

Parasitic Life Styles of Marine Dinoflagellates¹

D. WAYNE COATS

Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USA

ABSTRACT. Several genera of marine dinoflagellates contain species that have evolved parasitic life styles. Dinoflagellate infections have been reported for a wide range of host organisms including sarcodines, ciliates, free-living dinoflagellates, various invertebrates, and a few vertebrates. Some dinoflagellates even parasitize other parasitic dinoflagellates. Most species are obligately parasitic and rely on heterotrophy as their sole means of nutrition; however, some are mixotrophic, as they possess chloroplasts during part or all of their life cycle. Many are ectoparasites that use highly specialized structures to attach to their host and feed, while others are intracellular parasites that feed by osmotrophy. Parasitic dinoflagellates often have adverse effects on their host that can lead to reproductive castration or death. The ecological importance of parasitic dinoflagellates is particularly evident during epidemic outbreaks that cause mass mortality of host organisms. Species that infect fish can pose threats to aquaculture, while other species can make commercially important crustacea unpalatable. In the planktonic realm, parasitic dinoflagellates influence the structure and function of the microbial food web. They compete with copepods and other grazers by utilizing ciliates as hosts and can stimulate rapid recycling of nutrients by causing the decline of toxic and non-toxic red tides.

Key Words. Disease, crabs, epizootic, fish, parasitism, protists.

THE first well documented case of a parasitic life style among the dinoflagellates was provided more than a century ago when Pouchet (1885) described *Gymnodinium pulvisculus* (now *Oodinium pouchetii* Chatton) as an ectoparasite of appendicularia. By the early 1900's, research on parasitic dinoflagellates had blossomed under the leadership of the French protistologist Édouard Chatton, who along with his students and colleagues revealed a surprising diversity of parasitic taxa. Much of that early work emphasized morphological and developmental attributes of the many newly discovered parasites, while simultaneously demonstrating the ability of dinoflagellates to infect a broad array of protistan and metazoan hosts (e.g. Chatton 1920, 1952; Chatton and Biecheler 1935, 1936; Chatton and Hovasse 1938; Chatton and Poisson 1931). Jean and Monique (Enjumet) Cachon, working out of the marine lab at Villefranche-sur-Mer during the middle of this century, significantly expanded the study of parasitic dinoflagellates through numerous contributions on parasite cytology and life history. Their work, summarized in a synthetic review just over a decade ago (Cachon and Cachon 1987), encompassed light and electron microscopic investigations that provided insightful clues about the structure and function of dinoflagellate organelles, including the mitotic spindle apparatus, the flagellar rootlet system, and the pusule. More recent advances have come from German researchers (e.g. Drebes 1969; Drebes and Schnepf 1982; Elbrächter and Drebes 1978; Schnepf and Deichgräber 1984; Schnepf and Elbrächter 1992), whose studies on parasites of marine plankton have revealed intriguing feeding behaviors like "myzocytosis" (see Hansen and Calado 1999).

The body of literature on parasitic dinoflagellates has increased at an impressive rate over the past decade, due largely to concerns over dinoflagellates as disease agents in marine fisheries and a growing interest in the role of microbes in marine food webs. Information on host-parasite ecology is becoming more available (e.g. Coats et al. 1994, 1996; Kimmerer and McKinnon 1990; Love et al. 1993), and molecular tools are providing improved ways to identify infected hosts and parasite taxa (e.g. Field and Appleton 1996; Hudson and Adlard 1996; Smith, Levy and Noga 1992). The goal of this review is to briefly summarize parasitic behaviors of dinoflagellates, with particular attention to the ecological significance of parasitism by these microbes.

Taxonomic and trophic diversity. Differentiating between parasitic and predatory behaviors of dinoflagellates is often difficult, particularly when dealing with free-swimming species that attack and consume their host (or prey) on time-scales of minutes to hours (e.g. Drebes and Schnepf 1982; Elbrächter 1988). Consequently, some dinoflagellates have been classified as parasites on some occasions and as predators at other times, even for publications by the same authors (e.g. Pfiester and Popovský 1979; Popovský and Pfiester 1982). In reality, heterotrophic dinoflagellates fall along a predator-parasite continuum, for which trophic classification of intermediate forms becomes somewhat arbitrary. One approach to this dilemma has been to discriminate parasitic dinoflagellates as those forms that have morphologically different feeding and reproductive stages and that produce more than two daughter cells after each feeding event (Gaines and Elbrächter 1987). By this definition, dinoflagellates like *Paulsenella* spp. are considered parasites, as they lose their flagella and gymnodinioid shape after feeding and then divide as a series of encysted stages (primary, secondary, tertiary cysts, etc.) to produce 4-16 progeny (Drebes and Schnepf 1982, 1988). However, *Styrodinium listii*, originally described as a parasite of copepod and rotifer eggs (Drebes 1988), would not seem to qualify, as this species retains a gymnodinioid shape and latent motility throughout its life cycle, even while dividing as an encapsulated palmelloid stage to produce 16-32 progeny. Recently, Drebes and Schnepf (1998) refrained from referring to *Gyrodinium undulans* (= *Styrodinium listii*?) as a parasite.

Drebes (1984) estimated that about 140 of the roughly 2,000 species of extant dinoflagellates (approximately 7%) had been classified as parasites. Since then, at least nine additional species have been described (Coats 1988; Drebes 1988; Drebes and Schnepf 1988; Elbrächter 1988; Hudson and Shields 1994; Lom, Rhode, and Dyková 1993; McLean and Galt 1990; McLean and Nielson 1989), and many other apparently unique forms have been encountered, but not formally characterized (e.g. Drebes and Schnepf 1988; Hudson and Adlard 1996; Johnson 1985; Lawler 1980; Meyers, Lightner and Redman 1994; Mills and McLean 1991; Reimchen and Buckland-Nicks 1990; Wilhelm and Mialhe 1996). About 35 genera, representing four orders of dinoflagellates, the Phytodiales, Gymnodiniales, Blastodinales, and Syndiniales have been reported to include parasitic species (Table 1). The majority of these are parasites of marine and estuarine organisms, including a wide variety of protists, invertebrates, and vertebrates. Only the order Phytodiales contains predominately freshwater parasites, most of which utilize aquatic algae and plants as hosts. One notable exception is the marine species *Styrodinium gastrophilum*,

Corresponding Author: D. Coats—Telephone number: 301-261-4190 ext. 271; FAX number: 301-261-7894; e-mail: coats@serc.si.edu.

¹ Symposium presentation August 7, 1998, during a joint meeting of the Society of Protozoologists, American Phycological Society, and the International Society of Evolutionary Protistology, Flagstaff, AR.

Table 1. Dinoflagellate genera that have been characterized as endoparasites (I) or ectoparasites (X) of marine and freshwater organisms. Presence or absence of photosynthetic stages in the life cycles of the parasite is indicated by "+" and "-", respectively.

	Photo-synthetic life-history stage	Hosts													Reference ^a
		Algae	Sarcodines	Dinoflagellates	Ciliates	Cnidaria	Ctenophores	Platyhelminthes	Rotifer eggs	Annelids	Crustacea & eggs	Chaetognaths	Larvacea	Fish & eggs	
Gymnodiniales															
<i>Paulsenella</i>	-	X													14, 28
<i>Syltadinium</i>	-							X		X					22
<i>Schizochytriodinium</i>	-									X					25
Phytodiniales															
<i>Cystodinedria</i>	+	X													43, 44
<i>Cystodinium</i>	+	X													42
<i>Stylodinium</i>	+	X				X									11, 43, 44
Blastodiniales															
<i>Myxodinium</i>	-	X													12
<i>Caryotoma</i>			I												30, 31
<i>Protodinium</i>	+					X									7
<i>Cachonella</i>	-					X				X					3, 45
<i>Oodinium</i>	-		X			X	X			X		X	X		3, 6, 13, 40, 41
<i>Actinodinium</i>	-										I				19
<i>Blastodinium</i>	+										I				14, 46, 47
<i>Chytriodinium</i>	-										X				5, 23, 47
<i>Dissodinium</i>	+										X				24, 26
<i>Haplozoon</i>	-									I			I		3, 48, 49
<i>Apodinium</i>	-												X		8, 39
<i>Amyloodinium</i>	-							X							X 2, 22, 35, 36
<i>Crepidodinium</i>	+														X 36, 37
<i>Oodinioides</i>	-														X 36
<i>Piscinodinium</i>	+														X 36
Syndiniales															
<i>Atlanticellodinium</i>	-		I												9
<i>Dogelodinium</i>	-		I												3
<i>Keppenodinium</i>	-		I												3
<i>Merodinium</i>	-		I												15, 31, 32
<i>Solenodinium</i>	-		I												15, 32
<i>Amoebophrya</i>	-		I	I	I										1, 3, 34
<i>Cocoidinium</i>	-			I											17, 18
<i>Duboscquella</i>	-			I	I										3, 21
<i>Duboscquodinium</i>	-				I										16
<i>Hematodinium</i>	-										I				20, 33, 47
<i>Trypanodinium</i>	-										I				13
<i>Syndinium</i>	-										I				14, 38, 47
<i>Sphaeripara</i>	-											I			4, 10
<i>Ichthyodinium</i>	-													I	29, 36

^a References are: (1) Borgert 1898; (2) Brown 1934; (3) Cachon 1964; (4-8) Cachon and Cachon 1966, 1968, 1971a, b, 1973; (9 & 10) Cachon and Cachon-Enjumet 1964, 1965; (11 & 12) Cachon, Cachon, and Bougaheux 1965, 1969; (13-16) Chatton 1912, 1920, 1923, 1952; (17 & 18) Chatton and Biecheler 1934, 1936; (19) Chatton and Hovasse 1938; (20) Chatton and Poisson 1931; (21) Coats 1988; (22) Colomi 1994; (23) Dogiel 1906; (24 & 25) Drebes 1969, 1988; (26) Drebes and Schnepf 1988; (27) Elbrächter 1988; (28) Elbrächter and Drebes 1978; (29) Holland and Cachon 1952; (30) Hollande and Corbel 1982; (31) Hollande and Enjumet 1953; (32) Hovasse and Brown 1953; (33) Hudson and Shields 1994; (34) Koeppen 1899; (35) Landsberg et al. 1994; (36) Lom 1981; (37) Lom, Rohde, and Dyková 1993; (38) Manier, Fize, and Grizel 1971; (39) McLean and Galt 1990; (40) McLean and Nielsen 1989; (41) Mills and McLean 1991; (42) Pfister and Lynch 1980; (43 & 44) Pfister and Popovský 1979; Popovský and Pfister 1982; (45) Rose and Cachon 1951; (46) Sewell 1951; (47) Shields 1994; (48) Shumway 1924; (49) Siebert 1973.

which is an ectoparasite of Siphonophores (Cachon, Cachon and Bougaheux 1965). Non-marine parasites are also known for the Blastodiniales, where two species of *Piscinodinium* and the enigmatic, monotypic genus *Oodinioides* are ectoparasites of freshwater fish.

Somewhat less than half of the dinoflagellate genera infecting marine organisms are ectoparasites that use specialized holdfast organelles and/or modified peduncles for attaching to their host and obtaining nourishment (see Cachon and Cachon 1987 for discussion of attachment organelles and feeding structures). All

of the parasitic Phytodiniales and Gymnodiniales and about two-thirds of the Blastodiniales fall into this category, with species known to attack the following organisms: (1) marine protists, including diatoms (parasitized by *Paulsenella* spp.), the chlorophyte *Halosphaera* sp. (infected by *Myxodinium pipens*), and acantheria (by *Oodinium* sp.); (2) eggs of rotifers, copepods, euphausiids, shrimp, and fish (by *Chytriodinium* sp., *Dissodinium* spp., *Syltadinium* spp., and *Schizochytriodinium*); (3) adult and/or juvenile hydromedusae, siphonophores, ctenophores, annelids, chaetognaths, appendicularia, and fish (by

Amyloodinium ocellatum, *Apodinium* spp., *Cachonella* spp., *Crepidodinium* spp., *Oodinium* spp., and *Protodinium* spp.); and (4) the parasitic trematode *Neobenedenia melleni* (by *Amyloodinium ocellatum*); see references for Table 1.

By contrast, the Syndiniales are strictly endoparasitic, with many being cytoplasmic or intranuclear parasites of protists. Syndinian species are also known to invade the body cavity of appendicularia (parasitized by *Sphaeripara* spp.) and crustacea, including amphipods, copepods, crabs, and lobsters (infected by *Hematodinium* sp. and *Syndinium* spp.), as well as the eggs of copepods (by *Trypanodinium ovicola*), and fish (by *Ichthyodinium chabelardi*). Endoparasitic members of the Blastodiniales include: (1) *Caryotoma bernardi*, a poorly characterized intranuclear parasite of radiolaria; (2) *Actinodinium apsteini* and *Blastodinium* spp., which grow in the digestive tract of copepods; and (3) *Haplozoon* spp., curious "colonial" parasites that live attached to the intestinal wall of marine polychaetes; see references for Table 1.

Most parasitic dinoflagellates are obligate heterotrophs; however, the existence of one or more apparently photosynthetic life-history stages has been reported for eight genera (Table 1). Chloroplasts or photosynthetic pigments are most common among ectoparasitic forms, with only one endoparasitic genus, *Blastodinium*, having photosynthetic taxa. The importance of photosynthesis to the growth and survival of parasitic dinoflagellates is not well understood; however, species of *Cystodinedria*, *Cystodinium*, and *Stylodinium* appear to rely on photosynthesis during much of their life cycle and were long believed to be strict autotrophs (Cachon and Cachon 1987). Interestingly, pigmentation varies during the life-history of these algal parasites and is influenced by pigment characteristics of the host, suggesting that some parasitic dinoflagellates may temporarily retain cleptochloroplasts (Pfister and Lynch 1980; Popovský and Pfister 1982, 1990). *Crepidodinium*, an ectoparasitic genus that lives on the gills of marine and estuarine fish, is also thought to rely largely, if not exclusively, on phototrophy. *Crepidodinium* spp. cause little damage to their hosts and may be ectocommensals, rather than true parasites (Lom, Rohde and Dyková 1993). Photosynthesis can also play a significant role in the nutrition of endoparasites like *Blastodinium* sp., which acquires as much as half the energy needed for growth through phototrophy (Pasternak, Arashkevich and Sorokin 1984). Phototrophy may even enhance the dispersal of parasitic dinoflagellates, especially in species with photosynthetic, "free-living" dinospores (Stoecker 1999).

Life cycle. The asexual cycle of marine parasitic dinoflagellates typically involves a biflagellate zoospore (= dinospore) that is widely accepted as the infective agent, a growth stage (= trophont) that rarely resembles a dinoflagellate in gross appearance, and a sporogenic reproductive phase that generates large numbers of dinospores. Growth and reproduction need not be mutually exclusive, as trophonts of some parasites (e.g. *Blastodinium*, *Apodinium*, *Haplozoon*) produce a trophocyte and a gonocyte at the first division. The gonocyte undergoes rapid sequential divisions, to form multiple generations of sporocytes and dinospores, while the trophocyte continues to grow and divides less frequently to produce successive generations of trophocytes and gonocytes. In other taxa, growth of the trophont is accompanied by nuclear division with little or no cytoplasmic fission, thus forming a multinucleate cell (e.g. *Amoebophrya* infections of dinoflagellates) or a plasmodium/plasmodia (e.g. *Syndinium* and *Hematodinium* in crustacea). At maturity, these multinucleate trophonts undergo cytokinesis, perhaps accompanied by additional nuclear divisions, to produce dinospores. A more direct cycle is evident in genera like *Amyloodinium*, *Chytriodinium*, and *Dissodinium*, where growth of the trophont

to some terminal size is followed by repeated nuclear and cytoplasmic divisions leading to the differentiation of dinospores.

Sporulation in a number of species results in the formation of either large or small dinospores (= macrospores and microspores, respectively), with only one type arising from each host individual (e.g. Cachon 1964; Cachon, Cachon and Bouquahoux 1969; Coats 1988; Grassé in Chatton 1952; Meyers et al. 1987; Stickney 1978). The existence of morphologically distinct spore-types has long been suspected as evidence of a sexual cycle (Cachon and Cachon 1987); however, few data have been available to support that notion. Alternatively, production of spore types that differ in number and motility may reflect multiple dispersal strategies that ensure success of the parasite over a broad range of host densities and environmental conditions (Coats 1988; Meyers et al. 1990).

Early reports of isogamous fusion by dinospores of *Duboscquella aspida* (Duboscq and Collin 1910) and anisogamy in *D. anisospora* (Grassé in Chatton 1952) implied a sexual cycle, but provided no information on the fate of the presumptive zygote. More recently, Drebes and Schnepf (1988) described the complete sexual cycle of *Paulsenella chaetoceratis*, in which anisogamy leads to the formation of a motile zygote (= planozygote). The planozygote of *P. chaetoceratis* feeds on one or more diatom hosts before reproducing inside two successive "division cysts" to generate four meiospores. Meiospores can become vegetative cells directly, or form resting cysts that later germinate into vegetative cells. Drebes and Schnepf (1988) also reported production of temporary cysts and the possibility of resting cysts during the asexual cycle of *P. chaetoceratis*. Encystment is a logical survival strategy to contend with periods of low host abundance, yet cysts or cyst-like stages have only been reported for two other parasitic dinoflagellates [i.e. *Dissodinium pseudolunula* (Drebes 1981; John and Reid 1983) and *Duboscquella cacheroni* (Coats 1988)].

Dinospores are known to be responsible for spreading infections of many parasitic dinoflagellates and are assumed to serve that function for all species (Cachon and Cachon 1987). However, attempts to propagate some parasites (e.g. *Blastodinium*, *Hematodinium*, and *Syndinium*) by exposing naive hosts to dinospores or infected individuals have been unsuccessful (Shields 1994; Stickney 1978). In addition, field studies indicate that seasonal patterns in the sporulation of *Hematodinium* sp. and the availability of highly susceptible post-molt Tanner crabs are not consistent with parasite transmission via dinospores (Meyers et al. 1990). These results suggest that alternate pathways like cannibalism or transmission via an intermediate host may be important to the success of some parasitic dinoflagellates (Hudson and Shields 1994; Meyers et al. 1990; Shields 1994). Thus far, attempts to propagate *Hematodinium* infections via cannibalism have failed; however, species of this genus can be transmitted among crabs by injecting naive hosts with vegetative stages of the parasite (Hudson and Shields 1994; Meyers et al. 1987).

Host specificity. Species within genera of parasitic dinoflagellates usually infect similar types of host organisms (Table 1). *Oodinium* is a clear exception in this regard, as species forming the genus parasitize several different host phyla. *Amoebophrya* also shows a broad host range, with its representatives known to infect members of three major protistan taxa.

At the subgeneric level, parasitic dinoflagellates exhibit varying degrees of host specificity. The fish ectoparasite *Amyloodinium ocellatum* shows almost no host preference, with infections reported for over 100 species representing more than 40 families of fish (Lom 1981). *Amyloodinium ocellatum* has even been reported as a hyperparasite of a trematode parasite on the skin of gilt-head bream, *Sparus aurata* (Colorni 1994). At-

Table 2. Reported prevalence of parasitic dinoflagellates of protistan hosts.

Parasite	Host	Locality	Prevalence range, maximum, or (average)	References ^a
<i>Paulsenella</i> (in diatoms)				
<i>P. chaetoceratis</i>	<i>Streptothecha thamesis</i>	Wadden Sea, Germany	20%	5
<i>Amoebophrya</i> (in dinoflagellates)				
<i>A. cf. ceratii</i>	<i>Ceratium fusus</i>		0.8%	9
	<i>Ceratium</i> spp.	Kiel Bay, Germany	3–10%	6
	<i>Dinophysis norvegica</i>	Mahone Bay, Nova Scotia	2%	7
	<i>Gymnodinium sanguineum</i>	Chesapeake Bay	40% (4%)	2
	<i>Gymnodinium sanguineum</i>	Rhode River, MD	14% (1%)	4
	<i>Gyrodinium uncatenum</i>	Rhode River, MD	81% (2%)	4
	<i>Protogonyaulax catenella</i>	Sequim Bay, WA	30–40%	11
	<i>Protogonyaulax catenella</i>	Puget Sound, WA	2–47%	8, 9, 10
	<i>Scrippsiella trochoidea</i>	Rhode River, MD	33% (6%)	4
	<i>Scrippsiella</i> sp.	Nova Scotia	50%	7
<i>Duboscquella</i> (in ciliates)				
<i>D. aspida</i>	<i>Favella panamensis</i>	Chesapeake Bay	86% (24%)	3
	<i>Favella panamensis</i>	Indian River, FL	69% (12%)	3
<i>D. cachoni</i>	<i>Eutimninus pectinis</i>	Chesapeake Bay	50% (10%)	1

^a References are: (1) Coats and Heisler 1989; (2) Coats and Bockstahler 1994; (3 & 4) Coats et al. 1994, 1996; (5) Drebes and Schnepf 1982; (6) Elbrächter 1973; (7) Fritz and Nass 1992; (8) Nishitani and Chew 1984; (9) Nishitani, Erickson, and Chew, 1985; (10) Nishitani et al. 1984; (11) Taylor 1968.

tempts to transmit *A. ocellatum* experimentally, however, suggest that some fish may not be susceptible to infection or become resistant with age (Lawler 1980). Most of these less susceptible host species are able to tolerate very low oxygen concentrations or to produce large amounts of mucus that may prevent attachment of the parasite. *Crepidodinium* spp., on the other hand, are restricted to a handful of fish species. *Crepidodinium cyprinodontum* parasitizes five species of cyprinodontids, with a marked preference for *Fundulus majalis*, but has never been found on non-cyprinodontid hosts (Lawler 1967, 1968a,b). *Crepidodinium australe* appears even more host specific, with only the sand whiting (*Sillago ciliata*) found to be infected, despite examination of 1,862 fish representing 46 coastal species and 1,563 specimens representing 67 deep-water species (Rohde 1988, as cited in Lom, Rohde, and Dyková 1993).

The host-specificity of many parasitic dinoflagellates is difficult to evaluate, due to limited consideration of potential host taxa and geographic coverage. For example, *Myxodinium pipiens* is presumably restricted to the chlorophyte genus *Halosphaera*, yet this parasite is only known from one study of Mediterranean plankton. Similarly, the 10 species of *Haplazon*, most of which have been reported only once, are believed to be highly host specific, with each infecting a single host species (Shumway 1924; Siebert 1973).

Questions of host specificity are also complicated by limited species descriptions and/or the lack of recognized morphological traits for sorting taxa of some parasitic dinoflagellates. For example, infestations of various decapod crustacea have been attributed to *Hematodinium perezii* or *H. perezii*-like organisms (Chatton and Poisson 1931; MacLean and Ruddell 1978; Messick 1994; Newman and Johnson 1975), suggesting that this dinoflagellate has little host specificity. However, recent description of a second species, *H. australis* (Hudson and Shields 1994), along with molecular studies showing genetic divergence among *Hematodinium* infections of different crustacean hosts (Hudson and Adlard 1996) indicate higher species diversity and greater host specificity than previously recognized. *Amoebophrya ceratii*, a parasite of free-living dinoflagellates,

is another species that has long been thought to lack host specificity, despite differences in dinospore morphology and sites of infection among host taxa (Cachon 1964). However, epidemiological data for dinoflagellates of Chesapeake Bay are not consistent with a single-parasite/multiple-host hypothesis, and laboratory studies have shown that *A. cf. ceratii* ex *Gymnodinium sanguineum* fails to infect other potential host species (Coats et al. 1996). Molecular studies have also shown significant difference in small-subunit rRNA sequences of parasites from different host species (Gunderson, J. H., pers. commun.).

Parasite prevalence and impact on host populations. Parasitic dinoflagellates of planktonic protists appear most commonly in coastal and estuarine environments, where they typically maintain moderate to low infection levels (Table 2). However, some species (e.g. *Duboscquella* spp. and *Amoebophrya cf. ceratii*) produce epizootics that are usually associated with periodic or seasonal maxima in host abundance (Coats and Heisler 1989; Coats et al. 1996; Taylor 1968). While host availability clearly influences the occurrence of parasitic dinoflagellates, other factors may also be important in the formation of epizootics. For example, high infection rates have been linked to nutrient stress in photosynthetic hosts (Nishitani, Erickson, and Chew 1985; Nishitani et al. 1984), and behavioral differences between infected and uninfected hosts may limit the spread of infections in some systems (Coats and Bockstahler 1994).

Species that infect planktonic protists have generation times of 1–2 days (Coats and Heisler 1989; Coats and Bockstahler 1994; Drebes and Schnepf 1988) and all are lethal to their hosts; however, *Favella panamensis* can survive a single infection of *Duboscquella aspida* (Coats et al. 1994), and in some cases *Paulsenella chaetoceratis* only damages its host (Drebes and Schnepf 1982). Thus, it is not surprising that epizootic outbreaks are relatively short-lived and often coincide with declining host populations (Nishitani, Erickson and Chew 1985; Nishitani et al. 1984). Estimates of parasite-induced mortality indicate that epizootics of *Amoebophrya cf. ceratii* can account for the death of more than 50% of the host population each day (Coats et al. 1996), while average removal of tintinnids by *Du-*

Table 3. Reported prevalence of parasitic dinoflagellates of crustacean hosts.

Parasite	Host	Locality	Parasite prevalence maximum (average)	Reference ^a
Blastodinium				
<i>B. hyalinum</i>	Copepod (<i>Calanus finmarchicus</i>)	North Sea	60% (4%)	23
<i>B. sp.</i>	Copepod (<i>Euchaeta antarctica</i>)	Weddell Sea	7%	19
<i>B. spp.</i>	Copepods (multiple genera)	Gulf of Naples	<2%	7, 8
		Arabian Sea		20
		Mediterranean Sea		2
Syndinium				
<i>S. sp.</i>	Copepod (<i>Paracalanus indicus</i>)	Port Phillip Bay Australia	29% (6%) adult females	10
<i>S. sp.</i>	Copepod (<i>Paracalanus parvus</i>)	Gulf of Naples	13% adult females 30% juveniles	7, 8
<i>S. sp.</i>	Shrimp Eggs (<i>Pandalus borealis</i>)	Gulf of Maine	30%	21
Hematodinium				
<i>H. perezii</i>	Portunid & Cancer Crabs	Western France & Mid-Atlantic USA	4%	3, 12
	Blue Crab (<i>Callinectes sapidus</i>)	Southeast USA	30%	13
		Mid-Atlantic USA	100% (40%)	18
<i>H. australis</i>	Sand & Mud Crab (<i>Portunus pelagicus</i> & <i>Scylla serrata</i>)	Queensland Australia	4%	6
<i>H. sp.</i>	Tanner Crab (<i>Chionoecetes bairdi</i>)	Southeast Alaska	100% (26%)	15, 16
		Southeast Alaska	99% (68%)	4, 11
<i>H. sp.</i>	Snow Crab (<i>Chionoecetes opilio</i>)	Newfoundland	4% (<1%)	22
		Bering Sea	29%	17
<i>H. sp.</i>	Velvet Crab (<i>Necora puber</i>)	Western France	87% (33%)	24
<i>H. sp.</i>	Norway Lobster (<i>Nephrops norvegicus</i>)	Western Scotland	85% (22%)	5
<i>H. sp.</i>	Shrimp (<i>Pandalus borealis</i> & <i>P. platyceros</i>)	Gulf of Alaska & British Columbia	50%	1, 14
<i>H. sp.</i>	Benthic Amphipods	Northeast USA (13 species)	67% (5%)	9

^a References are: (1) Bower, Meyer, and Boutillier 1993; (2) Chatton 1920; (3) Chatton and Poisson 1931; (4) Eaton et al. 1991; (5) Fields et al. 1992; (6) Hudson and Shields 1994; (7) Ianora, Mazzocchi, and di Carlo 1987; (8) Ianora et al. 1990; (9) Johnson 1985; (10) Kimmerer and McKinnon 1990; (11) Love et al. 1993; (12) MacLean and Ruddell 1978; (13) Messick 1994; (14) Meyers, Lightner, and Redman 1994; (15–17) Meyers et al. 1987, 1990, 1996; (18) Newman and Johnson 1975; (19) Øresland 1991; (20) Sewell 1951; (21) Stickney 1978; (22) Taylor and Kahn 1995; (23) Vañe 1952; (24) Wilhelm and Mialhe 1996.

boscquella spp. can rival grazing pressure from zooplankton (Coats and Heisler 1989; Coats et al. 1994).

Parasitic dinoflagellates that infect crustacea generally show strong seasonal cycles, with lowest prevalence often occurring during colder months (e.g. Ianora et al. 1990; Kimmerer and McKinnon 1990; Love et al. 1993; Messick 1994). Infections frequently cause sexual castration and lead to mortality of the host; however, *Blastodinium* appears to be far less pathogenic than other genera (see Shields 1994 for detailed review). Crustacean eggs are destroyed when parasitized by dinoflagellates, with an unnamed species responsible for up to 30% egg mortality in northern shrimp *Pandalus borealis* (Stickney 1978).

Epizootics are known to occur in several planktonic and benthic crustacea (Table 3) and have significant impacts on host populations. In coastal Australian waters, *Syndinium* sp. has been estimated to cause about a third of the total mortality of the planktonic copepod *Paracalanus indicus* (Kimmerer and McKinnon 1990). Reports of parasitism by *Hematodinium* indicate nearly 100% mortality of infected Alaskan Tanner crabs (Love et al. 1993; Meyers et al. 1987), over 50% loss of blue crabs along the Delmarva Peninsula (Shields 1994), and 2–4 times higher death rates of infected Norway lobsters compared to uninfected individuals (Field et al. 1992). *Hematodinium* infections in decapods are not only lethal, but make the flesh of infected individuals unpalatable or of poor quality. Thus, epizootics of *Hematodinium* spp. have led to significant economic losses associated with reduced harvest of commercially important species, including Tanner crabs (*Chionoecetes bairdi*) off

North America and the velvet swimming crab (*Necora puber*) in Europe (Meyers et al. 1987; Wilhelm and Mialhe 1996).

The dinoflagellate fish parasites *Amyloodinium ocellatum* and *Crepidodinium* spp. are often quite prevalent in natural host populations, and epizootics of the fish egg parasite *Ichthyodinium chaberlardi* are known to occur along the coast of Portugal (Table 4). *Ichthyodinium chaberlardi* kills eggs that it attacks and is the only parasitic dinoflagellate that significantly affects natural fish populations. *Crepidodinium* spp. appear to cause little damage to their hosts, and *A. ocellatum* is rarely reported to kill hosts in nature (e.g. Kuperman, Matey and Barlow 1999). Similarly, an unnamed dinoflagellate that infects sticklebacks (*Gasterosteus* sp.) of Queen Charlotte Island, British Columbia, reaches peak prevalence of 99% with no discernible effect on its hosts (Reimchen and Buckland-Nicks 1990).

In closed systems, however, *A. ocellatum* is one of the most persistent and pathogenic ectoparasites of warm-water marine fish (Paperna 1984). It has been responsible for mass mortality of aquaria fish on many occasions (e.g. Brown 1934; Dempster 1955; Nigrelli 1936) and has caused significant loss of mariculture stocks. Lawler (1980) recorded the death of 300,000 juvenile Striped Bass (*Morone saxatilis*), equivalent to 75–80% of the stock, caused by *A. ocellatum* over a 2-day period. Even higher losses (up to 100%) have been reported on some occasions (e.g. Barbaro and Francescon 1985; Sandifer et al. 1993). The freshwater dinoflagellate *Piscinoodinium pillulare* causes

Table 4. Reported prevalence of parasitic dinoflagellates in natural fish populations.

Parasite Host	Prevalence	Locality	Reference
Amyloodinium			
<i>A. ocellatum</i> 42 teleost spp.	30%	Mississippi Sound	3
Crepidoodinium			
<i>C. cyprinodontum</i> <i>Fundulus majalis</i>	77%	North Carolina, Outer Banks	1
<i>Fundulus heteroclitus</i>	5%	North Carolina, Outer Banks	1
<i>Cyprinodon variegatus</i>	80%	North Carolina, Outer Banks	1
<i>Fundulus luciae</i>	8%	Virginia Coast	2
<i>C. australe</i> <i>Sillago ciliata</i>	58%	New South Wales, Australia	4
Ichthyodinium			
<i>I. chabelardi</i> Sardine Eggs	0.7–34%	Portuguese Coast	5, 6

^a References are: (1–3) Lawler 1968a, b, 1980; (4) Lom, Rohde, and Dyková 1993; (5 & 6) Meneses and Ré 1989, 1992.

similar problems in aquaculture systems (e.g. Shaharom-Harrison et al. 1990).

Ecological significance. Dinoflagellate parasitism represents an important aspect of marine planktonic food webs, particularly in enriched coastal settings where host densities are sufficiently high to promote epizootics. Infection by *Amoebophrya* cf. *ceratii* may retard or prevent the formation of dinoflagellate red tides (Nishitani, Erickson and Chew 1985), with epizootics able to facilitate the decline of blooms (Coats et al. 1996). By causing the destruction of bloom-forming hosts, parasitic dinoflagellates effectively recycle undergrazed phytoplankton production through the "microbial loop." Species that infect plankton ciliates have a somewhat different effect, as they compete for a preferred food source of zooplankton (Coats and Heisler 1989). Dinoflagellates that produce epizootics in crabs and lobsters may have a dramatic effect on benthic communities by removing species that serve as dominant organizers of in-faunal communities (Shields 1994).

ACKNOWLEDGMENTS

I wish to express my gratitude to the Society of Protozoologists for financial support and assistance in organizing this symposium and to my fellow participants for their camaraderie and inspiration. Preparation of this manuscript was supported by NSF Grant No. OCE-9730695.

LITERATURE CITED

- Barbaro, A. & Francescon, A. 1985. Parassitosi da *Amyloodinium ocellatum* (Dinophyceae) su larvae di *Sparus aurata* allevate in un impianto di riproduzione artificiale. *Oebalia*, **11**:745–752.
- Borgert, A. 1898. Beiträge zur Kenntnis in *Sticholonche zanclea* und *Acanthometridenarten* vorkommenden Parasiten (Spiralkörper Fol, *Amoebophrya* Köppen). *Z. Wiss. Zool.*, **63**:141–186.
- Bower, S. M., Meyer, G. R. & Boutillier, J. A. 1993. Disease of spot prawns (*Pandalus platyceros*) caused by an intracellular bacterium and a *Hematodinium*-like protozoa. Abstract. *J. Shellfish Res.*, **12**: 135A.
- Brown, E. M. 1934. On *Oodinium ocellatum* Brown, a parasitic dinoflagellate causing epidemic disease in marine fish. *Proc. Zool. Soc. Lond.*, **2**:583–607.
- Cachon, J. 1964. Contribution à l'étude des péridiniens parasites. Cytologie, cycles évolutifs. *Ann. Sci. Nat. Zool.*, **6**:1–158.
- Cachon, J. & Cachon, M. 1966. Ultrastructure d'un péridinien parasite d'Appendiculaires, *Neresheimeria catenata* (Neresheimer). *Protistologica*, **2**:17–25.
- Cachon, J. & Cachon, M. 1968. Cytologie et cycle évolutif des *Chytridinium* (Chatton). *Protistologica*, **4**:249–262.
- Cachon, J. & Cachon, M. 1971a. Ultrastructures du genre *Oodinium* Chatton. Différenciations cellulaires en rapport avec la vie parasitaire. *Protistologica*, **7**:153–169.
- Cachon, J. & Cachon, M. 1971b. *Protoodinium chattoni* Hovasse. Manifestations ultrastructurales des rapports entre le Péridinien et la Méduse-hôte: fixation, phagocytose. *Arch. Protistenk.*, **113**:293–305.
- Cachon, J. & Cachon, M. 1973. Les Apodinidae Chatton révision systématique rapports hôte-parasite et métabolisme. *Protistologica*, **9**: 17–33.
- Cachon, J. & Cachon, M. 1987. Parasitic dinoflagellates. In: Taylor, F. J. R. (ed.), *The Biology of Dinoflagellates*, Blackwell Sci. Publ., Oxford. p. 571–610.
- Cachon, J. & Cachon-Enjumet, M. 1964. Cycle évolutif et cytologie de *Neresheimeria catenata* (Neresheimer), Péridinien parasite d'Appendiculaires. Rapports de l'hôte et du parasite. *Ann. Sci. Nat. Zool.*, **6**: 779–800.
- Cachon, J. & Cachon-Enjumet, M. 1965. *Atlanticellodinium tregouboffi* nov. gen. nov. sp., Péridinien Blastuloidae Neresheimer, parasite de *Planktonetta atlantica* Borgert, Phaeodarié Atlanticellide. Cytologie, cycle biologique, évolution nucléaire au cours de la sporogénèse. *Arch. Zool. Exp. Gen.*, **105**:369–379.
- Cachon, J., Cachon, M. & Bouquaheux, F. 1965. *Stylo-dinium gastrophilum* Cachon, Péridinien Dinococcide parasite de Siphonophores. *Bull. Inst. Oceanogr.*, **65**, No. 1359, p. 8.
- Cachon, J., Cachon, M. & Bouquaheux, F. 1969. *Myxodinium pipiens* gen. nov., sp. nov., péridinien parasite d'*Halosphaera*. *Phycologia*, **8**:157–164.
- Chatton, É. 1912. Diagnoses préliminaires de Péridiniens parasites nouveaux. *Bull. Soc. Zool. France*, **37**:85–93.
- Chatton, É. 1920. Les Péridiniens parasites. Morphologie, reproduction, éthologie. *Arch. Zool. exp. et gén.*, **59**:1–475.
- Chatton, É. 1923. Les Péridiniens des Radiolaires. *C. R. Acad. Sci., Paris*, **177**:1246–1249.
- Chatton, É. 1952. Classe des Dinoflagellés ou Péridiniens, In: Grassé, P. P. (ed.), *Traité de Zoologie*, Masson et Cie, Paris, **1**:309–390.
- Chatton, É. & Biecheler, B. 1934. Les Coccidiniidae, Dinoflagellés coccidiomorphes parasites de Dinoflagellés, et le phylum des Phytodinozoa. *C. R. Acad. Sci., Paris*, **199**:252–255.
- Chatton, É. & Biecheler, B. 1935. Les *Amoebophrya* et le *Hyalosaccus*: leur cycle évolutif. L'ordre nouveau des Coelomastigina dans les Flagellés. *C. R. Acad. Sci., Paris*, **200**:505–507.
- Chatton, É. & Biecheler, B. 1936. Documents nouveaux relatifs aux Coccidiniidae (Dinoflagellés parasites). La sexualité du *Coccidinium mesnili* n. sp. *C. R. Acad. Sci., Paris*, **203**:573–576.
- Chatton, É. & Hovasse, R. 1938. *Actinodinium apsteini* n. g. n. sp.,

- Péridinien parasite entérocoelomique des *Acartia* (Copépodes). *Arch. Zool. Exp. Gen.*, **79**:24-29.
- Chatton, É. & Poisson, R. 1931. Sur l'existence, dans le sang des Crabes, de Péridiniens parasites: *Hematodinium perezii* n. g., n. sp. (Syn-*dinidae*). *C. R. Seances Soc. Biol.*, Paris, **105**:553-557.
- Coats, D. W. 1988. *Duboscquella cachoni* n. sp., a parasitic dinoflagellate lethal to its tintinnine host *Eutintinnus pectinis*. *J. Protozool.*, **35**:607-617.
- Coats, D. W. & Bockstahler, K. R. 1994. Occurrence of the parasitic dinoflagellate *Amoebophrya ceratii* in Chesapeake Bay populations of *Gymnodinium sanguineum*. *J. Euk. Microbiol.*, **41**:586-593.
- Coats, D. W. & Heisler, J. J. 1989. Spatial and temporal occurrence of the parasitic dinoflagellate *Duboscquella cachoni* and its tintinnine host *Eutintinnus pectinis* in Chesapeake Bay. *Mar. Biol.*, **101**:401-409.
- Coats, D. W., Adam, E. J., Gallegos, C. L. & Hedrick, S. 1996. Parasitism of photosynthetic dinoflagellates in a shallow subestuary of Chesapeake Bay, USA. *Aquat. Microb. Ecol.*, **11**:1-9.
- Coats, D. W., Bockstahler, K. R., Berg, G. M. & Snieczek, J. H. 1994. Dinoflagellate infections of *Favella panamensis* from two North American estuaries. *Mar. Biol.*, **119**:105-113.
- Colomi, A. 1994. Hyperparasitism of *Amyloodinium ocellatum* (Dinoflagellata: Oodiniidae) on *Neobenedenia melleni* (Monogenea: Capsalidae). *Dis. Aquat. Org.*, **19**:157-159.
- Dempster, R. P. 1955. The use of copper sulfate as a cure for fish diseases caused by parasitic dinoflagellates of the genus *Oodinium*. *Zoologica: New York Zool. Soc.*, **40**:133-138.
- Dogiel, V. 1906. Beiträge zur Kenntnis der Peridineen. *Mitt. Zool. Stn. Neapel*, **18**:1-45.
- Drebes, G. 1969. *Dissodinium pseudocalani* sp. nov., ein parasitischer Dinoflagellat auf Copepodeneiern. *Helgoländer. Wiss. Meeresunters.*, **19**:58-67.
- Drebes, G. 1981. Possible resting spores of *Dissodinium pseudolunula* (Dinophyta) and their relation to other taxa. *Br. Phycol. J.*, **16**:207-215.
- Drebes, G. 1984. Life cycle and host specificity of marine parasitic dinophytes. *Helgoländer Meeresunters.*, **37**:603-622.
- Drebes, G. 1988. *Syltodinium listii* gen. et spec. nov., a marine ectoparasitic dinoflagellate on eggs of copepods and rotifers. *Helgoländer Meeresunters.*, **42**:583-591.
- Drebes, G. & Schnepf, E. 1982. Phagotrophy and development of *Paulsenella* cf. *chaetoceratis* (Dinophyta), an ectoparasite of the diatom *Streptotheca thamesis*. *Helgoländer Meeresunters.*, **35**:501-515.
- Drebes, G. & Schnepf, E. 1988. *Paulsenella* Chatton (Dinophyta), ectoparasites of marine diatoms: development and taxonomy. *Helgoländer Meeresunters.*, **42**:563-581.
- Drebes, G. & Schnepf, E. 1998. *Gyrodinium undulans* Hulburt, a marine dinoflagellate feeding on the bloom-forming diatom *Odontella aurita*, and on copepod and rotifer eggs. *Helgoländer Meeresunters.*, **52**:1-14.
- Duboscq, O. & Collin, B. 1910. Sur la reproduction sexuée d'un Protiste parasite des Tintinnides. *C. R. Acad. Sci.*, Paris, **151**:340-341.
- Eaton, W. D., Love, D. C., Botelho, C., Meyers, T. R., Imamura, K. & Koeneman, T. 1991. Preliminary results on the seasonality and life cycle of the parasitic dinoflagellate causing bitter crab disease in Alaskan Tanner crabs (*Chionoecetes bairdi*). *J. Invert. Pathol.*, **57**:426-434.
- Elbrächter, M. 1973. Population dynamics of *Ceratium* in coastal waters of the Kiel Bay. *Oikos suppl.*, **15**:43-48.
- Elbrächter, M. 1988. Life cycle of *Schizochytriodinium calani* nov. gen. nov. spec., a dinoflagellate parasitizing copepod eggs. *Helgoländer Meeresunters.*, **42**:593-599.
- Elbrächter, M. & Drebes, G. 1978. Life cycles, phylogeny and taxonomy of *Dissodinium* and *Pyrocystis* (Dinophyta). *Helgoländer Wiss. Meeresunters.*, **31**:347-366.
- Field, R. H. & Appleton, P. L. 1996. An indirect fluorescent antibody technique for the diagnosis of *Hematodinium* sp. infection of the Norway lobster *Nephrops norvegicus*. *Dis. Aquat. Org.*, **24**:199-204.
- Field, R. H., Chapman, C. J., Taylor, A. C., Neil, D. M. & Vickerman, K. 1992. Infection of the Norway lobster *Nephrops norvegicus* by a *Hematodinium*-like species of dinoflagellate on the west coast of Scotland. *Dis. Aquat. Org.*, **13**:1-15.
- Fritz, L. & Nass, M. 1992. Development of the endoparasitic dinoflagellate *Amoebophrya ceratii* within host dinoflagellate species. *J. Phycol.*, **28**:312-320.
- Gaines, G. & Elbrächter, M. 1987. Heterotrophic nutrition. In: Taylor, F. J. R. (ed.), *The Biology of Dinoflagellates*, Blackwell Scientific Publ., Oxford, p. 224-268.
- Hansen, P. J. & Calado, A. J. 1999. Phagotrophic mechanisms and prey selection in free-living dinoflagellates. *J. Euk. Microbiol.*, **46**:382-389.
- Hollande, A. & Cachon, J. 1952. Un parasite des oeufs de Sardine: l'*Ichthyodinium chabelardi* nov. gen., nov. sp. (Péridinien parasite). *C. R. Acad. Sci.*, Paris, **235**:976-977.
- Hollande, A. & Corbel, J.-C. 1982. Ultrastructure, cycle évolutif et position systématique de *Caryotoma bernardi* Holl. et Enj. (Dinoflagellés Oodiniidés) parasite endocapsulaire des Thalassicolles (Radiolaires). *Protistologica*, **18**:123-133.
- Hollande, A. & Enjumet, M. 1953. Contribution à l'étude des Sphaerocollides (Radiolaires Collodaires et Radiolaires Polycyttaires) et de leurs parasites. Partie I: Thalassicollidae, Physematidea, Thalassophysidae. *Ann. Sci. Nat.*, **15**:99-183.
- Hovasse, R. & Brown, E. M. 1953. Contribution à la connaissance des Radiolaires et de leurs parasites Syndiniens. *Ann. Sci. Nat.*, **15**:405-438.
- Hudson, D. A. & Adlard, R. D. 1996. Nucleotide sequence determination of the partial SSU rDNA gene and ITS1 region of *Hematodinium* cf. *perezii* and *Hematodinium*-like dinoflagellates. *Dis. Aquat. Org.*, **24**:55-60.
- Hudson, D. A. & Shields, J. D. 1994. *Hematodinium australis* n. sp., a parasitic dinoflagellate of the sand crab *Portunus pelagicus* from Moreton Bay, Australia. *Dis. Aquat. Org.*, **19**:109-119.
- Ianora, A., Mazzocchi, M. G. & di Carlo, B. S. 1987. Impact of parasitism and intersexuality on Mediterranean populations of *Paracalanus parvus* (Copepoda: Calanoida). *Dis. Aquat. Org.*, **3**:29-36.
- Ianora, A., di Carlo, B. S., Mazzocchi, M. G. & Mascellaro, P. 1990. Histomorphological changes in the reproductive condition of parasitized marine planktonic copepods. *J. Plank. Res.*, **12**:249-258.
- John, A. W. G. & Reid, P. C. 1983. Possible resting cysts of *Dissodinium pseudolunula* Swift ex Elbrächter and Drebes in the Northeast Atlantic and the North Sea. *Br. Phycol. J.*, **18**:61-67.
- Johnson, P. T. 1985. Parasites of benthic amphipods: dinoflagellates (Duboscquodiniida: Syndiniidae). *Fish. Bull.*, **84**:605-614.
- Kimmerer, W. J. & McKinnon, A. D. 1990. High mortality in a copepod population caused by a parasitic dinoflagellate. *Mar. Biol.*, **107**:449-452.
- Koepfen, N. 1899. *Hyalosaccus ceratii* nov. gen. et sp., parazit 'Dinoflagellat'. *Kiev. Obshch. Estest.*, Zapiski, **16**:89-135.
- Kuperman, B. I., Matey, V. E. & Barlow, S. B. 1999. Ectocommensal and parasitic protozoans on fish, polychaetes, and crustaceans from the Salton Sea. Abstract. *J. Euk. Microbiol.*, **46**:6A.
- Landsberg, J. H., Steidinger, K. A., Blakesley, B. A. & Zondervan, R. L. 1994. Scanning electron microscope study of dinospores of *Amyloodinium* cf. *ocellatum*, a pathogenic dinoflagellate parasite of marine fish, and comments on its relationship to the Peridinales. *Dis. Aquat. Org.*, **20**:23-32.
- Lawler, A. R. 1967. *Oodinium cyprinodonotum* n. sp., a parasitic dinoflagellate on gills of Cyprinodontidae of Virginia. *Ches. Sci.*, **8**:67-68.
- Lawler, A. R. 1968a. Occurrence of the parasitic dinoflagellate *Oodinium cyprinodontum* Lawler, 1967 in North Carolina. *Virginia J. Sci.*, **19**:240.
- Lawler, A. R. 1968b. New host record for the parasitic dinoflagellate *Oodinium cyprinodontum* Lawler, 1967. *Ches. Sci.*, **9**:263.
- Lawler, A. R. 1980. Studies on *Amyloodinium ocellatum* (Dinoflagellata) in Mississippi Sound: natural and experimental hosts. *Gulf Res. Rep.*, **6**:403-413.
- Lom, J. 1981. Fish invading dinoflagellates: a synopsis of existing and newly proposed genera. *Fol. Parasitol.*, **28**:3-11.
- Lom, J., Rohde, K. & Dykov, I. 1993. *Crepidodinium australe* n. sp., an ectocommensal dinoflagellate from the gills of *Sillago ciliata*, an estuarine fish from the New South Wales coast of Australia. *Dis. Aquat. Org.*, **15**:63-72.
- Love, D. C., Rice, S. D., Moles, D. A. & Eaton, W. D. 1993. Seasonal prevalence and intensity of bitter crab dinoflagellate infection and

- host mortality in Alaskan Tanner crabs *Chionoecetes bairdi* from Auke Bay, Alaska, USA. *Dis. Aquat. Org.*, **15**:1–7.
- Manier, J.-F., Fize, A. & Grizel, H. 1971. *Syndinium gammari* n. sp. Péridinien Duboscquodinida Syndinidae, parasite de *Gammarus locusta* (Lin.). Crustacé Amphipode. *Protistologica*, **7**:213–219.
- McLean, S. A. & Ruddell, C. L. 1978. Three new crustacean hosts for the parasitic dinoflagellate *Hematodinium perezii* (Dinoflagellata: Syndinidae). *J. Parasitol.*, **64**:158–160.
- McLean, N. & Galt, C. P. 1990. *Apodinium floodi* n. sp., a dinoflagellate (Dinoflagellata: Apodiniidae) ectoparasitic on *Oikopleura labradoriensis* (Urochordata: Larvacea). *Dis. Aquat. Org.*, **9**:213–219.
- McLean, N. & Nielsen, C. 1989. *Oodinium jordani* n. sp., a dinoflagellate (Dinoflagellata: Oodiniidae) ectoparasitic on *Sagitta elegans* (Chaetognatha). *Dis. Aquat. Org.*, **7**:61–66.
- Meneses, I. & Ré, P. 1989. Infection of sardine eggs by a parasitic dinoflagellate (*Ichthyodinium chabelardi*) off Portugal. Abstract. *Rapp. P. V. Reun. Cons. Int. Explor. Mer.*, **191**:442A.
- Meneses, I. & Ré, P. 1992. Infection of sardine eggs by a parasitic dinoflagellate (*Ichthyodinium chabelardi* Hollande and Cachon) off the Portuguese coast. Abstract. *Bol. Inst. Esp. Oceanogr.*, **8**:201A.
- Messick, G. A. 1994. *Hematodinium perezii* infections in adult and juvenile blue crabs *Callinectes sapidus* from coastal bays of Maryland and Virginia, USA. *Dis. Aquat. Org.*, **19**:77–82.
- Meyers, T. R., Lightner, D. V. & Redman, R. M. 1994. A dinoflagellate-like parasite in Alaskan spot shrimp *Pandalus platyceros* and pink shrimp *P. borealis*. *Dis. Aquat. Org.*, **18**:71–76.
- Meyers, T. R., Koeneman, T. M., Botelho, C. & Short, S. 1987. Bitter crab disease: a fatal dinoflagellate infection and marketing problem for Alaskan Tanner crabs *Chionoecetes bairdi*. *Dis. Aquat. Org.*, **3**:195–216.
- Meyers, T. R., Botelho, C., Koeneman, T. M., Short, S. & Imamura, K. 1990. Distribution of bitter crab dinoflagellate syndrome in southeast Alaskan Tanner crabs *Chionoecetes bairdi*. *Dis. Aquat. Org.*, **9**:37–43.
- Meyers, T. R., Morado, J. F., Sparks, A. K., Bishop, G. H., Pearson, T., Urban, D. & Jackson, D. 1996. Distribution of bitter crab syndrome in Tanner crabs (*Chionoecetes bairdi*, *C. opilio*) from the Gulf of Alaska and the Bering Sea. *Dis. Aquat. Org.*, **26**:221–227.
- Mills, C. E. & McLean, N. 1991. Ectoparasitism by a dinoflagellate (Dinoflagellata: Oodiniidae) on 5 ctenophores (Ctenophora) and a hydromedusa (Cnidaria). *Dis. Aquat. Org.*, **10**:211–216.
- Newman, M. W. & Johnson, C. A. 1975. A disease of blue crabs (*Callinectes sapidus*) caused by a parasitic dinoflagellate, *Hematodinium* sp. *J. Parasitol.*, **61**:554–557.
- Nigrelli, R. F. 1936. The morphology, cytology and life-history of *Oodinium ocellatum* Brown, a dinoflagellate parasite on marine fishes. *Zoologica, N. Y.*, **21**:129–164.
- Nishitani, L. & Chew, K. K. 1984. Recent developments in paralytic shellfish poisoning research. *Aquaculture*, **39**:317–329.
- Nishitani, L., Erickson, G. & Chew, K. K. 1985. Role of the parasitic dinoflagellate *Amoebophrya ceratii* in control of *Gonyaulax catenella* populations. In: Toxic Dinoflagellates. Anderson, D. M., White, A. W. & Baden, D. G. (ed.), Elsevier Science Publ., New York, p. 225–230.
- Nishitani, L., Hood, R., Wakeman, J. & Chew, K. K. 1984. Potential importance of an endoparasite of *Gonyaulax* in paralytic shellfish poisoning outbreaks. In: Seafood Toxins. Ragelis, E. P. (ed.), ACS Symposium Series, **262**:139–149.
- Øresland, V. 1991. Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic waters. *Mar. Ecol. Prog. Ser.*, **78**:41–47.
- Paperna, I. 1984. Chemical control of *Amyloodinium ocellatum* (Brown 1931) (Dinoflagellida) infections: in vitro tests and treatment trials with infected fishes. *Aquaculture*, **38**:1–18.
- Pasternak, A. F., Arashkevich, Y. G. & Sorokin, Y. S. 1984. The role of the parasitic algal genus *Blastodinium* in the ecology of planktonic copepods. *Oceanology*, **24**:748–751.
- Pfiester, L. A. & Lynch, R. A. 1980. Amoeboid stages and sexual reproduction of *Cystodinium bataviense* and its similarity to *Dinococcus* (Dinophyceae). *Phycologia*, **19**:178–183.
- Pfiester, L. A. & Popovský, J. 1979. Parasitic, amoeboid dinoflagellates. *Nature*, **279**:421–424.
- Popovský, J. & Pfiester, L. A. 1982. The life-histories of *Stylocladus sphaera* Pascher and *Cystodinedria inermis* (Geitler) Pascher (Dinophyceae), two freshwater facultative predator-autotrophs. *Arch. Protistenk.*, **125**:115–127.
- Popovský, J. & Pfiester, L. A. 1990. Dinophyceae (Dinoflagellida). In: Ettl, H., Gerloff, J., Heynig, H. & Mollenhauer, D., (ed.), Süßwasserflora von Mitteleuropa. Begründet von A. Pascher, 6, Jena, Gustav Fischer Verlag, p. 272.
- Pouchet, G. 1885. Nouvelle contribution à l'histoire des Péridiniens marins. *J. Anat. Physiol.*, Paris, **21**:28–88.
- Reimchen, T. E. & Buckland-Nicks, J. 1990. A novel association between an endemic stickleback and a parasitic dinoflagellate. 1. Seasonal cycle and host response. *Can. J. Zool.*, **68**:667–671.
- Rose, M. & Cachon, J. 1951. *Diplomorpha paradoxa*, n. g., n. sp. Protiste de l'ectoderme des Siphonophores. *C. R. Acad. Sci., Paris.*, **233**:451–452.
- Sandifer, P. A., Hopkins, J. S., Stokes, A. D. & Smiley, R. D. 1993. Experimental pond grow-out of red drum, *Sciaenops ocellatus*, in South Carolina. *Aquaculture*, **118**:217–228.
- Schnepf, E., & Deichgräber, G. 1984. "Myzovytosis", a kind of endocytosis with implications to compartmentation in endosymbiosis. *Naturwissenschaften*, **71**:218–219.
- Schnepf, E. M. & Elbrächter, M. 1992. Nutritional strategies in dinoflagellates: a review with emphasis on cell biological aspects. *Eu. J. Protistol.*, **28**:3–24.
- Sewell, R. B. S. 1951. The epibionts and parasites of the planktonic Copepoda of the Arabian Sea. *John Murray Expedition 1933–34, Sci. Rep. Br. Mus. (Nat. Hist.)*, **9**:255–394.
- Shaharom-Harrison, F. M., Anderson, I. G., Siti, A. Z., Shazili, N. A. M., Ang, K. J. & Azmi, T. I. 1990. Epizootics of Malaysian cultured freshwater pond fishes by *Piscinoodinium pillulare* (Schäperclaus 1954) Lom 1981. *Aquaculture*, **86**:127–138.
- Shields, J. D. 1994. The parasitic dinoflagellates of marine crustaceans. *Ann. Rev. Fish Dis.*, **4**:241–271.
- Shumway, W. 1924. The genus *Haplozoon*, Dogiel. Observations on the life history and systematic position. *J. Parasitol.*, **11**:59–74.
- Siebert, A. E., Jr. 1973. A description of *Haplozoon axiothellae* n. sp., an endosymbiont of the polychaete *Axiothella rubrocincta*. *J. Phycol.*, **9**:185–190.
- Smith, S. A., Levy, M. G. & Noga, E. J. 1992. Development of an enzyme-linked immunosorbent assay (ELISA) for the detection of antibody to the parasitic dinoflagellate *Amyloodinium ocellatum* in *Oreochromis aureus*. *Vet. Parasit.*, **42**:145–155.
- Stickney, A. P. 1978. A previously unreported peridinian parasite in the eggs of the northern shrimp, *Pandalus borealis*. *J. Invert. Pathol.*, **32**:212–215.
- Stoecker, D. K. 1999. Mixotrophy among dinoflagellates. *J. Euk. Microbiol.*, **46**:397–401.
- Taylor, D. M. & Khan, R. A. 1995. Observations on the occurrence of *Hematodinium* sp. (Dinoflagellata: Syndinidae), the causative agent of bitter crab disease in Newfoundland snow crab (*Chionoecetes opilio*). *J. Invert. Pathol.*, **65**:283–288.
- Taylor, F. J. R. 1968. Parasitism of the toxin-producing dinoflagellate *Gonyaulax catenella* by the endoparasitic dinoflagellate *Amoebophrya ceratii*. *J. Fish. Res. Bd. Canada*, **25**:2241–2245.
- Vane, F. R. 1952. The distribution of *Blastodinium hyalinum* in the North Sea. *Challenger Soc.*, **3**:23–24.
- Wilhelm, G. & Mialhe, E. 1996. Dinoflagellate infection associated with the decline of *Necora puber* crab populations in France. *Dis. Aquat. Org.*, **26**:213–219.