Chapter 10
Animals in Coastal Benthic Ecosystem and Aquaculture Systems

The best way to observe a fish is to become a fish
Jacque Yves Cousteau

Animals are secondary and higher level producers in any ecosystem. Health of animals at each trophic level is important for efficient energy transfer to trophic levels above. Many marine animals are also cultivated in aquaculture for human use. Hence, their health is also of economic importance to human society. Following their death by natural mortality, disease, and incomplete predation by other animals, they are decomposed by bacteria and fungi which recycle nutrients in the ecosystem. The littoral and sublittoral zones of coastal seas are home to a large diversity and population of benthic animals. These include meiobenthos such as nematodes, amphipods, and polychaetes, as well as macrobenthos such as crustaceans, molluscs, and fish. Many of these are cultivated in aquaculture. The balance of health of marine animals when they are alive and their decomposition and recycling of nutrients upon their death are crucial to the marine ecosystem.

A high diversity of fungi belonging to Mycetae as well as Straminipila are widely associated with animals as symbionts and saprotrophs. Mutualistic fungi play a role in maintaining the health of animals. Saprophytic fungi decompose dead animals and their fecal matter. Most of what we know about fungi in the marine ecosystem pertains to their role as parasites and pathogens. Many members of marine Oomycetes (Straminipila) as well as terrestrial species of fungi are widely prevalent as animal parasites.

10.1 Nonpathogenic Symbiotic Fungi in Animals

Diverse fungi occur in a variety of invertebrates without causing any external disease symptoms.

Obligate as well as facultative marine fungi are frequently found in invertebrates.

S. Raghukumar, *Fungi in Coastal and Oceanic Marine Ecosystems*,
DOI 10.1007/978-3-319-54304-8_10

- Sea urchins (Phylum Echinodermata) harbor fungi in their guts.
  - The irregular sea urchin *Echinocardium cordatum* (Pennant) collected from a muddy sediment at a depth of 28 m from the Baltic Sea harbors a variety of microorganisms in its guts (Thorsen 1999). An obligately anaerobic fungus belonging to the Neocallimastigomycota appears to be a resident in its guts (Fig. 10.1). Motile spherical cells of 4–6 μm with an extremely long, posteriorly directed flagellum resembling zoospores were found in the gut and coelomic fluid. Thalli, zoosporangia, and zoospores of the chytrid fungus have been found in various parts of its gut. Cells of the chytrid as well as zoospores are abundant in the anoxic anterior cecum of the gut, along with bacteria and protozoa. This fungus may be mutualistic with the symbiont, with a similar function as in terrestrial ruminant animals.
  - Thraustochytrids have been cultured from the guts of another sea urchin, *Lytechinus variegatus* collected from the Gulf of Mexico (Wagner-Merner et al. 1980). Straminipilans also appear to be associated intimately with other invertebrates. The thraustochytrid *Ulkenia visurgensis* (Ulken) Gaertner has been detected using an immunofluorescence detection method in the coelenterons and hydranth of a hydroid from the west coast of India (Raghukumar 1988). The aplanochytrid, *Aplanochytrium (Labyrinthuloides) yorkensis*, was first isolated from the mantle cavity of the oyster *Crassostrea virginica* (Perkins 1973).

- Trichomycetes, a group of mycetaen fungi belonging to Glomeromycota, colonize the digestive tracts of many marine arthropods. These fungi are believed to

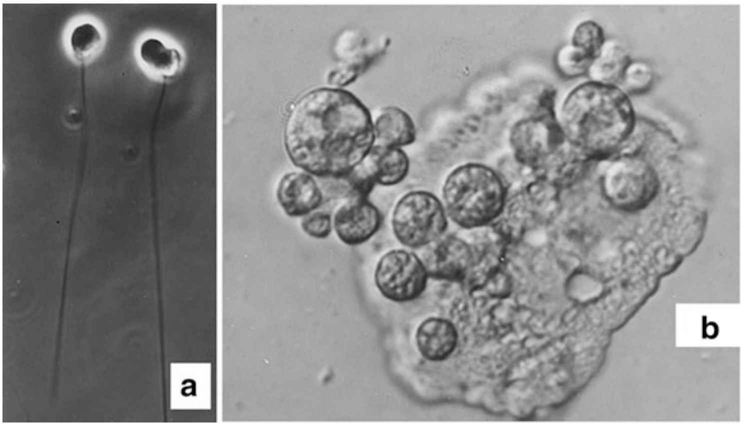

Fig. 10.1 Some commensalistic or mutualistic fungi in animals. (**a**, **b**) A fungus resembling anaerobic Neocallimastigomycota in gut of the sea urchin *Echinocardium cordatum*. (**a**) Zoospores with a posterior flagellum from the coelomic fluid. (**b**) Particulate material from the anterior cecum, inhabited by nonmotile spherical cells resembling the fungus (**a** and **b**: Source: Thorsen, M.S. 1999. Abundance and biomass of the gut-living microorganisms (bacteria, protozoa and fungi) in the irregular sea urchin *Echinocardium cordatum* (Spatangoida: Echinodermata). Marine Biology 133:353–360)

live in a mutualistic association with their hosts. Their thallus either consists of branched, septate filaments attached to the host cuticle by a holdfast or may be unbranched, nonseptate, and coenocytic (http://www.nhm.ku.edu/~fungi/). Trichomycetes cannot be cultured and have to be detected by direct microscopy methods. These fungi have been found in a number of marine arthropods, isopods, decapods, and amphipods (Misra and Lichtwardt 2000). One particular study found several members of Eccrinales belonging to Trichomycetes in crustaceans of the littoral region of the San Juan archipelago, Washington (Hibbits 1978).

- A number of marine-derived fungi have been obtained from the sponges *Amphimedon viridis, Axinella corrugata, Dragmacidon reticulata, Geodia corticostylifera, Mycale laxissima*, and *Mycale angulosa* and the ascidians *Didemnum ligulum* and *Didemnum* sp. collected at 5–10 m from the coast of Sao Paulo, Brazil. Culturing following surface sterilization yielded facultative marine fungi belonging to Ascomycota, Basidiomycota, and Mucoromycota (Menezes et al. 2010). Marine-derived fungi have also been detected from sponges along the coast of Hawaii, using DGGE analysis of ITS or SSU rRNA sequences. These fungi included the PCG environmental sequence groups belonging to Ascomycota as well as the Hy-An group belonging to Basidiomycota (Gao et al. 2008). Most fungi belonged to hitherto unidentified taxa. Among the identified ones, most belonged to *Trichoderma, Penicillium, Aspergillus* and *Fusarium*. The ascidian *Didemnum* sp. harbored the highest diversity of filamentous fungi.
- Yeasts have been isolated from a variety of marine animals, such as the Mexico shrimp *Penaeus setiferus*, shrimp eggs, sponges, and other invertebrate material collected from the North Atlantic Ocean, guts of the fiddler crab, *Uca pugilator,* shellfish, and intestine of farmed rainbow trout (*Salmo gairdneri*) (Kutty and Philip 2008). Yeasts appear to be abundant in internal fluids of some animals, such as those of the guts of fiddler crab and the liquid portion of the shellfish. A variety of yeasts have been identified. Red-pigmented yeasts dominated and composed about 90% of the isolates from the rainbow trout. Other yeasts are *Trichosporon cutaneum, Rhodotorula glutinis, Candida parapsilosis, Pichia guilliermondii, Pullularia pullulans, Debaryomyces hansenii, Torulopsis candida, Trichosporon cutaneum*, *Debaryomyces hansenii*, *Saccharomyces cerevisiae, Rhodotorula rubra* and *R. glutinis*.

10.2 Animal Diseases Caused by Fungi

Parasitism is as much a natural, ecological strategy as commensalism and mutualism are. Natural or man-made environmental changes may induce physiological stress in organisms and make them susceptible to diseases. Under such conditions, organisms which are mildly parasitic or even mutualistic may become highly virulent and cause infections of epidemic proportions that affect the population of the host organisms (Harvell et al. 1999). New diseases have often emerged through host or range shifts of known pathogens.

Fungal infections are common in both wild and cultivated marine animals (Porter 1986; Polglase et al. 1986; Shields and Overstreet 2007; Ramaiah 2006; Hyde et al. 1998; Hatai 2012; Marano et al. 2012). Fungi parasitize almost all groups of marine animals in the oceans. In addition to their importance in the marine ecosystem, infectious diseases, including fungal infections, are a major problem for aquaculture industries. Marine fishes, prawns, and crabs are very popular seafood. Finfish and shellfish seed production and culture are important economic activities. Most of our knowledge on fungal parasites of marine animals comes from diseases of commercially useful ones.

10.2.1 Fungi that Cause Animal Diseases

Fungi belonging to the Oomycetes, Straminipila have an enormous host range and are probably most important as marine invertebrate parasites, especially in the seed production of marine crustaceans such as shrimps and crabs (Marano et al. 2012; Hatai 2012). This includes species belonging to *Atkinsiella* (Atkinsiellales, Saprolegniomycetes), *Haliphthoros, Halioticida*, and *Halocrusticida* (Haliphthorales), *Lagenidium* (Peronosporales), and *Sirolpidium* (Olpidiopsidales) (Beakes et al. 2014) (Fig. 10.2; Table 10.1).

- **Members of "Haliphthorales" are exclusively marine and occur as parasites of molluscs, crustaceans, or their eggs** (Beakes et al. 2014). Members of this group produce irregularly branched mycelial thalli. Part of the thallus is converted into the reproductive structures, the zoosporangia, while others remain vegetative (eucarpic thallus). Species of this order can be cultured on artificial media. Large segments of the thalli convert into zoosporangia. All genera form very long narrow hypha-like exit tubes from which the biflagellate zoospores escape in uniseriate fashion.
- **Species of *Lagenidium,* particularly *L. callinectes* Couch, infect and kill many invertebrate eggs and embryos**. This oomycete was first discovered in eggs of the blue crab *Callinectes sapidus* from Chesapeake Bay and described by the renowned mycologist John N. Couch in 1942. The fungus was later reported to infect ova of the barnacle *Chelonibia patula*. *Lagenidium chthamalophilum* Johnson infects ova of the barnacles *Chthamalus fragilis*. *Lagenidium callinectes* represents the greatest fungal threat in cultivation of marine decapods. Presence of the fungus can be observed as brown or gray patches in the clutch. Dead eggs are opaque and smaller than healthy ones. Infection is generally more on eggs in the periphery of the clutch. The fungus rarely penetrates more than 3 mm of the clutch. Eggs die prematurely. The fungus may infect 100% of eggs and kill all of them under severe conditions. Older clutches are attacked more heavily than recently laid ones. Larvae are also

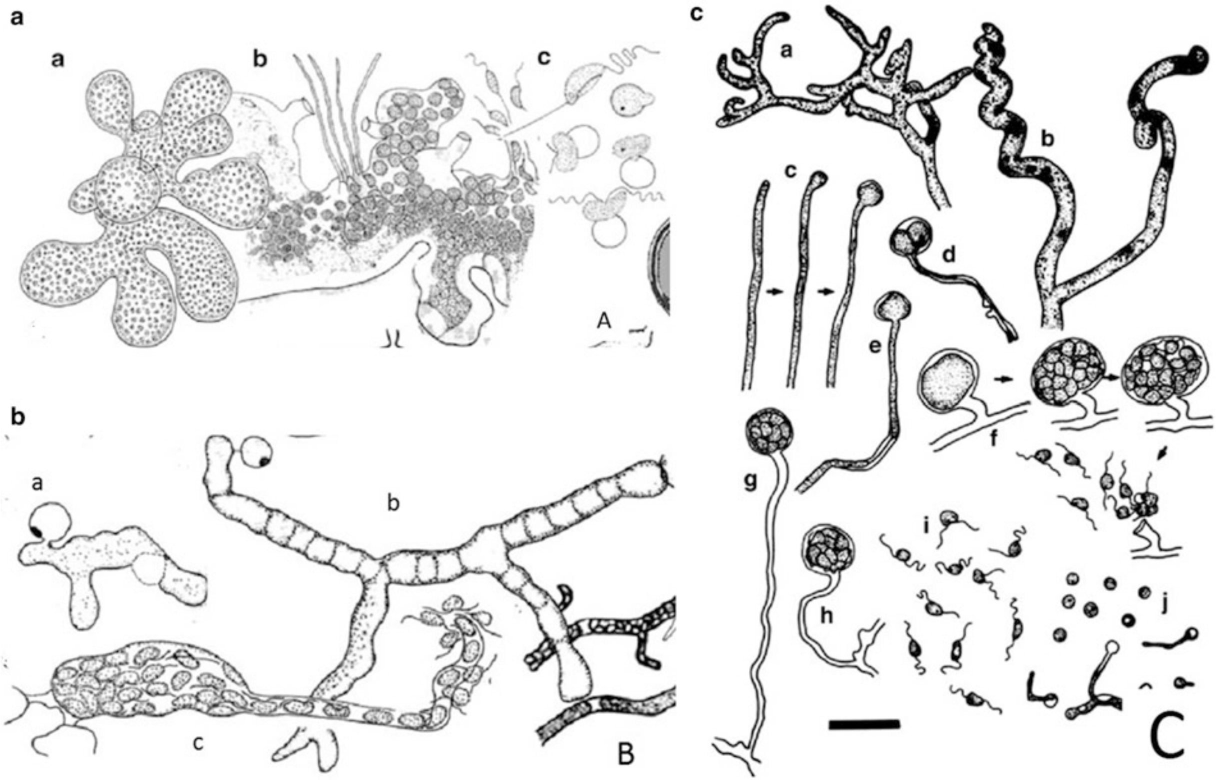

Fig. 10.2 Oomycete parasites of marine animals. (**a**) *Atkinsiella dubia*. (a) lobate thalli; (b) zoosporangia; (c) biflagellate zoospores. (**b**) *Haliphthoros milfordensis*. (a) Encysted zoospores; (b) lobate thalli; (c) zoosporangia. (**c**) *Lagenidium callinectes*. (a, b) Vegetative thallus. (c–h) Zoosporangium formation. (i, j) Liberation of biflagellate zoospores (Source: **a** and **b**: Beakes, G.W. et al. Systematics of the Straminipila: Labyrinthulomycota, Hyphochytriomycota, and Oomycota. In: Systematics and Evolution, 2nd Edition The Mycota VII Part A. D.J. McLaughlin and J.W. Spatafora (Eds.) Springer-Verlag. **c**: Hatai, K. 2012. Diseases of Fish and Shellfish Caused by Marine Fungi. In: Raghukumar, C. (ed.). Biology of Marine Fungi. Springer Verlag)

Table 10.1 Examples of diseases caused by Oomycetes in marine animals

Fungus	Hosts
Lagenidium	• *L. callinectes*—ova of the blue crab, *Callinectes sapidus, Artemia salina;* ova of the barnacle, *Chelonibia patula*; eggs and zoeae of the marine crabs, *Portunus pelagicus, Cancer magister, Neopanope texana, Pinnotheres ostreum, Portunus trituberculatus, Scylla serrata;* American lobster, *Homarus americanus* • *L. chthamalophilum*—ova of the barnacle, *Chthamalus fragilis. C*ultivated crustaceans, e.g., white shrimp, *Penaeus setiferus*, the Dungeness crab, *Cancer magister*, and the American lobster, *Homarus americanus* • *L. scyllae*—ova and larvae of the mangrove crab, *Scylla serrata*, in Philippines • *L. thermophilum*—eggs and larvae of mangrove crab, *Scylla serrata*, affecting the seed production in Bali, Indonesia, *Penaeus monodon, Crangon vulgaris, Palaemon serrat*us (as *Leander serratus*) • *L. marinum*—bivalves *Barnea candida, Acanthocardia echinata* (as *Cardium echinatum*), *Mytilus edulis*
Haliphthoros	• *H. milfordensis*: endoparasite of eggs of the oyster drill, *Urosalpinx cinerea*; juveniles of the American lobster, *Homarus americanus, H. gammarus*; brine shrimp *Artemia salina;* adults of the white shrimp, *Penaeus setiferus*, *Farfantepenaeus duorarum* (as *Penaeus duorarum*), *Penaeus japonicus, P. monodon, Litopenaeus setiferus* (as *P. setiferus*); crabs, *Callinectes sapidus, Portunus pelagicus, P. pisum, P. trituberculatus, Pinnotheres* spp., *Scylla serrata;* in abalone, *Haliotis gigantea (sieboldii), Japan; Penaeus monodon* in Nha Trang, Vietnam; gill lesions of juvenile kuruma prawns, *Penaeus japonicus*, with black gill disease. • *H. philippinensis:* larvae of the jumbo tiger prawn, *Penaeus monodon* in Philippines; crab *Scylla serrata;* oyster *Crassostrea virginica;* hard clam *Mercenaria mercenaria* (as *Venus mercenaria*)
Halodaphnea (Halocrusticida)	• *H. hamanaensis*—Eggs and larvae of *Scylla serrata* • *H. parasitica*—Rotifer *Brachionus plicatilis*, crab *Portunus trituberculatus* • *H. awabi*—Abalone (*Haliotis gigantea (sieboldii)*), • *H. okinawaensis*—zoea of the crab *Portunus pelagicus*, *Eroicheir japonicus*; crab *Scylla serrata* • *H. panulirata*—Philozoma of spiny lobster (*Panulirus japonicus*) • *H. baliensis*—crab *Scylla serrata*
Atkinsiella dubia	• Abalone, *Haliotis gigantea (sieboldii)* Crabs—eggs of pea crab, *Pinnotheres pisum* in England, eggs of *Gonoplax rhomboids,* gills of swimming crab, *Portunus trituberculatus,* Japan, *Eriocheir japonicus, Gonoplax angulata, Hyas* sp., *Macropodia* sp., *Oregonia, Portunus depuratus, Typton spongicola*
Halioticida noduliformans	Abalone—*Haliotis medae*, Japan, gills of wild mantis shrimp, *Oratosquilla oratoria* in Tokyo Bay, Japan
Sirolpidium	Eggs and larvae of the prawn *Penaeus monodon*

attacked. The fungus penetrates the exoskeleton, grows rapidly within the body of the larva, and replaces the internal tissues, particularly the striated muscles (Polglase et al. 1986). An isolate from the blue crab grew better on simple sugars (e.g., fructose, glucose) than on complex carbohydrates and polysaccharides and required vitamin B1 (Bahnweg and Bland 1980). Most strains are obligately marine, but isolates from the American lobster and the Dungeness crab *Cancer magister* do not require NaCl (Bahnweg and Gotelli 1980). Infection starts through germination of encysted zoospores that form a germ tube which penetrates the host and grows rapidly. The vegetative thallus consists of coenocytic, intramatrical hyphae. These grow rapidly, ramify in the host, and replace the host tissues. They reproduce by means of zoospores produced in zoosporangia. The zoosporangium is first delimited by a septum from the vegetative hyphae. Sporangia develop long discharge tubes. Following this, cytoplasm is discharged (5–30 min) into a gelatinous vesicle. Flagellar formation precedes cleavage, and the flagella can be observed actively beating inside the sporangium (Gotelli 1974). Cleavage is rapid and spore release occurs within 10 min of sporogenesis. From 20 to 200 zoospores are produced by a single sporangium. The pyriform zoospores, 10 by 13 μm, have two flagella arising from a groove that spans the length of the spore (Shields and Overstreet 2007).

Many terrestrial species of fungi, such as species of *Fusarium*, are opportunistic pathogens and have been reported to be associated with shell disease of marine crustaceans and lobsters.

10.2.2 Infections of Shrimps and Prawns

Fungal diseases frequently pose a huge problem in prawn hatcheries.

- ***Penaeus monodon***, the highly rated giant tiger prawn or the Asian tiger shrimp, is the second largest cultivated aquaculture prawn in the world. Eggs and larvae of the prawn in the hatchery of an aquaculture facility in Thailand, were reported to have been infected by ***Lagenidium thermophilum*** K. Nakam., Miho Nakam., Hatai & Zafran in August 2000 (Muraosa et al. 2006). A new species, ***Haliphthoros philippinensis*** Hatai, Bian, Batic. & Egusa, was isolated from larvae of the jumbo tiger prawn, *Penaeus monodon* in Philippines (Hatai et al. 1980). This species grows in a wide range of temperature, even up to 36 °C. The anamorphic, opportunistic, terrestrial fungus *Fusarium* may infect all stages of the prawn (Ramaiah 2006). In Vietnam, a new *Fusarium* infection, caused by ***F. incarnatum*** (Roberge) Sacc., occurred in black tiger shrimp, *Penaeus monodon* (Khoa and Hatai 2005). Infected shrimps showed typical signs of black gill disease and mortalities about a month prior to harvest. Optimal temperature for the fungus ranged from 20 to 30 °C. The fungus grew very well at 35 °C, but not at 5 and 40 °C.

Haliphthoros milfordensis Vishniac was isolated from larvae of *Penaeus monodon* in Nha Trang, Vietnam (Chukanhom et al. 2003).

- **The kuruma prawn, *Penaeus japonicus***, is another highly prized cultured prawn. Many fungi cause the "black gill disease" of juveniles of this prawn (Fig. 10.3a, b). The oomycete *Halipthoros milfordensis* was reported from black gill lesions at a private farm in August 1989 in Japan. The fungus *Fusarium* seems to be an important agent of the disease. *Fusarium* infection was first reported from black gill disease of pond-cultured kuruma prawn in Japan in 1972. Subsequently, the fungus has been implicated in a number of such infections. The fungi *Fusarium solani* (Mart.) Sacc., *F. moniliforme* J. Shield, and *F. oxysporum* Schltdl have also been isolated from kuruma prawn with black gill disease in Japan. Among these, *F. solani* appears to be an important pathogen (Fig. 10.3c). The pathogenicity of anamorphic fungi *Plectosporium oratosquillae* and *Acremonium* sp., isolated from mantis shrimp in kuruma

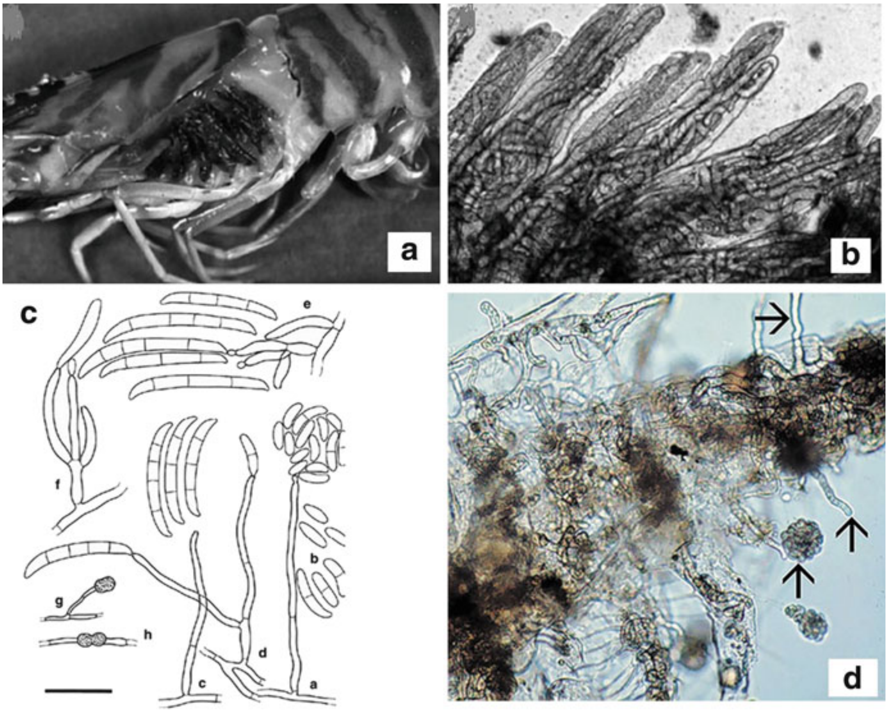

Fig. 10.3 Fungal parasites of marine crustaceans. (**a**, **b**) The black gill disease of the kuruma prawn, *Penaeus japonicus*. (**a**) The typically black gills. (**b**) Hyphae of the parasite *Haliphthoros milfordensis*. (**c**) Conidia of *Fusarium solani,* causal agent of black lesions in *Penaeus japonicus*. (**a**–**c**: Source: Hatai, K. 2012. Diseases of Fish and Shellfish Caused by Marine Fungi. In: Biology of Marine Fungi (Ed.: C. Raghukumar, Springer). (**d**) Mycelium of *Lagenidium callinectes* pervading larvae of *Penaeus setiferus*. Zoosporangia with zoospores have emerged (*arrows*) (Courtesy: Dr. D.H. Lightner, Aquaculture Pathology Laboratory, University of Arizona)

prawn *Penaeus japonicus*, has been established by intramuscular injection of conidial suspensions. Cumulative mortality in kuruma prawn reached 100% when injected with a conidial suspension of *Acremonium* sp. The prawns showed typical black gills, and the clinical sign was similar to that of prawn naturally infected with fungus. The prawn is an important cultured crustacean in Japan and lives in the same environmental conditions.

- **The mantis shrimp, *Oratosquilla oratoria***, is an economically important and delicious culinary crustacean species. The famous Japanese "sushi" is made from the meat of mantis shrimp. This shrimp is a dominant benthic species in coastal Japan. Gill lesions from the wild mantis shrimp from Tokyo, Japan, harbored the oomycete *Halioticida noduliformans*. The fungus grows in an aerobic environment. In culture, it grows well at 15–25 °C, with optimal temperature of 20 °C.

  Two anamorphic fungi, *Plectosporium oratosquillae* and *Acremonium* sp., cause mortality of the mantis shrimp by infecting the gills which turn brown due to discoloration. Animals injected with conidia of the two species result in brown spots in the gill filaments similar to the clinical sign of mantis shrimp naturally infected with the fungi and subsequently in death. Hyphae and conidia are found in the gill filaments and heart, and the hyphae become encapsulated by hemocytes in the gill filaments and the base of gills. The result confirmed that these two anamorphic fungi were pathogenic to mantis shrimp. The antifungal agent voriconazole is an efficient antifungal agent against *Acremonium* sp. (Duc et al. 2010).
- **Adult northern shrimp, *Pandalus borealis*, cultured at the Japan Seafarming Association (JASFA) was infected by *Salilagenidium myophilum*** (Hatai & Lawhav.) M.W. Dick *(Pythium myophilum, Lagenidium myophilum*) which grew in the abdominal muscles and swimmeret. Lesions became filled with hyphae. The fungus could grow at temperatures of 5–25 °C. It also infected larvae of the coonstripe shrimps, *Pandalus hypsinotus*. The disease caused 100% mortality at Hokkaido in Japan (Nakamura et al. 1994).
- **The cultivated white shrimp *Penaeus setiferus* is often infected by *Lagenidium callinectes* and *Haliphthoros milfordensis***.
- A species of the yeast ***Kluyveromyces*** was isolated from the heart tissue of subadult penaeid shrimp ***Penaeus chinensis*** during tissue culture (Tong and Miao 1999).
- The yeast ***Metschnikowia bicuspidata*** (Metschn.) T. Kamienski, a pathogenic yeast of aquatic invertebrates, infected aquaculture-reared, disease-free ***Artemia*** (Moore and Strom 2003).

10.2.3 Infection of Crabs and Lobsters

- **The gazami crab, Japanese blue crab** or horse crab, *Portunus tuberculatus,* is the most fished pelagic crab species in the world. It is being cultivated in China. An explosive epidemic disease, now called milky or "emulsification" disease, has appeared in cultured *Portunus trituberculatus* since 2001 in Zhoushan, Zhejiang Province, China, leading to high mortality of this crab and great economic loss in this area. Infected crabs are emaciated and a milky liquid flows out from cut legs. The causal organism is the yeast *Metschnikowia bicuspidata*. The yeast can produce similar symptoms in the muscle, heart, and hepatopancreas when inoculated artificially. The use of "killer yeasts" to control the disease has been suggested. "Killer yeasts" can be applied to control growth of pathogenic yeasts in humans, animals, and plants. Such yeasts produce low molecular mass proteins or glycolipid toxins that kill the target pathogen. A strain of *Pichia anomala* (E.C. Hansen) Kurtzman was subsequently identified for the purpose (Wang et al. 2007b). Gills of this swimming crab was seen to be infected also by *Atkinsiella dubia* (D. Atkins) Vishniac in Japan. Heavy mortalities reaching 100% among gills of swimming crab have been observed. Infected zoeal larvae were filled with numerous aseptate hyphae. Zoea of this crab is also infected by *Haliphthora milfordensis*.

- Another pelagic crab, the blue **swimmer crab or flower crab, *Portunus pelagicus***, is vulnerable to a fungal disease. Eggs and zoeae of these crabs may be infected by ***Lagenidium thermophilum and Halocrusticida okinawaensis*** (K. Nakam. & Hatai) K. Nakam. & Hatai.
- **The mud crab or the mangrove crab, *Scylla serrata***, is a dominant crab of Indo-Pacific mangroves and is now widely cultivated. **Several fungi cause diseases in this crab.** In 1997, fungal diseases occurred in the eggs and zoeae of the mangrove crab, *S. serrata,* at the Gondol Research Station for Coastal Fisheries, Bali, Indonesia. The mortality rate reached almost 100% in the larvae. The infected larvae were whitish in color and filled with numerous aseptate hyphae. *Lagenidium callinectes, L. scyllae* Bian et al., *Haliphthoros milfordensis*, *Halocrusticida baliensis* Hatai, Roza & T. Nakay sp. nov., and *H. (Atkinsiella) hamanaensis* Bian & Egusa have all been reported as parasites in eggs and larvae of this crab (Hatai et al. 2000; Hatai 2012). A new fungus named *Lagenidium thermophilum* was isolated from the diseased mangrove crabs in 1993 at Gondol Research Station for Coastal Fisheries, Bali, Indonesia. This thermotolerant fungus grows rapidly between 15 and 45 °C and has an optimum at 30–40 °C (Nakamura et al. 1995). *Haliphthoros philippinensis* Hatai, Bian, Batic. & Egusa and *H. milfordensis* are known to abort eggs of captive *Scylla serrata* before hatching in several hatchery runs at the Aquaculture Department of Southeast Asian Fisheries Development Center in lloilo, Philippines (Leaño 2002).
- A 100% mortality of larvae of the **Japanese mitten crab, *Eriocheir japonicus***, is known to have been caused by infections, the main parasite being ***Atkinsiella dubia***.
- Live eggs of the subtidal yellow **rock crab, *Cancer anthonyi*, become infected by the chytrid fungus *Rhizophydium littoreum*** Amon, which otherwise is generally known to be a saprobe on its dead eggs. About 14–52% infections have been recorded throughout the year at sites along the west coast of North America. The chytrid probably is a facultative parasite with a low degree of virulence.

- **Eggs of the blue crab, *Callinectes sapidus*, pea crab, *Pinnotheres pisum*, and the Dungeness crab, *Cancer magister*, are prone to attack by *Lagenidium callinectes***. Up to 50% of the eggs in the former succumb to the infection. Eggs of pea crab *Pinnotheres pisum* and the angular crab *Gonoplax rhomboides* are also parasitized by *Atkinsiella dubia* (Atkins) Vishniac. This fungus as well as *Halocrusticida hamanaensis* infect crustacean eggs freshly detached from ovigerous females (Porter 1986). The embryos of the crabs *Dyspanopeus texana, Panopeus herbstii*, and *Pinnotheres ostreum* are also susceptible to infection by *Lagenidium callinectes* (Polglase et al. 1986; Shields and Overstreet 2007).
- **The Black Mat Syndrome in the Tanner Crab *Chionoicetes bairdi* is caused by the biotrophic, ascomycetous fungus *Trichomaris invadens*** Hibbets, Hughes et Sparks (Polglase et al. 1986). The carapace turns black because of the growth of the fungus and presence of ascocarps. The hyaline hyphae penetrate the exoskeleton and grow in the epidermis. In advanced cases, the hyphae invade the connective tissue of the animal, presumably preferring to grow along lines of low physical weakness. The symptoms of the disease indicate that this disease could severely affect the health of the crab. As is typical of biotrophic parasites, the fungus cannot be grown in the absence of the host and has not been cultured so far.
- **The American lobster, *Homarus americanus***, is cultured in California for food. The animals are **host to the pathogens *Lagenidium callinectes* and *Haliphthoros milfordensis***. The fungi penetrate and fill larvae with mycelia giving a white, opaque appearance. Appendages or body filled with white mycelia, vegetative fruiting structures are visible under dissecting microscope. The anamorphic ascomycete fungus *Fusarium* also causes a disease in American lobsters. The fungus is an opportunistic parasite and invades the animal through damaged or dead tissues.
- **Philozoma of the diseased spiny lobster, *Panulirus japonicus,* in Japan has been reported to harbor the parasite *Halocrusticida (Atkinsiella) panulirata***. The spiny lobster *Palinurus elephas* is known to be infected by a fungus which extensively invades and destgroys the shell (see Kohlmeyer and Kohlmeyer 1979).
- **Hermit crabs have been reported to be infected by *Fusarium*** species.
- Exoskeleton of the crab *Carcinus maenas* is infected by *Periconia prolifica* that causes ‘burnspots’ and black nodules in the hepatopancreas (see Kohlmeyer and Kohlmeyer 1979).

10.2.4 Bivalves and Gastropods

- The bivalve, the abalone, is a greatly valued traditional food. **Mariculture of the northern abalone, *Haliotis kamtschatkana*, and the red abalone, *H. rufescens*, has been attempted** in view of their declining natural populations. This has been beset with serious problems, including a fungal disease.

One of these is a disease caused by the aplanochytrid *Aplanochytrium (Labyrinthuloides) haliotidis* (S.M. Bower) C.*A. Leander* & D. Porter (Fig. 10.4). The high mortality of up to 100% of juvenile abalones caused by this disease in 1980s is considered to be one of the reasons why the mariculture facility on Vancouver Island, British Columbia, in the West coast of Canada was closed down (Bower 1987, 2000; Bower and Meyer 2005).

The fungal infection causes destruction of head and foot tissues of the juvenile abalones which are less than 4 mm in shell length and younger than

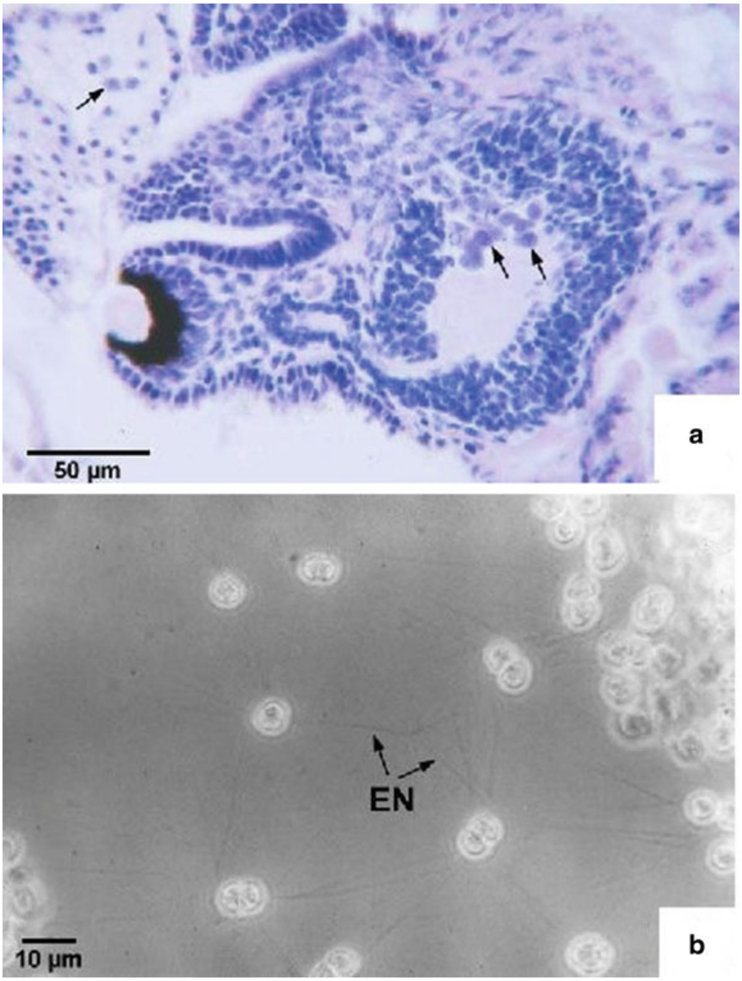

Fig. 10.4 *Aplanochytrium* disease of the abalone *Haliotis kamtschatkana*. (**a**) Histological section of a juvenile abalone with *Aplanochytrium haliotidis* (*arrows*) within the nerve ganglion and in surrounding tissues. (**b**) Cells of *Aplanochytrium haliotidis* in culture showing ectoplasmic net elements (EN, *arrows*) (Courtesy: Dr. Susan M. Bower)

6 month. Over 90% of the 100,000 small abalones in the British Columbia raceway succumbed to infection within 2 weeks of detection in a raceway. Abalones greater than 5 mm in shell length were more resistant to infection and mortality compared to those which were about 25 mm in shell length. Cells of the aplanochytrid could be detected in internal tissues. The fungus might be capable of infecting other bivalves if it gains access to internal tissues. Thus, small Pacific oysters (*Crassostrea gigas*) with damaged shells became infected, although those with intact ones were not affected. The scallop (*Patinopecten yessoensis)* was also resistant to infection.

The aplanochytrid grows vegetatively by binary divisions of cells. Mature cells are released into the water upon death. They produce biflagellate zoospores which may again infect live abalone. *Labyrinthuloides haliotidis* grew well on a wide variety of nutrient media and could also grow on pine pollen, which is used as a standard bait to culture labyrinthulomycetes.

Various control measures were considered. Exposure to chlorine, the anti-fungal compound cyclohexamide, and ozone treatment of incoming water have been recommended. Many of these are not practical for various reasons. A major precaution is to physically separate broodstock from the progeny, disinfecting fertilized eggs and rearing of the progeny in treated (disinfected) water until they reach a shell size of more than 5 mm. Quarantine practices are also recommended.

A few other species of abalone are also susceptible to fungal diseases. *Haliotis sieboldii* held in aquaria with circulating sea water adjusted to 15 °C by a cooling system in Japan has been infected by the oomycete *Haliphthoros milfordensis*. Tubercle-like swellings are produced on the mantle and melanized lesions on the peduncle. The fungus grew at a temperature range of 4.9–26.5 °C, with optimum of 11.9–24.2 °C. It grew best in shrimp extract medium at 25 °C.

Haliotis midae imported from the Republic of South Africa, *Haliotis rufescens* imported from the Republic of Chile and the United Mexican State, and *Haliotis sieboldii* collected in Japan were seen to have been infected by the oomycete *Halioticida noduliformans* Muraosa & Hatai. Here too white nodules were produced on the mantle.

- Many oysters such as *Ostrea edulis*, *Crassostrea gigas*, *Saccostrea cucullata*, *Crassostrea cucullata*, and *C. angulata* are prone to a wart disease caused by the mycetaen fungus *Ostracoblabe implexa* (Golubic et al. 2005; Raghukumar and Lande 1988). The fungus pervades the shells of the oysters. It is characterized by spindle-shaped swellings along the hypha. The fungus is probably an opportunistic pathogen, which normally resides in the shells without causing a disease. However, in the case of a disease, the hyphae grow through the shell, eventually penetrating the inner surface. The disease is limited to the shell, first appearing as small round white spots, which are slightly raised and have a clear center. These spots coalesce. “Conchiolin warts” are formed on the inner surface of the shell and can cause severe thickening of the shell margin. If the area beneath the adductor muscle is infected, attachment is weakened and closing of the shell is compromised due to excessive shell production in that area. Distortion can render the oyster unmarketable. Proliferation of the fungus is restricted to waters where temperatures exceed 22 °C for more than 2 weeks. Hence, shallow beds are more severely affected than deep growing sites. Infections have been reported from Europe, India, and Canada (both Pacific and Atlantic coasts).

- **Hatchery-related mortalities of the oyster *Crassostrea virginica* by the oomycete *Sirolpidium zoophthorum* Vishniac have been reported** along eastern U.S. Larvae and post-metamorphic juveniles measuring up to 400 μm in diameter are affected. The fungus spreads throughout the soft tissues, resulting in their disintegration. The long discharge tubes of the zoosporangia protrude outside the shell and release motile biflagellate zoospores. The disease is transmitted through zoospores. Over 90% of larvae can be killed within 2 days. Zoospores of *S. zoophthorum* can germinate and grow on nutrient agar in the absence of bivalve larvae. The disease is believed to be because of poor husbandry. The disease also occurs in natural populations of the oyster.
- **Eggs of the oyster drill, *Urosalpinx cinerea*, have been reported to become infected with *Haliphthoros milfordensis*.**
- **The edible "hard clam" or quahog, *Mercenaria mercenaria,* caused by a thraustochytrid, now termed the Quahog parasite or QPX (Quahog Parasite Unknown),** is widespread in North and Central America. A serious disease of the clam emerged in Provincetown, Massachusetts, USA, in 1993. About 90% of the clams were affected, threatening to shut down the clam industry (Powell 2005). Hatchery-reared and commercially harvested clams throughout the northeastern coast of North America have been affected. Infected clams are weak. Their shells become partially opened, allowing the lodging of sand inside. Tan nodules develop within the clams. Such clams are more likely to be consumed by predators, leading to mortalities. As the siphon sucks in seawater, particles that are not taken into the gut are discarded. These "pseudofaces" may harbor QPX, initiating the infection at the clam's siphon. The QPX thraustochytrid is believed to be a saprobe in the surrounding water and may be an opportunistic pathogen. In culture, the thraustochytrid grows best between 20 °C and 23 °C. Production of abundant mucus by the parasite is believed to promote inflammatory response of the clam and also protect the thraustochytrid from phagocytic hemocytes and humoral antimicrobial agents. Mortalities peak in summer and early fall (Garcia-Vedrenne et al. 2013).
- The fungi ***Curvularia* sp., *Exserohilum rostratum*** (Drechsler) K.J. Leonard & Suggs, and an unidentified species were regularly isolated from fungal lesions in juveniles of the **boring clam *Tridacna crocea***, which is cultured in Australia (Norton et al. 1994).
- Natural populations of the **nudibranch *Tritonia diomedea*** from the North American Atlantic coast, as well as laboratory, often contract a disease called the yellow spot disease or ringworm. Symptoms consist of large yellow spots in the subepidermal tissues, up to 1.5 mm in diameter. This may lead to erosion of surface layers. Cells of a **thraustochytrid** are found in the amoebocytes of the nudibranch and is probably the cause of the disease (McLean and Porter 1987).

10.2.5 Cultured Fish

A number of commercially cultured fish are infected by opportunistic parasites belonging to terrestrial species of fungi (Hatai 2012).

- **The devil stinger, *Inimicus japonicus* is parasitized by the anamorphic fungus *Ochroconis humicola*.** Symptoms of the disease include necrotic surface lesions that become sloughed off, leaving the trunk muscles exposed in the form of a crater. Hyphae of the fungus pervade the lesions. This fungus also infects the red sea bream, *Pagrus major*, and marbled rockfish, *Sebasticus marmoratus*. Body lesions are caused on the surface in both cases. Yet another anamorphic fungus *Fusarium oxysporum* also infects the red sea bream. Kidneys of the fish have been noticed to become swollen and discolored, although the disease did not cause external symptoms.
- **Juveniles of the cultured striped jack, *Pseudocaranx dentex*, at a fish farm in Japan also became infected by *Ochroconis humicola*** *during* April 2004. Moribund fish had a distended abdomen. About 25% of the fish died. Fungal hyphae were found in the musculature, spleen, and kidney. Resistant fish showed inflammatory reaction involving mycotic granulomas and granulation tissues. The isolate grew at 10–30 °C, but not at 35 °C. The isolate could grow up to 9% NaCl indicating that *O. humicola* could grow in an environment with a wide range of salinity. *Exophiala* sp. is another parasite of the striped jack.
- **In Japan, infection by *Exophiala xenobiotica* occurred in cultured striped jack, *Pseudocaranx dentex***, in 2005. One hundred out of 35,000 fish died per day and mortalities continued for 1 month. Diseased fish showed swelling of the abdomen and kidney distension. Fungal hyphae and conidia were found in gill, heart, and kidney.
- **Caged rainbow trout *Salmo gairdneri* becomes infected by a thraustochytrid**.

10.2.6 Other Animals

- Cephalopods are often parasitized by thraustochytrids. The thraustochytrid *Ulkenia amoeboidea* (Bahnweg and Sparrow) Gaertner as well as a labyrinthulid are associated with a fatal ulcerative dermal necrosis in the lesser octopus, *Eledone cirrhosa* (Polglase et al. 1986). Amoebocyte in the octopus only partially encapsulates the pathogens, resulting in a more serious disease compared to that in the nudibranch *Tritonia diomedea* (see above), where the encapsulation appears to be complete. Thraustochytrids are also found in gill lesions of the squid *Illex Illecebrosus*. **Many fungi have caused epizootics in mariculture, resulting in high mortalities and economic losses. Several crustaceans, such as shrimps, crabs, lobsters, as well as bivalves and fish have been affected seriously. Most of these diseases are caused by**

oomycetan fungi and facultative marine fungi. A number of trials have been carried out on antifungal substances in aquaculture. Malachite green has been tried in shrimp culture to reduce zoospore motility and infection. Trifluralin and captan reduced mortality rates when exposed for 96 h and caused minimal larval mortalities. Furanace was effective against *H. milfordensis* in shrimp aquaculture.

- **The littoral marine nematode *Rhabditis marina* Bastian becomes infected by three species of oomycetes**: *Gonimochaete latitubus, Haptoglossa heterospora*, and *Myzocytiopsis vermicola*. *Haptoglossa* is an obligate parasite of rhabditid nematodes (Marano et al. 2012). *Myzocytiopsis vermicola* is parasitic in adults and larvae, but does not infect eggs of the nematode.
- **The rotifer, *Brachionus plicatilis,*** bred in a concrete tank as food supply for seed production of crustaceans and fishes has been reported to be infected by ***Halocrusticida (Atkinsiella) parasitica***.
- The whole body of the **amphipod *Podocerus brasiliensis*** was found to be invaded by ***Rhodotorula minuta***. Seki and Fulton showed that the tissues of living **marine copepods (*Calanus plumchrus*) were attacked by *Metschnikowia*** sp. Fize et al. (1970) reported a *Metschnikowia* sp. parasitizing living copepods (*Eurytemora velox*) in southern France (Kutty and Philip 2008).
- Many captive marine mammals develop a variety of mycotic infections (see Chap. 11).

Fungal pathogens of animals are likely to continue as a major problem, because many of them are difficult to eradicate and cause death of their hosts (Hyde et al. 1998).

However, no effective strategies are available even now to counter fungal diseases in aquaculture practices.

10.3 Saprobic Fungi in Marine Animals

Soft tissues of dead animals are decomposed much more rapidly compared to plant material, since they are relatively less recalcitrant to decomposition. Under these circumstances, bacteria have a greater advantage compared to filamentous, mycetaen fungi, which require time to colonize and establish themselves in decomposing tissues. Hence, the role of such fungi in decomposition of soft animal tissues may be negligible compared to bacteria. However, the role of straminipilan fungi in such decomposing tissues is not known.

Compared to soft tissues, parts of animal tissues that are less labile to degradation may be vulnerable to fungal degradation. Some of these are the calcareous shells and chitinous exoskeleton of invertebrates and bones of vertebrates. Fungi play a role in decomposition of all these three animal remains. Calcium carbonate shells are secreted by molluscs (gastropods and bivalves). The calcium carbonate is embedded in a matrix of the horny protein conchyolin made up of quinone-tanned proteins. Chitinous exoskeletons are secreted by crustaceans. Chitin is a polymer of N-acetylglucosamine. Bones of marine vertebrates, including fish and mammals, are a matrix made up of calcium phosphate and collagen.

Calcareous shells secreted by marine animals such as molluscs, barnacles, and corals become colonized by endolithic fungi upon the death of the animals (Fig. 10.5; Kohlmeyer and Kohlmeyer 1979; Golubic et al. 2005; Raghukumar 2008). Endolithic organisms in calcareous shells comprise cyanobacteria, green algae, red algae, and fungi. Many such shells are often cast on intertidal beaches where they can be collected and studied (Fig. 10.5a). Endolithic fungi were discovered more than 130 years ago by the French phycologists Edouard Bornet and Charles Flahault, who described the fungus *Ostracoblabe implexa* in oyster shells (Sect. 10.2.4). Willy Hőhnk in Germany reported the presence of endolithic fungi from shells in the 1930s. Filaments of endoliths can be directly detected under a stereoscopic microscope.

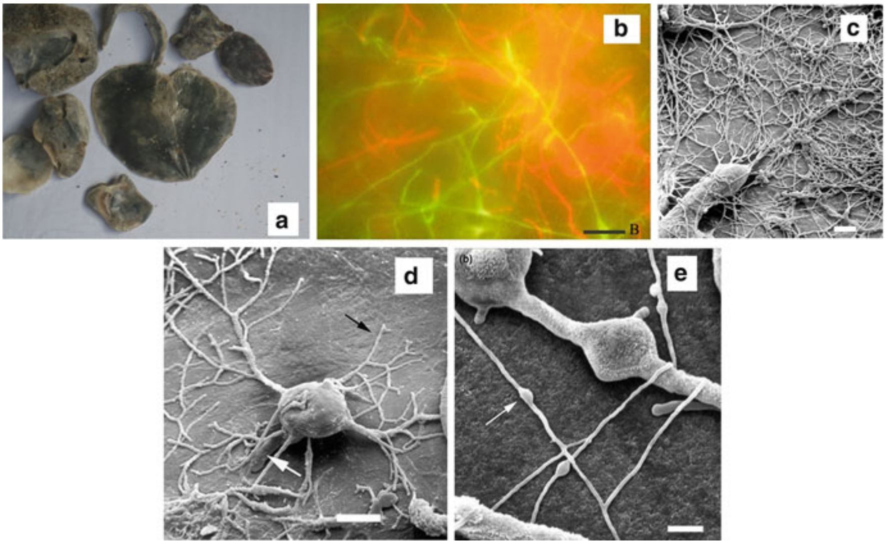

Fig. 10.5 Endolithic fungi in calcareous shells of molluscs. (**a**) Shells of the windowpane oyster *Placuna placenta* and others darkened possibly of colonization by endolithic fungi and algae (S. Raghukumar). (**b**) Epifluorescence microscopy of autofluorescing cyanobactria (*red*) and Calcofluor stained *green* fungal mycelia in windowpane oyster shells (Source: C. Raghukumar 2008. Fungal Diversity 31:19–35. With permission of Dr. Kevin Hyde.) (**c**–**e**) Resin casts of calcareous animal shells. (**c**, **d**) Dense networks of tapering fungal borings in a bivalve shell fragment from shallow coastal waters. Bar represents 10 μm. (**e**) The fungus *Ostracoblabe implexa* in calcareous shells spread next to a much larger tunnel of the endolithic *green* alga *Phaeophila dendroides*. (**c**–**e**) (Reprinted from Trends in Microbiology 13:229–235, Golubic, S. et al. Dense networks of tapering fungal borings permeate a bivalve shell fragment in shallow coastal waters. 2005. With permission from Elsevier)

- **Filamentous fungi and algae pervade and grow within calcareous animal shells.** It is often difficult to distinguish between filaments of green algae, cyanobacteria, and fungi. Chelation and removal of the calcium carbonate shells using EDTA is a way of detecting fungal hyphae. Fungi and algae can be simultaneously distinguished by epifluorescence microscopy. Algae can be distinguished by red autofluorescence and the fungi by a blue fluorescence following staining with the optical brightener Calcofluor (Raghukumar 2008; Fig. 10.5b).
- **The resin-cast method** provides a clear picture of the branching pattern of endolithic organisms in shells (Fig. 10.5c, d). The method yields **three-dimensional plastic casts of the endoliths or their empty borings that were previously within the shell. SEM observations of the surface features of these resin casts reveal details not visible with conventional light microscopy** (Golubic et al. 1975).
- Photosynthetic algae and fungi display a difference in their colonization of shells (Golubic et al. 2005). Fungi prefer to grow within organic lamellae of the shells and apparently make use of the organic matrix for the nutrition. On the other hand, endolithic algae, which cannot utilize the organic material, seem to prefer the mineral portion. They are often confined and crowded within particular crystallites, apparently unable to digest and penetrate the surrounding organic lamellae. Fungal ramifications often arise from bag-shaped swelling and frequently display dichotomous branching and fine tapering of the hyphae. These features are not common in endolithic cyanobacteria and algae. Bag-shaped swellings of endolithic fungi are often connected to the substrate surface by wider tunnels, which probably serve for the dispersal of spores.
- Endolithic fungi cause bioerosion of calcareous shells (Sect. 9.1.2). During growth, fungi produce tunnels of uniform diameter within the shells.
- Diverse fungi, including obligately marine mycetaen fungi, facultative marine fungi, and straminipilan fungi colonize calcareous shells. The fungus *Ostracoblabe implexa* is an example (see Sect. 10.2.4; Fig. 10.5e). **The obligately marine ascomycete, *Pharcidia balani* (Winter) Bausch, is a common and cosmopolitan endolith in various barnacles, snails, and limpets.** Shells of wood boring shipworms found in the borer tunnels are often colonized by lignicolous fungi, such as *Arenariomyces trifurcatus* Höhnk, *Arenariomyces triseptalas* Kohlm., *Corollospora maritima* and *Corollospora pulchella* Kohlm., *Antennospora quadricornuta, A. salina, Hydea pygmaea*, and *Humicola alopallonella* Meyers & R.T. Moore. These fungi reside in the wood, from where they invade the calcareous shells (Kohlmeyer and Kohlmeyer 1979). Shells of barnacles and bivalves that are brought to the laboratory and incubated for several months may yield ascocarps and basidiocarps of ascomycetes and basidiomycetes, respectively, developing on them (Ananda et al. 1998). These presumably arise from the endolithic hyphae of the fungi that inhabit the shells. Most of these ascomycetes belong to the so-called "arenicolous fungi" such as *Corollospora maritima* that produce fruiting bodies adhering to sand grains,

while drawing nutrition from another source. The most common ones found along the west coast of India were the ascomycetes *Corollospora maritima* Werdermann, *C. angusta* Nakagiri el Tokura, *C. cinnamomea* Koch, and *Arenariomyces parvulus* Koch. Shells of balanids and the gastropod *Turritella* had the highest density of ascocarps, while cuttlebone samples showed the highest diversity.

- **A thraustochytrid with the characteristics of the genus *Schizochytrium* was found in carbonate shell fragments** that were baited in coastal US waters (Porter and Lingle 1992). Thraustochytrids were particularly abundant in fragments of mussel shells, which have more organic matrix than clam or oyster shells. The thraustochytrid has an unusual morphology of elongated, tapered, and sometimes branched thalli that were divided into many vegetative cells. Observations suggested that the thraustochytrid was responsible for the formation of tunnels and cavities, thus causing bioerosion.

The exoskeleton of tunicates is made of tunicin, which is an animal cellulose. **The ascomycete *Antennospora quadricornuta,* isolated from tunicates has been shown to grow well on pure tunicin and degrade it** (Kohlmeyer and Kohlmeyer 1979).

Chitinous exoskeleton of dead crabs harbor thraustochytrids (Bongiorni et al. 2005b). Two thraustochytrids isolated from this substrate produced a wide variety of enzymes, including esterase, esterase lipase, lipase, leucine, cystine and valine arylamidase, acid and alkaline phosphatase, naphthol-AS-BI-phosphohydrolase, β-galactosidase and β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase, and L-aminopeptidase. Interestingly, these enzymes were produced as ectoenzymes that were adsorbed to the cell surface, rather than exoenzymes that were secreted into the environment. The presence of chitinase (N-acetyl-β-glucosaminidase) indicate that thraustochytrids may play an important role in the process of degradation of this biopolymer present in the carapace of crustaceans. Crab exoskeleton collected from intertidal beaches of the west coast of India did not initially reveal any fungi (Ananda et al. 1998). However, after prolonged moisture chamber incubation for several months, a high density of ascocarps of two obligate marine fungi, *Corollospora angusta* Nakagiri & Tokura and *C. maritima*, were noticed. This indicates that fungal mycelia may be present in chitinous shells of dead animals. These grow subsequently and reproduce on these shells.

- A number of fungi are found as symbionts and saprotrophs in marine animals.
- Fungal infections are common in both wild and cultivated marine animals.
- Many fungi such as species belonging to thraustochytrids, yeasts, and Trichomycetes live as commensals in invertebrates.
- A number of marine-derived fungi have been detected in sponges.

(continued)

- Fungi belonging to the Oomycetes are probably the most important parasites of marine animals and often affect seed production of marine crustaceans such as shrimp and crabs.
- Fungal diseases affect eggs and larvae of a number of economically important crustaceans, such as the giant tiger prawn, the kuruma prawn (“black gill disease”), the cultivated white shrimp, the mantis shrimp, the gazami crab, Japanese blue crab or horse crab, the mangrove crab*, t*he American lobster, and the Japanese mitten crab.
- Many other species of shrimps, prawns, crabs, and molluscs are also affected.
- The most important oomycete parasites of marine invertebrates are *Lagenidium callinectes and other Lagenidium species; Haliphthoros milfordensis;* as well as other species of the genus, *Salilagenidium myophilum, Sirolpidium zoophthorum, Atkinsiella dubia, and Halocrusticida* spp. Yeasts belonging to *Kluyveromyces, Metschnikowia bicuspidata*, and *Pichia anomala* have been reported as parasites. Many terrestrial species of fungi, such as species of *Fusarium*, are opportunistic pathogens and have been reported to be associated with shell disease of marine crustaceans and lobsters.
- Many molluscs are also affected by fungal parasites. Cultured abalone, *Haliotis rufescens*, is affected by the aplanochytrid *Aplanochytrium haliotidis*. The edible “hard clam” or quahog, *Mercenaria mercenaria*, is parasitized by the QPX thraustochytrid.
- A number of commercially cultured fish are infected by opportunistic parasites belonging to terrestrial species such as *Ochroconis humicola* and *Exophiala xenobiotica*
- Many other straminipilan parasites occur in invertebrates such as cephalopods and nematodes
- No effective strategies are available even now to counter fungal diseases in aquaculture practices.
- Saprobic fungi may be much more common in recalcitrant body parts such as exoskeletons of invertebrates, rather than on easily degradable soft tissues of dead animals.
- Calcareous shells secreted by marine animals such as molluscs, barnacles, and corals become colonized by endolithic fungi.
- The resin-cast method provides a clear picture of the branching pattern of endolithic organisms in shells. Endolithic fungi cause bioerosion of calcareous shells. Fungi produce tunnels of uniform diameter within shells.
- Diverse fungi, including obligately marine mycetaen fungi, facultative marine fungi, and straminipilan fungi, colonize calcareous shells.
- Only a few fungi are known in chitinous exoskeleton.

Future Directions

1. Animal guts may harbor mutualistic fungi, particularly yeasts, Trichomycetes, and thraustochytrids. Their diversity and role are not known.
2. Most studies on fungal diseases are from aquaculture animals. The importance of fungal diseases in wild animals is not known.
3. Do fungi with an r-strategy, such as yeasts and thraustochytrids, have a role in decomposition of soft tissues of animals?
4. Molluscan shells are almost invariably colonized by fungi. What is their diversity, nutrient substrates, and role in recycling organic matter?