flagella emerging from only one of the anterior "flagellar" pores. They designated the larger pore the flagellar pore and the smaller pore, the auxillary pore.

In the Caribbean *Prorocentrum* species I have studied, thecal or valve maturation obscured or changed surface ornamentation in some specimens, e.g. pores and pits can "fill-in" with age, and valve surfaces can become rugose with age. Since *Prorocentrum* can divide longitudinally in mitosis and do not always produce daughter cells within the old theca, the parent valve can be different from the newly formed daughter valve. This process could account for some of the dimorphism observed between left and right valves.

Few of the benthic forms recently described as new species fit neatly into Dodge's (1975) five distinct sections for *Prorocentrum* based on presence or absence of pores, poroids, anterior spines and valve spines. Dodge's arbitrary groupings and species synonymies should be re-evaluated using recent advances in SEM.

A sexual life cycle has not been described for any *Prorocentrum* species although I believe such cycles exist and produce hypnozygotes that are ovoid, smooth and uniformly brown like *Protoperidinium*. Such cells have been observed inside old valves.

2.4. Other genera

Although *Amphidinium* is toxic under laboratory conditions, I know of no instance where it has been documented to cause fish kills in nature even though *A. carterae* can "bloom." Therefore, *Amphidinium* and *Dinophysis fortii,* which has been associated with shellfish illness, are not the major organisms known to elaborate neurotoxins and will not be discussed taxonomically although further studies will probably show that certain *Dinophysis, Thecadinium* and unarmored species produce toxic substances responsible for DSP.

2.5. General systematic perspectives

Taxonomy is the classification of species based on type material, or individual material which is usually fixed and preserved. Systematics is the study of population parameters using a biological or evolutionary species concept of successful interbreeding and speciation through time/space by reproductive or geographical isolation which produces sympatric or allopatric sibling species respectively. In the last decade, dinoflagellate taxonomy has advanced to a systematic approach using sexual life history data and population crosses, electrophoretic analyses for biochemical genetics, chromosome numbers, and other advanced techniques.

Since many dinoflagellate species are "cosmopolitan," one wonders how many strains or sibling species are involved in a specific species complex. I cannot accept that a cosmopolitan species is of one unit stock even though these are planktonic organisms subject to wide dispersal in one form or another. Although biochemical techniques such as isozyme electrophoresis and mitochondrial DNA restriction enzyme analyses have at times been disputed, the analytical refinement of such techniques continues and with new data come new advances. The work of Beam and Himes (cf. 1982) and Schoenberg and Trench (1980) demonstrated the usefulness of breeding groups, DNA content, isozyme patterns, host specificity and infectivity (for *Symbiodinium microadriaticum*), slight morphological differences, antigen-antibody studies and the like in identifying genetic strains of two species complexes. Beam and Himes (1982) characterized 28 sibling species of *Crypthecodinium cohnii* with only 7 strains being of wide distribution. Schoenberg and Trench (1980) characterized 12 "electrophoretic strains" of *S. microadriaticum* from 17 invertebrate hosts (40 isolates). Recognizing and accepting the concept of sibling species in homothallic, and no doubt heterothallic, species complexes may explain different growth and response characteristics among isolated strains but what does such separation and identification really mean; how can it be applied? It can be applied to evolutionary schemes, host-symbiont interactions, subpopulation parameters and dispersal patterns, variability in toxin production, quality of food organisms for aquaculture, and similar aspects; but of what use is it to routine phytoplankton surveys when phytoplanktonologists are working with individual cells? A sibling species cannot be identified by one or two cells unless they are isolated, cultured and tested as a population. Are we to do as some ciliate systematists have done and name each sibling species a new "species" (e.g. Sonneborn 1975)?

In fisheries, the matter is clearer. Fisheries managers, in developing regulations, must address the number of stocks of a given species. For example, different geographic stocks may have different growth rates or sex ratios thus affecting recommended size limits by area or catch quota by area. Different stocks may have different spawning areas and different recruitment patterns thus affecting area/seasonal closures and area/seasonal availability.

Not all dinoflagellates may reproduce sexually. These, by definition, could not represent a species complex of sibling components. I suspect that all estuarine and neritic dinoflagellates do indeed have a sexual cycle although few have been documented. On the other hand, it would be counterproductive for oceanic species to produce hypnozygotes. If they do have sexual cycles, the species are probably homothallic and the cycle may only go as far as a planozygote. Again, how can the concept of sibling species and a species complex be applied to toxic dinoflagellate systematics? One obvious answer is that species should be identified as to area of occurrence, particularly in estuaries and nearshore areas. Some examples are: *Protogonyaulax tamarensis* (Perch Pond, MA), *P. tamarensis* (Salt Pond, MA), *P. tamarensis* (Gulf of Maine), *P. tamarensis* (Bay of Fundy, Canada), *P. tamarensis*

ation of toxins will be a serious problem in the development of chemical assays." Table 2 shows presence and relative abundance of nine toxins discussed by Shimizu (1978, 1979). Hall et al. (1979) found heterogeneous toxin distributions in bivalves less than 25 km apart.

All of the now 12 toxins (including saxitoxin, neosaxitoxin, gonyautoxins I–VIII) have similar chemical structures with differing substituents at carbon 1, 11, and 13, and interconversions leading to saxitoxin have been documented; however, different fractions have different potencies (Hall et al. 1980; Kobayashi and Shimizu 1981; Shimizu and Hsu 1981; Baden 1983). Saxitoxin (2,045 MU/μmol; MU = Mouse Unit) and gonyautoxin III (2,234 MU/μmol) are the most potent (Genenah and Shimizu 1981). Figure 21 shows several possible interconversions.

Kobayashi and Shimizu (1981) speculated that, "Furthermore, the marked difference in toxicity observed between (3) and (7) [gonyautoxins III and VIII] may be due to important differences in the binding mechanism between the toxin molecules and sodium channels." PSP-type toxins block Na influx by binding to receptor sites (1 : 1) near the sodium channel, inhibiting action potentials and nerve transmission impulses. The principal site of action is the peripheral nervous system and associated muscles with secondary activity on the central nervous system.

Lethal dose for PSP-like toxins is weight and species related. Generally, as with other toxins (cf. Baden 1983), oral administration is less potent than intraperitoneal (5–10 μg/kg with mice, see Collins 1978) with intravenous (3.4 μg/kg with mice) being the most potent route, but this may depend on the composition of the extract administered. If death occurs, it is by respiratory failure and not cardiac arrest. Not all animals exposed to PSP toxins suffer mortality due to intoxication. Bivalves such as scallops, oysters, mussels, and clams can accumulate and store the toxins in the hepatopancreas; other filter feeders such as tunicates are also capable of bioaccumulation without adverse effects (Oshima et al. 1982b). Non-filter feeding marine invertebrates such as some gastropods that are surface grazers and some xanthid crabs (Kotaki et al. 1981; Yasumoto et al. 1981) also harbor PSP toxins in varying fractions and levels of toxicity. Differences in filtering or depuration rates can account for some toxin level variation among species, but so can the possibility of metabolic alteration within the animal, as shown in Table 3.

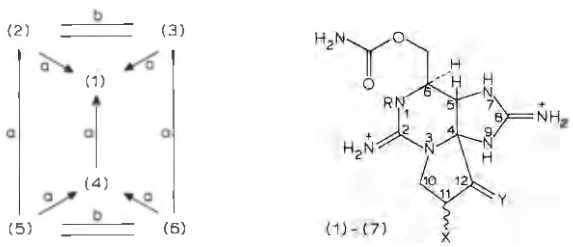


Fig. 21. Paralytic shellfish toxins and their interconversions. After Shimizu and Hsu 1981.

Table 3.

Distribution of toxins from *G. tamarensis* (=*G. excavata*) and scallops.

Compound	% of total toxin*	
	G. excavata	Scallops
α11-(OSO_3)STX (*3*)	~9	58
β11-(OSO_3)STX (*4*)	41	11
α11-(OSO_3)neoSTX (*5*)	~9	3
β11-(OSO_3)neoSTX (*6*)	30	<1
neoSTX (*2*)	11	1
STX (*1*)	0	20
Unknown toxin	0	7

*Percentages determined using a combination of TLC and ion-exchange chromatography. (After Wichmann et al. 1981.)

All planktivorous feeders and browsers are potentially harmful to higher consumers, e.g. vertebrates and man, if these lower animals can accumulate, sequester or bind the neurotoxins and remain unharmed. Man is the most visible victim in PSP intoxications, then birds which feed on bivalves and crabs, then fish. White (1981, 1982a) has documented that various marine fish are susceptible to PSP toxins through the food chain. Death is so rapid in acute incidents that accumulation of toxins in muscle tissue does not occur. White reported that adults and larvae could be affected and suggested that such recurrent events could impact recruitment.

3.2. Neurotoxic shellfish poison and ciguatera (lipid soluble poisons)

Neurotoxic Shellfish Poison (NSP) produced by *Ptychodiscus brevis* and ciguatera produced by *Gambierdiscus* and possibly several *Prorocentrum* spp. have many similarities in chemical structure, e.g. polyether configurations, symptomatology, and physiological activity, yet there are distinct differences. Ciguatera is a tropical fish-borne disease whereby the neurotoxin(s) or its derivatives are accumulated through the food web and bioconcentrated in the flesh of higher carnivores, particularly reef fishes. The causative organisms that produce the original toxic compounds are benthic dinoflagellates closely associated with or attached to macroalgae. Contrarily, NSP is caused by the planktonic, vegetative stage of a dinoflagellate which is speculated to have a temporary benthic resting stage. This species, *Ptychodiscus brevis,* causes water column blooms up to 1.8×10^8 cells/liter and concentrations above 2.5×10^5 liter, can kill fish through respiratory inhibition. Although it can kill fish and some invertebrates, *P. brevis* toxin(s) accumulates in shellfish such as oysters, clams, and coquinas without harming them. At >50 MU/100 gram tissue, the toxins can cause human illness if toxic shellfish meats

metabolites and what are the common pathways for species of such divergent evolutionary affinities and ecological habitats is not currently known.

The function(s) of toxins, if there is one, is speculative. In red tide bloom species that produce monospecific or near monospecific blooms, toxins could act as inhibitors to other species. For example, Freeberg et al. (1979) demonstrated that filtrates from *P. brevis* cultures inhibited the growth of 18 out of 28 phytoplankters tested. In addition, toxin extracts inhibited 8 out of 12 phytoplankters tested including two dinoflagellate species known to co-occur in initial stages of blooms. This suggests that *P. brevis* produces an inhibitory ectocrine that kills or retards the growth of competitive species, and that the inhibitor may be the toxin(s). *Ptychodiscus* red tides have distinct developmental phases; initially at <50,000–100,000 cells/liter the phytoplankton community is mixed with both diatoms, dinoflagellates and microflagellates. Above this concentration, monospecific dinoflagellate blooms develop as if this species outcompeted other components in an isolated stable water mass. At the termination of the bloom, the phytoplankton community is mixed with other dinoflagellates and diatoms. I believe that termination is often due to mixing and dilution of a conditioned water mass whereby inhibitors and/or self-stimulators are diluted to the point of not supporting *P. brevis'* growth (0.2–0.5 divisions/day). Whatever the inhibitor is chemically, it could also be self-stimulatory to *P. brevis,* particularly if the substance was a chelator or ionophore. Fenical (1982) stated that brevetoxin B's polyether structure with its various side groups could function as an ionophore. Murakami et al. (1982) pointed out that PLT_2 from *Prorocentrum lima* and ciguatoxin from *Gambierdiscus toxicus* are both highly oxygenated polyether structures with potential ionophoretic capabilities. Although these species are benthic and do not cause red tides, the similarity in structure, and possibly function, of these polyether toxins is of interest. Therefore, such toxin(s) could act primarily as a metabolic inhibitor or secondarily as an ionophore facilitating the transport of cations across membranes. However, other bloom species that are not toxic also are capable of monospecific development, again in a restricted water mass initially. Perhaps the metabolic pathways are similar with different end products, or perhaps toxins do not figure in population development and other released endocrines are involved in biological conditioning and exclusion. If dinoflagellate toxins were defensive in nature then one would expect that they all would be exotoxins; they are not.

3.3. Assays

One aspect of toxins as relates to human health is the detection method used in shellfish monitoring programs. Some methods take a day, others a week, depending on toxin extractability and bioassay organism used. PSP is mainly tested by mouse bioassay, although a fluorometric test was developed by Bates and Rapoport (1978). The fluorometric test does not detect total toxicity and needs refinements (Shimizu

and Ragelis 1979). The mouse bioassay for PSP and NSP is cumbersome and not cost effective; it requires maintaining mice in a certain weight range. Additionally, death time versus toxin level is not linear. In PSP, the mouse bioassay has been standardized against saxitoxin (STX), and although STX has high potency it is usually in lesser quantities than the other toxic fractions and may not be the predominant orally toxic fraction. In NSP, the mouse bioassay has the same problems and lacks standardization. As Baden et al. (1982) have demonstrated, T17 is the predominant orally toxic fraction and i.p. injection into mice could underestimate or overestimate potential toxicity to humans. Therefore, various research groups are pursuing rapid immunoassays for PSP and NSP, as well as ciguatera. Immunoassay requires that a purified nonproteinaceous toxin be conjugated to a protein so that antisera can be produced in a host animal, e.g. rabbit. Researchers have already produced antigen complexes for some toxins and are working on NSP. Some day field immunoassay kits that require little incubation time will be available to detect PSP, NSP, DSP, and ciguatoxin and these tests will have a higher sensitivity than any current method.

4. ECOLOGY

Steidinger (1973) discussed conditions favoring red tides under the subheadings of Seed Populations, Nutrients and Growth Factors, and Hydrologic and Meteorologic Factors. Later, this concept was formalized into suggested sequential stages in the development of all red tide bloom events: initiation, followed by support and then maintenance (Steidinger 1975a,b). Evans and Taylor (1980) rightfully chose to divide "maintenance" into its two component stages, that of accumulation, or rather concentration, and dispersal. It is now accepted that there are four developmental stages in dinoflagellate bloom dynamics and that the first two, initiation and growth, may have common denominators in the form of salinity, temperature and light variables. The latter two, concentration and dispersal (including termination by dilution), also have common denominators in the form of hydrographic features.

Steidinger (1973), in explaining the materialization of red tides, said "Ryther [1955] stated, 'Thus, there is no necessity to postulate obscure factors which would account for a prodigious growth of dinoflagellates to explain red water. It is necessary only to have conditions favoring the growth and dominance of a moderately large population of a given species, and the proper hydrographic and meterological conditions to permit the accumulation of organisms at the surface and to effect their future concentrations in localized areas.' In this context, red tides can develop in waters without excessive nutrients or extremely high cell counts. Yet, certain prerequisites are necessary to *initiate* and *support* even moderate blooms, e.g., light, temperature, nutrients, and growth factors. Ryther's statement is an extremely important concept in understanding and explaining red tides because, in fact, winds,

tides, currents, convergences, divergences, and pycnoclines act as *concentrating mechanisms for planktonic organisms; they can create discrete patches or streaks* of red water. In addition, the same forces can *disperse* high cell concentrations and lessen the effects of an outbreak." All Steidinger (1973, 1975a,b) did was interpret and expand on Ryther's original observations and deductions by adding the source of seed populations and conceptualizing sequential stages in bloom dynamics. In the last 10 years, much of the red tide research on *Protogonyaulax* and *Ptychodiscus* has concentrated on these developmental stages, particularly initiation and concentration, and the concept of localized areas of accumulation of resting seed population(s), termed "seed beds", first introduced by Steidinger in 1974.

The ecology of toxic dinoflagellates has historically only addressed water column bloom dynamics, but more recently the ecology of ciguatera-causing organisms has received intense investigation since the identification of *Gambierdiscus toxicus* and *Prorocentrum* spp. from Pacific and Atlantic benthic habitats. Their population dynamics differ entirely from that of classical red tide or "red water" events because of their epiphytic association with tropical and subtropical macroalgae. Yet, the chemistry and physiological activity of the toxins produced by these benthic species is similar to other polyether toxins isolated from *P. brevis* and *Dinophysis fortii,* planktonic bloom species.

4.1. Initiation and growth of planktonic bloom species

Seed populations, or an inoculum, are a prerequisite to increased dinoflagellate cell concentrations. Benthic resting stages, either as spores, cysts, or hypnozygotes were speculated to contribute to the occurrence and/or seasonality of marine dinoflagellates by Braarud (1962), Prakash (1967), Wall and Dale (1968), Wall (1971), Reid (1972), and Steidinger and Ingle (1972). Later, Steidinger (1974) introduced the concept of seed beds for dinoflagellate bloom species whereby dormant resting stages accumulate in localized areas and re-inoculate the overlying water column. This then is the source of planktonic blooms in marine waters as it often is in freshwater lakes and ponds.

Many researchers recognize that excystment of benthic resting stages such as hypnozygotes, does not automatically create planktonic blooms; it merely provides an inoculum that must increase by vegetative division and growth before blooms are detectable. Also, it should be emphasized that red tides are not sudden population explosions due to increased mitotic division rates. Instead, they are normal population increases (typically up to 1 division day) that are confined (growth rate exceeds diffusion and loss) or physically concentrated by boundary layers, frontal systems, or convection cells (see Ryther 1955; Steidinger 1973; Margalef et al. 1979), sometimes in concert with the organism's vertical migratory behavior (see Seliger et al. 1970; Tyler and Seliger 1978; Tyler et al. 1982).

Benthic hypnozygotes with thick, layered cell walls have been documented for

both armored and unarmored dinoflagellate bloom species, e.g. *Protogonyaulax tamarensis* (Dale 1977; Anderson and Wall 1978; Turpin et al. 1978), *Gonyaulax monilata* (Walker and Steidinger 1979), *Gyrodinium uncatenum* (Tyler et al. 1982), and *Gyrodinium fissum* (L.M. Walker, unpublished), among others. A diversity of benthic resting stages when excysted have produced motile stages representing *Heterocapsa, Scrippsiella, Peridinium, Gonyaulax, Protoperidinium, Gymnodinium, Gyrodinium, Polykrikos,* and others; most of these are thought to be hypnozygotes or dormant 2N cells. *Ptychodiscus brevis* produces planozygotes and is suspected to produce hypnozygotes (Walker 1982). In some cases, these benthic cells with reduced cytoplasm and lowered metabolism have been documented to act as seed beds (Anderson and Morel 1979; Walker and Steidinger 1979, personal observations; Tyler et al. 1982) and thus account for the repeated occurrence of a bloom species in a specified locale and time frame. For example, most blooms of *Gonyaulax monilata* occur in August and September in the Gulf of Mexico and its estuaries. The same timing holds true for several back canals and a causeway in Tampa Bay. Steidinger and Haddad (1981) reasoned that all estuarine and inshore dinoflagellate bloom species produced hypnozygotes.

Scientists previously have speculated that induction of the sexual cycle and production of gametes was a survival mechanism in response to poor growth conditions, e.g. reduced nutrients. The demonstration that some species' sexual cycle could be artificially induced through inorganic depletion in culture media added to the basis of this speculation. However, documentation of sexual stages *in natura* is not extensive because of the timing of events, particularly with gamete production and fusion. Planozygotes are often the same size and shape of motile, vegetative cells but can be identified by the presence of two longitudinal and two transverse flagella and/or nuclear aspects. Cysts or hypnozygotes have been observed in plankton collections, but their origin was not known. Recently, Tyler et al. (1982) observed that *Gyrodinium uncatenum* planozygotes appeared at the end of a bloom while Anderson (personal communication) has observed *Protogonyaulax tamarensis* planozygote formation in the early stages after several vegetative divisions. Steidinger and Haddad (1981) speculated on internal storage product levels, or other possible chemical gradients, determining the induction of the sexual cycle and later the timing of excystment. The timing of zygote formation can and does influence the area of deposition or accumulation of hypnozygotes which is more important in allochthonous blooms such as *Ptychodiscus brevis* which originate 18–74 km offshore and can be transported by frontal systems, winds, and tides to inshore waters.

Not all hypnozygotes excyst nor do they necessarily excyst in synchrony, rather mature zygotes may have temporally limited, phased germination which may be related to metabolic activity and threshold levels of stored oil or starch reserves, and therefore temperature. Anderson (1980) has demonstrated the importance of temperature changes in *P. tamarensis* excystment both in the laboratory and *in situ*. Watras et al. (1982) developed a model to predict the timing of *P. tamarensis* water

column blooms (vegetative division) in relation to temperature and salinity but not population declines. Support or growth then still relates to temperature and salinity, as does germination or initiation. This is probably true for many planktonic bloom species. However, at the termination of blooms, temperature, salinity and even major nutrients were favorable for growth, therefore they reasoned that other factors such as predation, encystment, micronutrients, or advection overrode temperature and salinity influences in growth.

The mapping of seed populations or localized seed beds as suggested by Steidinger (1975b) and done by Lewis et al. (1979) and Anderson et al. (1982b) for New England waters, has its obvious value in forecasting potential areas of impact depending on the adequacy of sediment analyses (Anderson et al. 1982a) and interpretation of hydrographic influences. Mapping of benthic resting stages has its advantages over mouse bioassay or chemical assay of shellfish meats at selected stations because, as Anderson et al. (1982b) and Baden (1983) have pointed out, different *P. tamarensis* populations can have different levels of toxicity depending on the toxic fractions present and their conversion to more toxic fractions such as saxitoxin. Therefore, toxicity may not always be detectable because of detection levels and seasonal occurrence. In estuaries and ponds, the main impact area is confined unless the population is dispersed into nearshore coastal waters.

In coastal waters, blooms, initiating in deeper waters through germination of hypnozygotes, can inoculate other areas by being transported, either longshore or inshore. Therefore, the absence of a seed bed of a toxic dinoflagellate in a specific area does not always mean that an area will not be impacted because nearby water column populations (from other seed bed sources) could inoculate other water masses. Once inoculated, the area could have recurrent outbreaks depending on the production and future viability of benthic hypnozygotes in the new locale. Based on the above, it also would seem that the question of whether PSP outbreaks are spreading is open to discussion since in many areas, the potential of a bloom has always been there but not in numbers sufficient to cause problems. Unusual current events and/or some of man's activities (e.g. shellfish relaying) could introduce large numbers of a seed population, thus maximizing the potential for recurrent outbreaks of PSP as occurred in 1982 in Massachusetts.

4.2. Concentration and dispersal of planktonic bloom species

Many different physical mechanisms such as winds, tides, pycnoclines, upwellings, currents, and resultant convergences or divergences of varied types can actively or passively concentrate motile dinoflagellate populations. Some of these mechanisms are dependent on the organism's positive and negative phototactic responses. In some species, survival and dispersal is dependent upon their ability to migrate through water mass boundaries such as pycnoclines. In other species, or in the same species under different environmental and physiological conditions, inhibition of

vertical migratory behavior also may retain the population in a moving water mass (see Tyler and Seliger 1981). Kamykowski (1981) tested four dinoflagellate bloom species in relation to their ability to migrate through artificially created thermoclines. He found that all four species migrated through thermal differentials of 7°C, but that absolute temperatures and inferred tolerances were more critical than the size of the differential. Kamykowski concluded that "A multi-parameter response matrix is required to model coupling between organisms and biologically-active physical mechanisms realistically."

In two different bloom species, *Prorocentrum minimum* var. *marie-lebouriae* and *Gyrodinium uncatenum,* Tyler and associates (1981, 1982) have demonstrated that the downwelling convergence at an estuarine frontal boundary (halocline) concentrates, or rather entrains, either vegetative or resting stages in a moving subsurface lens, thus effecting dispersal over large distances. Such large frontal systems with their associated boundaries also occur in coastal waters and entrainment and dispersal along this boundary can occur as in estuarine systems (see Holligan 1978, 1979; Haddad and Carter 1979; Steidinger and Haddad 1981). The boundary layer then becomes a stable environment for growth and is fronted by mixed and stratified water masses (see Pingree et al. 1978; Heaney and Eppley 1981). According to researchers working on frontal boundary systems in the North Atlantic Ocean, vertical sheer can introduce a dinoflagellate population or patch at one point but it will spread along the frontal region by horizontal diffusion or mixing. Margalef et al. (1979) stated, "It is our opinion that in such places [upwelling regions], red tides are often associated with relatively sharp contacts between turbulent water and more stabilized volumes ... All marine fronts associated with upwelling or with tides are potential places for multiplication of red tide organisms, especially for the species more able to counteract decaying turbulence ..."

Steidinger and Haddad (1981) discussed these parameters in relation to stable, defined water masses, "If the population develops in a defined water mass, a bloom can develop and become monospecific by lack of predation, inhibitory exclusion, or competitive advantage through physiological rates or nutrient utilization ... Once the integrity of the water mass and/or boundary layer is disrupted, dilution and mixing can create unfavorable conditions for support in open, marine coastal waters if the receiving waters are not environmentally suitable." Both statements were in relation to coastal or shelf frontal systems; however, the concept of a defined water mass can be applied to estuaries, lagoons, or ponds that have poor flushing, low water exchange, and therefore high residency times. Monospecific blooms or above background levels of toxic dinoflagellates can be reached in these areas for the same reasons, "lack of predation, inhibitory exclusion, or competitive advantage through physiological rates or nutrient utilization". In some areas, such as the Massachusetts ponds that Anderson is studying, pycnoclines or other boundary layers are not a factor in bloom development and transport. The important factor is the confinement of the water body and minimal loss through advection.

Mueller (1979), Gordon et al. (1980), Steidinger and Haddad (1981), Munday and Zubkoff (1981), and Haddad (1982) among others have all shown the application of remote sensing, either from aerial photography or satellite imagery, in the detection of high chlorophyll areas due to dinoflagellate blooms. Often these same images show upwellings, eddies, and other thermally differentiated surface features. The fact that thermal features can be detected from various satellite platforms, e.g. GOES, NESS, and Nimbus 7 satellites, without concurrent ground truthing, makes this an attractive tool for predicting red tides on shelves when such red tides are coupled to oceanic current intrusions and eddies. GOES and Coastal Zone Color Scanner (CZCS) imagery from Nimbus 7 have been used by Haddad to show this coupling for West Florida Shelf *Ptychodiscus brevis* red tides and their transport along the coast. Murphy et al. (1975) used Landsat imagery to delineate turbidity and movement of West Florida Shelf water through the Florida Keys in conjunction with drift bottle studies to illustrate the transport of a 1972 *P. brevis* bloom to the Florida east coast. Since 1972, *P. brevis* blooms have been transported, via entrainment, from the west to east coasts in 1977 and 1980. Therefore, since blooms take 2–4 weeks to develop offshore (up to 0.5 divisions/day), presumably in a boundary layer, being able to detect specific oceanic features associated with initiation would enable a short-term predictive tool. F. Vukovich (Research Triangle Institution, NC, personal communication) is working on a predictive model for surface transport in the eastern Gulf. He can use satellite data to determine surface water temperatures along boundary systems within 0.5°C and infer salinity, thereby deriving geostrophic flow to predict surface transport. In one drogue test, his model had a correlation coefficient of 0.8.

Although satellite imagery can be used in certain areas, e.g. continental shelves and large estuaries, for bloom detection and potential prediction, it cannot be used in small estuaries or ponds because of resolution limits. For example, CZCS resolution is 800 m while Landsat is 80 m and GOES is 8 km. Currently, blooms of *Protogonyaulax tamarensis* in Massachusetts salt ponds can be forecast by the maturity of benthic hypnozygotes based on cytological features alone but only several days beforehand (Anderson, personal communication). If seed beds have been mapped for specific areas of toxic dinoflagellate blooms, then a "maturity index", say by percentage, may be a successful predictive tool, although it is time consuming and not synoptic. The advantage of satellite imagery, if readily available within 1–5 days, is that it is synoptic for large areas and entire coastlines.

4.3. Benthic ciguateric species

Since *Gambierdiscus toxicus* was identified as the toxic organism causing the tropical fish poisoning called ciguatera in 1977, various researchers have studied this organism and its toxic properties. However, the ecology of this species and other suspect ciguateric species in the genus *Prorocentrum* are not well known. *Gambier-*

discus toxicus and other epiphytic dinoflagellates occur on a variety of macro-algae including filamentous, foliose and calcareous forms (see Yasumoto et al. 1979; Taylor 1979b; Yasumoto et al. 1980a; Shimizu et al. 1982; and others). The species also occurs in benthic debris and rubble but is most abundant on red and brown algae, e.g. *Hypnea, Jania, Spyridia, Turbinaria, Sargassum,* and others of tropical or sub-tropical occurrence. As an epiphyte, it is usually attached to the host by a mucous thread and is not normally encountered in planktonic sampling with water samples or nets unless the collection followed a turbulent event. Other dinoflagellate epiphytes or those of benthic habitat found in association with *G. toxicus* at both Atlantic and Pacific reef sites known to be ciguateric are *Prorocentrum lima, P. concavum, P. emarginatum, P. mexicanum, P.* spp., *Ostreopsis ovata, O. siamensis, O. lenticula, Coolia monotis, Thecadinium* sp., *Scrippsiella subsalsa, Amphidinium carterae,* and others. This benthic assemblage may change slightly in composition and drastically in numbers of any given species (Yasumoto's work and personal observation). Since several toxic species of this benthic dinoflagellate assemblage occur in non-ciguateric areas and in temperate waters, toxicity should be verified for each study area and not assumed. Strain differences may include low toxin production or nontoxicity as occurs in other dinoflagellates discussed in this present synthesis.

Many red and brown algae are "leaky" and therefore may, in essence, create a phycosphere of high dissolved organic load; epiphytes such as *G. toxicus* and *P. lima* may be physiologically adapted to these enriched micro-environments. The assemblage composition may depend on nutritional requirements and the ability to function heterotrophically at low light or at night, as well as the ability to produce mucoid attachment processes.

Banner (1976) presented an interesting review of historical literature and research, including: 1) verification that ciguatoxin is trophically transmitted and appears in herbivores first, then carnivores with the top reef carnivores being the most toxic; 2) detrital feeding fish also become ciguatoxic thus implicating a small causative organism; 3) "In both the Pacific and Caribbean, ciguatera seems largely confined to islands and is not found along continental margins," and 4) not all disturbed reef areas (dredging, blasting, storms, etc.) become ciguateric. The latter point is important ecologically because it had been speculated that reef disturbances which killed coral provided new substrate for colonization by algae or other possible causative organisms. Besada et al. (1982) speculated that rafting of macroalgae with attached toxic dinoflagellates could seed suitable areas; this hypothesis is appealing and would be plausible after certain storm events. Yasumoto et al. (1980a) found little correlation with distribution of *G. toxicus* and basic nutrients. However, they also noted that "... strong light intensity and low salinity act as deterrent factors and may affect the distribution of this organism", and that "It may be also advantageous for the organism to live in turbulent places because the silt, sand, and other sediments can be removed from its surface."

Besada and collegues found *G. toxicus* in an intertidal pool while Baden (personal

communication) and others have found benthic toxic dinoflagellates, either *Gambierdiscus* or *Prorocentrum,* in harbors or bays near docks. These inshore occurrences of demonstrated toxic dinoflagellate populations raise a question concerning the distribution of ciguateric fish and their assumed association only with reef areas.

5. CONTROL OF MONOSPECIFIC DINOFLAGELLATE BLOOMS

Since red tides can cause shellfish poisoning and/or fish kills, thus affecting the economy through reduced shellfish sales and tourism, the question of control often arises in the public's mind. The question then becomes whether or not red tides can be controlled and if so, do we want to control red tides or do they serve a "purpose".

Various means of control have been postulated, such as: introducing a predator, competitor, parasite, or pathogen; removing necessary trace metals by chelation; adding toxic or lytic chemicals or growth inhibitors; changing optimal environmental parameters, such as light; artificially introducing turbulence and turbidity; and many others. All methods proposed to date involve treating the symptoms, i.e. water column motile populations, and not the cause, i.e. benthic resting populations that initially seed the water column. In coastal or large estuary blooms, treatment may involve millions of m^3, and depending on whether the origin of the bloom is auto- or allochonthous, treatment may have to be daily with each tidal cycle due to reinoculation. *Ptychodiscus brevis* red tides will be used as an example.

The first attempt at controlling Florida red tides occurred in the 1950s when copper sulfate was sprayed from planes and dragged in bags behind boats. Copper was suggested as a control agent because it is a demonstrated algicide and because federal researchers showed management agencies and the public that adding copper pennies to an aquarium of cultured *P. brevis* killed the cells; they settled to the bottom and the water cleared (Robert M. Ingle, personal communication). No one followed that demonstration by placing fish in the aquarium. If they had, the fish would have died because lysed cells release endotoxins. Any disruptive chemical, even freshwater, that lyses cells will increase the toxicity of the growth medium. The toxin(s) are quite stable in media for weeks, even in light and at elevated temperatures. The actual treatment of Tampa Bay waters was totally unsuccessful because of the vast area affected and because copper sulfate increases toxicity of the water by lysing *P. brevis* cells. Copper, although successful in controlling nuisance algae in freshwater lakes, was not effective in an open marine system containing an endotoxic species. Additionally, copper treatment can lead to decomposition of killed animals and then anoxia, creating a temporarily unsuitable habitat for fish.

"Red tide" cannot be seen at the water surface unless it is very concentrated and although dense populations of *P. brevis* are patchy in time/space, lower concentrations (10^3–10^4 cells/liter) exist between these hot spots both horizontally and verti-

cally. Thousands of square miles have been affected. *Ptychodiscus brevis* is not surface-bound and may be distributed throughout the water column unless restricted by a thermocline. Consequently, large volumes of water would need treatment. Local patches could not be controlled successfully because water is transitory and a fixed site would be reinoculated by surrounding water or tidal action. Florida red tides initiate 18–74 km offshore and can occupy areas from inside bays to at least 30 km offshore, concurrently. Consequently, chemical treatment, and other methods as discussed later, will be ineffective in controlling Florida red tides once they reach the threshold level for bloom proportions.

Martin et al. (1973) suggested ciliates (hypotrichs?) as a predatory control based on an observed decline in *P. brevis* cell numbers and a corresponding increase in cell debris with the addition of ciliate cultures. However, the study did not eliminate the possibility of interspecific competition. These authors suggested predation or phagotrophy as the mechanism of control. Indeed, hypotrichs are common contaminants in marine isolates and often outcompete phytoplankton species in culture if a POC substrate is available, e.g. settled cell debris. Although ciliate predators, e.g. tintinnids, are known to feed on dinoflagellate blooms, predation of *P. brevis* by any zooplankter is not commonly observed in field samples. Steidinger and Joyce (1973) pointed out that if a selected predator consumed 1,000 *P. brevis* cells/day, it would take 26 trillion predators to treat a 5 mi^2 area (at 2×10^9 *P. brevis* cells/m^3) just to a depth of 1 meter. If 1 million predators/5 gal could be harvested and lypholized every 2 weeks, it would take 10 years using a pond of 500,000 gal capacity to treat this small area just once. Just as important as feasibility is the fact that a successful predator (one that is not killed) would accumulate the toxin, as White (1981, 1982a) has shown for *Protogonyaulax* and pteropods, and therefore become a toxic vector to higher trophic levels. Would this approach truly be a solution regardless of cost?

Another control method, as suggested by Kutt and Martin (1975), Eng-Wilmot and Martin (1977), Hitchcock and Martin (1977), McCoy and Martin (1977), Moon and Martin (1980, 1981) and other collaborators is the use of a blue-green alga identified as *Gomphosphaeria aponina,* a brackish/marine, blue-green alga. This organism elaborates a sterol surfactant named "aponin" that is reported to cause irreversible cytolysis in *P. brevis* (Moon and Martin 1980). Living *G. aponina* cells through the elaboration and release of this bioactive compound also cause cytolysis of *P. brevis* within 4–10 days and the resultant media becomes toxic to seawater-adapted *Poecilia sphenops* (freshwater black mollies). In one experiment, extracted aponin incubated with *P. brevis* cultures (50 ml) for 24 hours killed the mollies within 627 ± 111 min (0.2 ml aponin residue) to 28 ± 7 min (3.0 ml aponin residue) while *P. brevis* alone killed the fish at 407 ± 79 min. Thus, high concentrations of aponin increased toxicity of the medium by lysis of *P. brevis*, but lysis was dose related and at low doses aponin was speculated to "mitigate" toxicity (McCoy and Martin 1977) based on the mean of 5 death times. If it takes 3.5×10^6 *G. aponina*

cells/liter to cause a 60% mortality of *P. brevis* after 10 days of confinement, then 3.5×10^9 cells/m^3 or 9.1×10^{15} cells/mi^2 would be needed to treat 1 mi^2 to a 1 m depth, once. If it takes 30 ppm (although cytolysis initiates at 1 ppm) of crude aponin extract to produce about a 93% mortality in *P. brevis* cultures then 77.7 metric tons would be needed to treat 1 mi^2 to a 1 m depth. If aponin, the extract, were proposed as a control rather than living cells then it would require 2.9×10^9 liters of *G. aponina* culture to produce the 77.7 metric tons since extraction yields only 0.027 g per liter. Since *P. brevis* is not surface restricted during blooms, treatment should apply to more than 1 m depth because water movement and mixing will reinoculate the top meter. The extract, aponin, is hydrophobic and therefore would not disperse readily unless bound to a carrier or pressure released from the bottom. Also, living *G. aponina* may lose its reproductive potential in the water column if cells sink as they do in unaerated culture vessels.

Maestrini and Bonin (1981) in their synthesis of "allelopathic relationships between phytoplankton species" cited aponin as having "no effect on fishes, crustaceans, and bacteria" and therefore may be a suitable control agent. However, only 2 species of freshwater mollies and 1 euryhaline minnow, 1 crustacean (*Artemia*), 1 polychaete, and 1 phytoplankter (*Prymnesium parvum,* up to 20% kill for 10 to 100 μliter per 10 ml culture) have been tested. Also, fish eggs, fish larvae, other adult fish, penaeid shrimp, meroplankton such as crab larvae and veligers, and other phytoplankters, such as naked phytomicroflagellates which numerically dominate estuarine and coastal waters of Florida have not been tested. The fate of lysed *P. brevis* cells increasing toxicity of sea water and causing kills of a variety of animals has not been tested adequately.

Maestrini and Bonin also stated that "Martin and associates postulated that *G. breve* should have optimal proliferation during mid-spring and late autumn, and *G. aponina* may proliferate during late spring and early summer and autumn. As a matter of fact, several red tides have occurred during late autumn and one during mid-spring, exactly during the postulated periods, namely when *G. aponina* cannot grow, supporting the opinion that the mechanisms postulated from *in vitro* experiments really occur *in situ.*" Actually, based on historic data, the "optimal proliferation" of *P. brevis* is in late summer, mid-autumn, not mid-spring and late autumn. Since 1947, red tides have only initiated twice in spring while summer-autumn has accounted for 21 red tides, exactly the time when *G. aponina* reportedly proliferates. Therefore, the speculation that *P. brevis* blooms because of the absence of *G. aponina* growth is invalid. *Ptychodiscus brevis* red tides initiate 18–74 km offshore while *G. aponina* is a nearshore, benthic cyanobacterium. At initiation the two species are widely separated geographically. In addition, *P. brevis* is a bloom species while *G. aponina* is not. Therefore, it is physically impossible for *G. aponina* to control *P. brevis* growth *in natura,* as suggested by Meastrini and Bonin.

Although contolling Florida red tides after they reach critical concentrations in the coastal water column ($>5–10 \times 10^3$ cells/liter), is not feasible because of area, volume, and hydrographic influence, control of seed beds may be possible, if seed

beds are localized accumulations. A question some scientists have then asked is whether or not contol is advisable, or do apparently destructive red tides serve a function in the system. Any answer to this question is one of speculation since community interrelationships such as succession, diversity, efficiency and stability are not totally understood.

Florida red tides with their associated patch reef and inshore fish kills could act as some types of natural fires or other perturbations. Forest fires burn unevenly leaving some of each habitat intact whilst those that are affected, change. In general, fires return successional patterns to earlier and more dynamic conditions and increase habitat efficiency and productivity. They control disease, particularly fungal diseases, remove unfit species, provide more suitable habitats for a greater variety of animals, and allow the invasion of pioneer species (Kozlowski 1974). In addition, natural fires increase the availability and amount of organic and inorganic nutrients or essential elements (Kozlowski 1974; Christensen and Muller 1975), and according to Keeley and Zedler (1978) "It seemed likely that the burned stands would eventually reach a state of development comparable to that shown in the preburn stand without any significant shifts in composition."

In comparison, Florida red tides can defauniate patch reefs in 13 m–33 m offshore, but as with certain types of fires not all reefs are affected nor total populations, and it takes a year for them to return to a similar ichythofaunal composition (Smith 1976). Smith stated "Minimum species replacement, but wide fluctuations in abundance characterized reef-fish succession following the red tide." The same is true for estuarine, intertidal infaunal kills. Dauer and Simon (1976) demonstrated that polychaetes repopulated a defauniated sandy beach in Tampa Bay within 2 years and that the new population structure, once recruited and established was similar to pre-red tide conditions. They stated "The pattern of a relatively stable species composition with great changes in the distribution of individuals among species through time has previously been reported for the marine environment." Therefore, based on limited studies, it would appear that red tides have short-term affects (2–5 years) on eventual community structure. During this time of repopulation, growth, and "instability" there can be, theoretically, increased system efficiency.

Margalef (1968) spoke of ecosystem stability in two different ways, that of achieving a steady state under constant conditions and that of achieving stability by having a high resistance to destructive changes originating outside the system. Margalef considered environmental perturbations as exploitations and said "Exploitation has a rejuvenating effect on exploited ecosystems. It is sufficient to add a protozoan to a senescent culture of algae to observe a rejuvenation in the plant population, with a higher energy flow per unit biomass and a more juvenile composition of plant pigments. In a way, the addition of a new trophic level to a system means a certain amount of rejuvenation of other trophic levels, increasing turnover." This is what happens in partially altered or defauniated ecosystems wherein

pioneer or opportunistic species recruit to these areas. The system becomes a mosaic of low maturity/high turnover and high maturing/high biomass and perhaps one fuels the other energetically.

In relating community structure and interactions to terrestrial production and harvest, Odum (1971) stated "the fluctuations, however, whether due to natural causes or arranged by the farmer are necessary to a harvest system. They also help keep out more complex associations of animals and plants that would divert energies from the harvest." Odum in a section entitled "Energy Channeling by the Addition of an Extreme" discussed the interjection of an extreme fluctuation into a system and the resultant lower diversity but higher production, "If it is possible to add an extreme to which the natural components must adapt, diversity drops out and the yields, although less, may be sufficiently channeled to provide a harvest for man." Patch reef communities in the eastern Gulf of Mexico do adapt to fluctuations such as red tides, storms and hurricanes, cold water intrusions, and other extremes or they wouldn't exist. Perhaps such environmental impacts allow the harvest of more desirable, higher trophic species or as Odum stated "... a simpler system with a large net yield may replace the complex one with many low yields". Additionally, fishermen report higher catches of shrimp and stone crabs following red tides. Such increased yields may be related to less predation, higher food availability, or reduced interspecific competition. Systems under pulsed stress survive and it may be that the components of the system are dependent on environmental extremes to avoid becoming mature, more vulnerable systems subject to total collapse in the event of a catastrophic fluctuation as suggested by Vogl (1980) in discussing perturbation-dependent ecosystems.

The example above relates to Florida red tides or to red tides with extensive marine mortalities; it does not intend to imply that *Protogonyaulax* red tides, which mainly cause toxic shellfish, act in a similar role.

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