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Parasites of fish from the Salton Sea, California, U.S.A.

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Key words: Oreochromis mossambicus, Bairdiella icistia, Gillichthys mirabilis, ectoparasites, *Amyloodinium ocellatum, Ambiphrya ameiuri, Cryptobia branchialis, Gyrodactylus olsoni, Gyrodactylus imperialis*, pathogenicity

Abstract

Parasitological monitoring was carried out from 1997 to 1999 in a highly saline (41–45 g/l) lake in southeastern California, Salton Sea. A total of 1473 fishes were examined. Young tilapia, *Oreochromis mossambicus*, croaker, *Bairdiella icistia*, and mudsucker, *Gillichthys mirabilis*, were found infected by ectoparasites. Some persistent foci of fish infestations were found around the perimeter of the lake. The diversity of parasites was limited to three protozoan species, *Amyloodinium ocellatum* (Dinoflagellida), *Ambiphrya ameiuri* (Peritricha), *Cryptobia branchialis* (Bodonida: Kinetoplastida), and two metazoans, the monogeneans *Gyrodactylus olsoni* and *G. imperialis*. Both *A. ocellatum* and *A. ameiuri* infested fish from spring through fall. The greatest infestations occurred in summer (29–40°C) in the case of *A. ocellatum* and in spring and autumn (22–27°C) in the case of *A. ameiuri*. High parasite loads caused severe damage to such respiratory organs as gills and skin. They may depress respiration and osmoregulation and, in combination with other environmental factors, cause fish suffocation and death. These parasites may play a major role in juvenile fish mortality.

Introduction

The Salton Sea (33° 25′ N, 115° 50′ W) is a highly saline lake located in an arid region of North America. This largest lake in California, with surface area of 980 km^2, was accidentally established in 1905–07. During unusual high flows, the Colorado River broke through irrigation canal headworks and poured into the Salton Sink, lakebed of former Lake Cahuilla (Carpelan, 1961a; Cohen et al., 1999). At that time, endemic freshwater fish came in with the Colorado River flows and successfully colonized the new-formed lake (Walker et al., 1961).

Two major tributaries, the Alamo and New rivers, provide most freshwater input into the Sea. Collecting wastewater from agriculture and municipalities, these rivers also deliver selenium, boron, DDE, DDT, and salts to the lake where they have been found in low concentrations in the biota (Setmire et al., 1993). With no outlets, high rate of water evaporation and permanent inflows of agricultural wastewater, the Salton Sea underwent over the next decades progressive increase in salinity up to 45 g/l, eutrophication, and contamination with pesticides and metals (Setmire, 1993; Cohen et al., 1999). The fish fauna at the Salton Sea decreased and by the 1930s, only the desert pupfish *Cyprinodon macularius* Baird and Girard, endemic to the Salton Sink, was present (Walker et al., 1961). From 1929 to 1956, 36 species of non-native marine and anadromous fish mainly from the Sea of Cortez, Mexico, were introduced to the Salton Sea. By the 1960s, three of them, orangemouth corvina, *Cynoscion xanthulus* Jordan and Gilbert; bairdiella, *Bairdiella icistia* (Jordan and Gilbert); and sargo, *Anisotremus davidsoni* (Steindachner) formed a productive and popular recreational fishery (Black, 1988).

By the mid 1960s, a breeding population of the redbelly tilapia, *Tilapia zillii* Gervain, originating from stockings into irrigation canals and drains was found on the Salton Sea. In 1979, another cichlid, the Mozambique tilapia, *Oreochromis mossambicus* Peters, had established a breeding population there (Black, 1988). This aggressive exotic cichlid probably escaped to the Sea from a private tropical fish farm

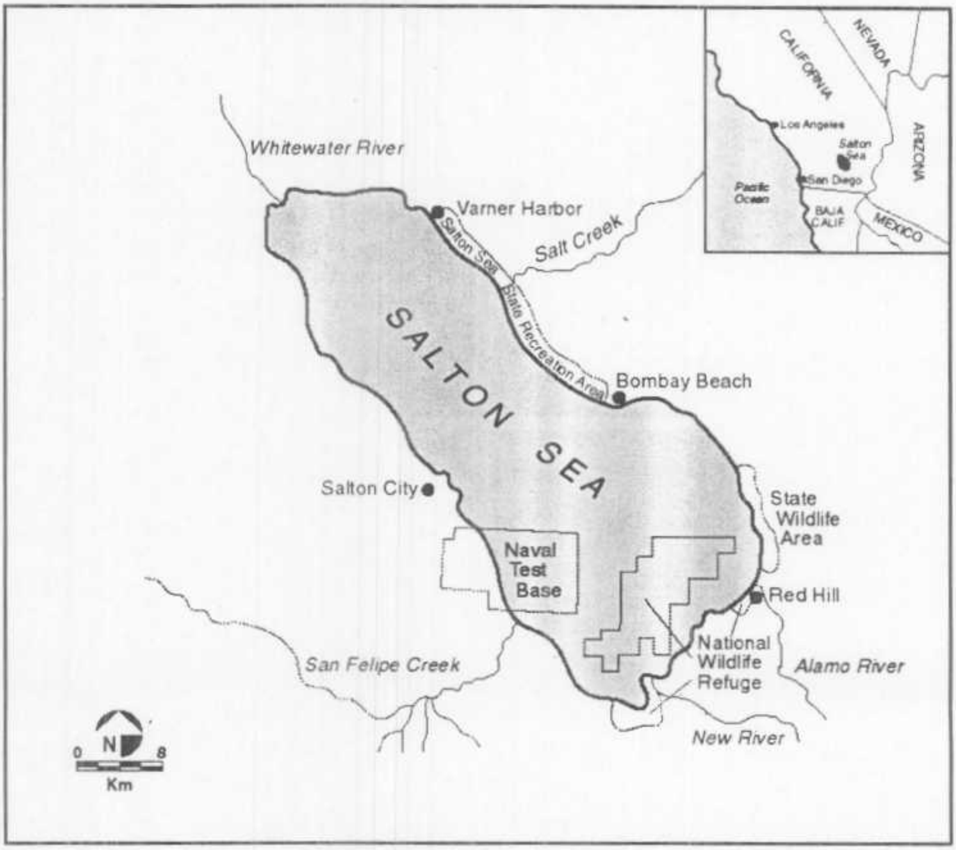


Figure 1. Map of the Salton Sea. Sites of fish sampling.

A full parasitological examination was carried out on 1172 specimens of young tilapia. 245 croakers, and 56 mudsuckers, *Gillichthys mirabilis* Cooper (Table 1). Under dissecting and compound microscopes all specimens were examined for ectoparasites on the general body surface, gills, fins, and tail and for endoparasites in the digestive tract, liver, spleen, gonads, and kidney. Prevalence and intensity of fish infestation by parasites was determined in fresh unstained specimens. Prevalence was defined as percentage of fish infected. Intensity of infestation by protozoan ectoparasites was defined as number of parasites per fish and was determined as high (+++, 100–1000 per fish), medium (++, 20–100 parasites per fish, and low (+, 1–20 per fish). For metazoan ectoparasites the intensity of infestation was defined simply as the number of parasites for the organ infected. Parasites were measured with an ocular micrometer and photographed using Kodak film and a Zeiss light microscope. Mean dimensions were measured for 50 specimens of each parasite species found on the fish. Some fish infected by ectoparasites were chosen for studying by scanning electron microscopy (SEM).

Scanning electron microscopy

Gill arches of large and middle-sized fish (2.0–6.8 cm) and whole bodies of very young fish (1.0–2.0 cm) were fixed in cold Karnovsky fixative for at least 2 h, postfixed in 1% osmium tetraoxide for 1 h and dehydrated using a graded ethanol with the final change in absolute ethanol. Then, specimens were critical-point-dried with liquid CO2 and all specimens were mounted on stubs. For examination of gills of the smallest fish (1.0–1.2 cm), the left opercula were removed from 10 specimens from each location on each sampling date using fine-tipped forceps to expose the gill baskets. Fish gills and whole fish bodies were sputter-coated with palladium and examined with a Hitachi S2700 scanning electron microscope at an accelerating voltage of 10 kV.

Results

Only ectoparasites were found on the fish from the Salton Sea. These included three species of protozoan parasites: *Amyloodinium ocellatum* (Brown) Brown and Hovasse (Dinoflagellida), *Cryptobia branchialis* Nie (Bodonida: Kinetoplastida), and *Ambiphrya ameiuri* (Thompson, Kirkegaard, Jahn) (Peritricha) and two species of metazoan parasites *Gyrodactylus olsoni* Mizelle & Kritsky, and *Gyrodactylus imperialis* Mizelle & Kritsky. (Monogenea).

Parasite morphology and foci of infestation

Amyloodinium ocellatum, a dinoflagellate, is a dangerous and destructive parasite of thermophilic marine fish (Brown, 1934; Lawler, 1980; Paperna, 1984; Landsberg et al., 1995). It is tolerant of high salinity and temperature. Its direct life cycle includes three intermittent stages: the actively feeding, parasitic trophont that is attached to the fish gills and body, the reproductive encysted tomont that resides in sediments, and free-swimming, infective dinospores (Brown, 1934). Epizootics of amyloodiniosis in public aquaria and aquaculture are explosive and may lead to severe reduction or total losses of fish populations (Brown, 1934; Lawler, 1977; Paperna, 1980; Sandifer et al., 1993; Noga & Levy, 1995). In nature, however, the prevalence and intensity of fish infestation by *A. ocellatum* are generally quite low (Lawler, 1980; Alvarez-Pellitero et al., 1993). To our knowledge, there are only two cases of high fish infestation by *A. ocellatum* being associated with mortality events in the wild (Overstreet, 1993; Kuperman & Matey, 1999), one of these cases being at the Salton Sea.

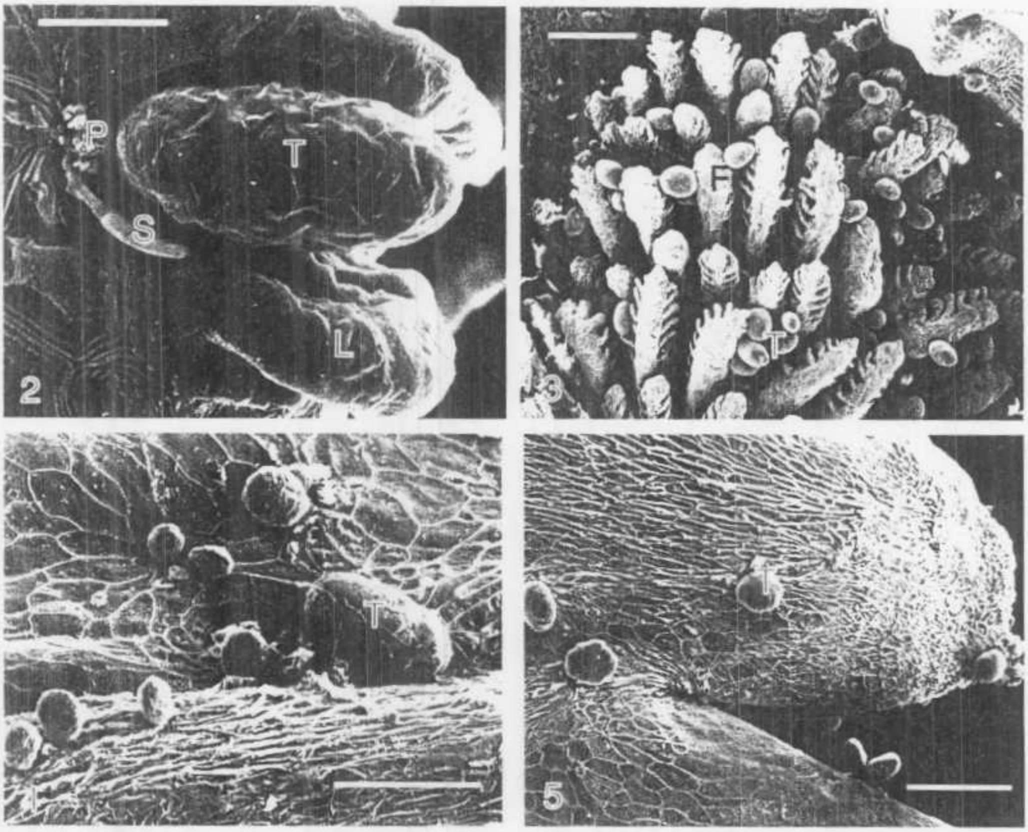
The general structure and ultrastructure of the trophonts of *A. ocellatum* found on young tilapia and croaker from the Salton Sea were described in detail in our previous paper (Kuperman & Matey, 1999). Sac-like or pyriform trophonts, 50–129 × 20–35 μm in size, attach to the host cells with a short stalk or peduncula (Fig. 2). Numerous protoplasmic projections, rhizoids and the long tentacle-like stopomode, protruding from the holdfast disk of the peduncula provide tight adhesion of parasite to fish epithelial tissues (Fig. 2).

The major sites of trophont attachment on the fish body are gills, skin, fins, and tail. Gills were found infected by *A. ocellatum* in young fish of all sizes (1.0–6.0 cm). In tilapia and croaker, trophonts are distributed along gill filaments, on their tips and between secondary lamellae (Figs 2 and 3). In heavy infestations, trophonts are found on gill arches and gill rakers as well. Skin is affected in very young specimens (1.0–2.2 cm long) that have no scales. Groups of trophonts are attached to the thin epithelium covering the fish body (Fig. 4). Fins, including caudal fins, are also found to be infected in these same young fish. Parasites are located along the blood vessels and in clusters at the tips of fins (Fig. 5).

Ambiphrya ameiuri, a sessiline peritrich, was first found in the US on *Ictalurus punctata* and *I. melas melas* in freshwater aquaculture facilities (Thompson et al., 1946; Davis, 1947). *A. ameiuri* accompanied ictalurids that were imported from the US into fish farm facilities of different European countries (Banina, 1981; Trombitsky et al., 1992; Lom, 1995). In Russian aquaculture, *A. ameiuri* has been found not only on young *I. punctata* but also on yearling salmonids and cyprinids (Banina, 1981). *A. ameiuri* has become common on fry in fish hatcheries. In small numbers, they cause no injury but severe infestation may lead to fish kills (Lom & Dykova, 1992). *A. ameiuri* was first found in the wild in Rybinsk Reservoir on the Volga River in Russia on young of some cyprinid species (Kuperman et al., 1994). To our knowledge, there are no reports of these peritrichs on fish from marine environments or saline lakes.

At the Salton Sea, *A. ameiuri* was found on young tilapia and croaker (1.0–2.5 cm) in 1998–1999. The size and shape of *A. ameiuri* depended on their location on the fish. Barrel-like forms (35–40 × 25–28 μm) were on gills, conical ones (60–65 × 15–19 μm) on fins and tail, and both cylindrical (45–52 × 24–26 μm) and conical ones on fish skin (Figs 6 and 7). *A. ameiuri* found on the Salton Sea fish had cell surface ultrastructure typical for this species. They were covered by a cross-striated pellicle from the apical to the basal part of the cell. They had a bundle of aboral cilia protruding from the peristome cavity, a prominent equatorial belt of rows of long cilia, and a flattened plate-like base, the scopula (Fig. 7). The scopula was flexible, rather wider (about 40 μm in diameter) than the rest of the cell and served for attachment of parasite to fish.

In fish from the Salton Sea, *A. ameiuri* infested the same organs as did *A. ocellatum*, but most were

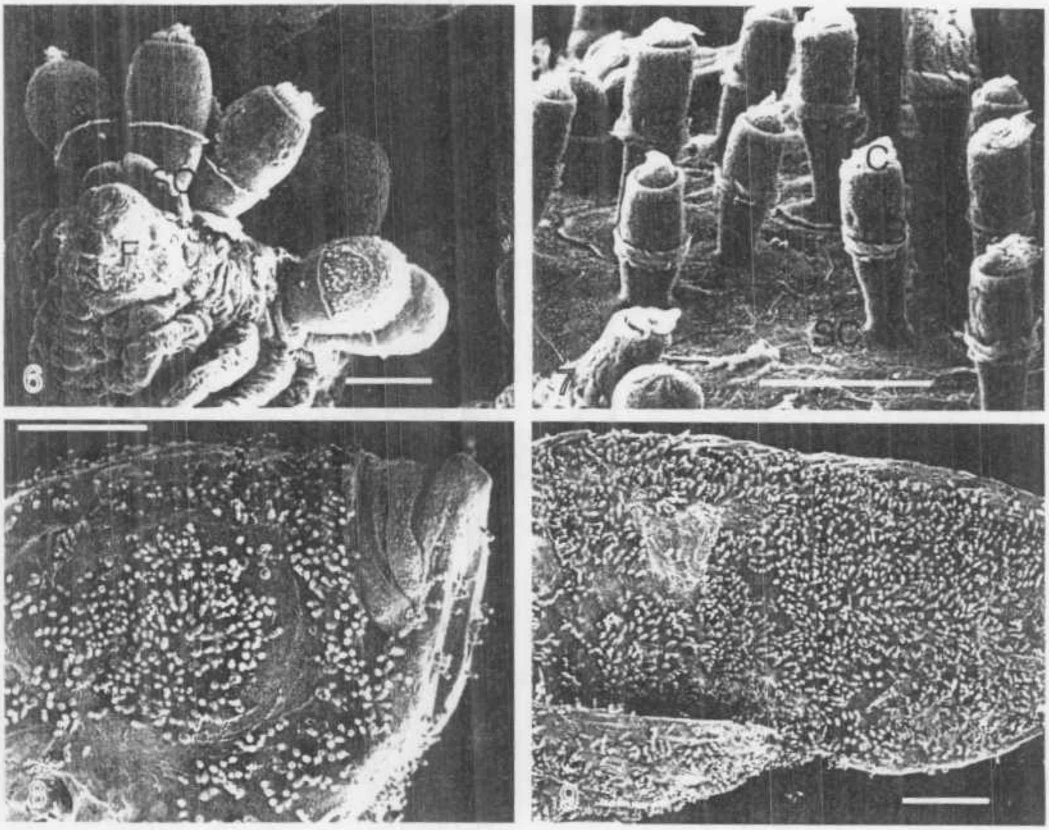


Figures 2–5. Amyloodinium ocellatum on different organs of tilapia. SEM. Figure 2. Trophont in the interlamellar space of gill. Figure 3. Heavy infestation of gills, swelling of filaments and fusion of lamellae; trophonts of *A. ocellatum* on tilapia skin (Figure 4), and tail (Figure 5). F, gill filament; L, secondary lamella; P, peduncula with rhizoids; S, stopomode; T, trophont. Scale bars: Figure 2 = 20 μm; Figures 3, 5 = 100 μm; Figure 4 = 50 μm.

found on the skin. Especially dense concentration of *A. ameiuri* was noted on the head (Fig. 8). In heavy infestations, the whole fish body, including fins and tail, were carpeted by the peritrichs (Fig. 9). We never saw the same level of infestation on the gills (Fig. 6).

Cryptobia branchialis is one of only five ectoparasitic species among the 52 nominal species in this genus (Woo & Poynton, 1995). *Cryptobia* spp. are common parasites (or ectocommensals) of freshwater fish in aquaculture and natural waterbodies in Europe, Asia, North America and Philippines (Chen, 1956; Bauer et al., 1969; Lom, 1980; Natividad et al., 1986). They also infect marine fish in the USA, France, and Israel (Burreson & Sypek, 1981; Blanc et al., 1987; Diamant, 1990). Sites of infections are fish gills, skin, and fins. Cryptobias reproduce by longitudinal fission, detach, and become free-living in the water. Parasites brought into the gill chamber via the mouth can attach to gills and reinitiate the cycle. In aquaculture, *Cryptobia* spp. can destroy the gill epithelium of susceptible fish in heavy infestations, and cause formation of thrombi and eventually, death (Chen, 1956). In nature, where intensity of infestation is usually low, the parasite is regarded as nonpathogenic (Lom, 1980).

The only infestation by *C. branchialis* was found on very young tilapia at Bombay Beach in 1997. The organism was pear shaped or elongated (7.5–11.6 × 2.8–4.6 μm), rounded at the anterior end and tapered posteriorly (Fig. 10). Two flagella protruded from the flagellar pocket at the anterior tip of the body. The short anterior flagellum curved freely out from the cell, while the long, posterior, recurrent flagellum served to attach the parasite to epithelial tissue. *C. branchialis*



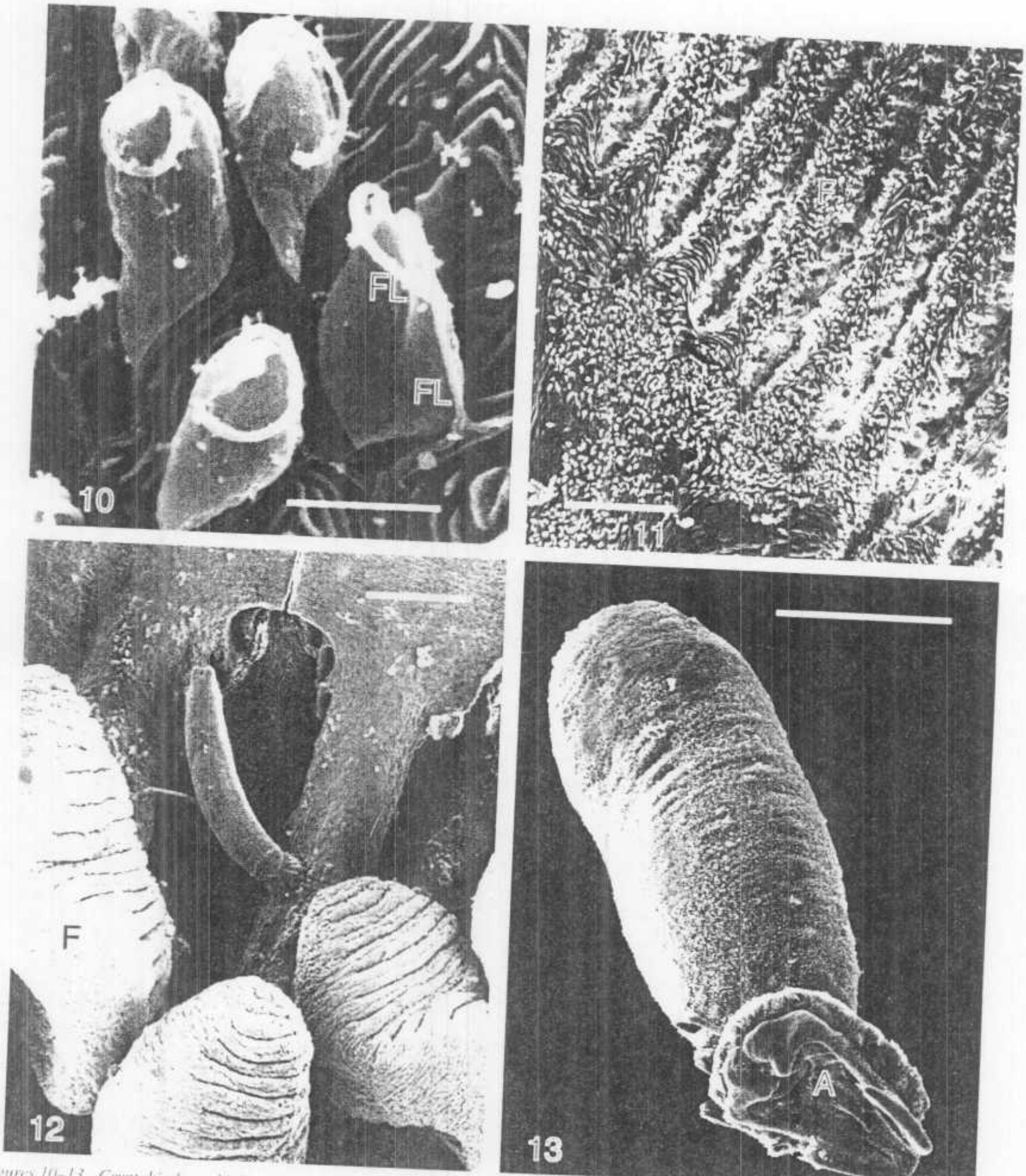
Figures 6–9. Ambiphrya ameiuri. SEM. Barrel-like form on the gills of croaker (Figure 6), cylindrical *A. ameiuri* on the tilapia skin (Figure 7), eye and head (Figure 8), on its body surface and pelvic fin (Figure 9) of tilapia. C, cilia; EB, equatorial belt; SC, scopula. Scale bars: Figure 6= 20 μm; Figure 7 = 50 μm; Figures 8, 9 = 500 μm.

was found only on the gills. It occurred along gill filaments, between secondary lamellae, on gill arches and even concentrated between gill rakers (Fig. 11).

Monogeneans of the genus *Gyrodactylus* are ectoparasites found worldwide on freshwater, brackish water and marine fish (Cone, 1995). They are common parasites of cultured and wild-living fish, especially salmonids, in northern Europe, USA, and Canada (Malmberg, 1993; Cone, 1995; Soleng & Bakke, 1997; Soleng et al., 1998). Due to their viviparity and rapid reproduction, gyrodactylids often cause disease problems in aquaculture. Epizootics of gyrodactylosis have been registered in hatcheries that are crowded or have poor environmental conditions (Cone et al., 1983; Malmberg, 1993). In the wild, the level of infestation by *Gyrodactylus* spp. usually is quite low, and these parasites are not an important fish health problem.

In 1967, two species of gyrodactylids, *Gyrodactylus olsoni* and *G. imperialis*, were found on the skin of the longjaw mudsuckers inhabiting drainage canals connected to the Salton Sea (Mizelle & Kritsky, 1967). In 1970, no gyrodactylids were detected on 12 mudsuckers from the Salton Sea (Martin & Multani, 1970). We found both *G. olsoni* and *G. imperialis*.

G. olsoni was found on mudsuckers from two locations, Bombay Beach and Red Hill in 1998 (Table 1). These small worms, averaging 312 μm in length, were found primarily on pelvic, pectoral and caudal fins, especially on their margins, but also on gills and sometimes on skin (Fig. 12). The opisthaptor, a well-developed attachment organ of *G. olsoni* was armored with 16 marginal hooks and a central pair of ventrally directed anchors, averaging 48 μm in length (Fig. 13). The base of each anchor was perforated and each anchor was bent into a 90–180° arc.



Figures 10–13. *Cryptobia branchialis* and *Gyrodactylus olsoni* on the gills. SEM. Figure 10. *C. branchialis*, general view with microridges of cells of gill epithelium in background. Figure 11. Heavy infestation of tilapia gills by *C. branchialis*. Figure 12. *Gyrodactylus olsoni* on the gill filament of longjaw mudsucker. Figure 13. *G. olsoni*, general view of parasite showing attachment organ with anchors. A, anchor; FL, flagella. Scale bars: Figure 10 = 5 μm; Figures 11, 12 = 100 μm; Figure 13 = 50 μm.

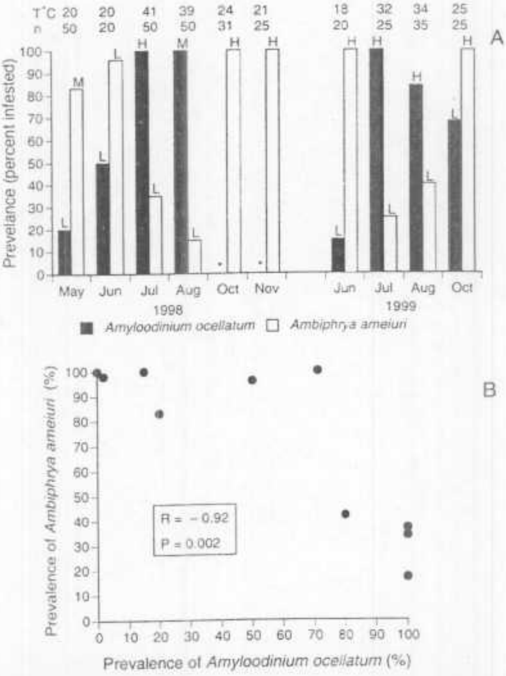


Figure 14. (A) Seasonal variation in infestation of tilapia in Varner Harbor, 1998–1999, by *Amyloodinium ocellatum* and *Ambiphrya ameiuri*. At top of figure are given water temperatures measured at 20–30 cm depth at time of collection of fish and sample sizes. Intensity of infestation is designed as low (L), medium (M), and high (H). Asterisks (*) denote the complete absence of parasites. (B) Negative correlation between prevalences of infestation of the two species of parasites.

Adult worms contained one or two embryos with fully formed anchors.

G. imperialis was found in 1998 on the fins and gills of tilapia from Bombay Beach. It was smaller than *G. olsoni*, with an average length of 261 μm. *G. imperialis* also has a well developed opisthaptor bearing 16 marginal hooks and two centrally located anchors, averaging 332 μm in length. Anchors formed a 30–40° arc. Full-formed embryos were found in the uterus of gravid specimens.

Seasonal dynamics of fish infestation by ectoparasites

Amyloodinium ocellatum and *Ambiphrya ameiuri*. Prevalence and intensity of the infestation by *A. ocellatum* and *A. ameiuri* were assessed most intensively for fish from Varner Harbor. Chi-squared tests demonstrated strong temporal variation in prevalence shown by both *A. ocellatum* (χ^2= 218.5, df=9, $P<0.001$) and *A. ameiuri* (χ^2= 162.9, df=9, $P<0.01$) (Fig. 14A). Correlation analysis documented a negative correlation between the occurrences of the two parasites (Fig. 14B).

In May 1998, when daytime, nearshore water temperature was about 22°C, 20% of tilapia examined were infested by *A. ocellatum* and 83% by *A. ameiuri*. The intensity of infestation by *A. ocellatum* was low, and these parasites were found mainly on the gills. *A. ameiuri* infested fish with medium intensity, and dozens of peritrichs were attached to the skin, fins (including caudal), and gills.

In June 1998 (water temperature 26°C), 50% of fish examined were infested by *A. ocellatum*, and 96% by *A. ameiuri*. However, intensity of infestation was low in both cases. Only few trophonts of *A. ocellatum* were found on the gills. Solitary peritrichs were placed on the fins, sometimes on skin near the fins but not on the gills.

In July–August, when water temperature was 39–41°C, 100% of fish were infested by *A. ocellatum*. Intensity of infestation was maximal in July, when hundreds of parasites were found on the gills, skin, fins, tail, and internal surface of gill covers (Fig. 3). In August, intensity of infestation was medium, and only gills and skin were infested. The peak of infestation by *A. ocellatum* coincided with decreasing of the infestation by *A. ameiuri*. Both prevalence and intensity of infestation by the second parasite were at their lowest levels.

In October and November (daytime water temperature 24 and 21°C) infestation by *A. ocellatum* was not detected. At the same time, 100% of fish were infested by *A. ameiuri* with high intensity. Hundreds of parasites covered the fish with especially high concentrations on the head and fins (Figs 8 and 9), and lower ones on gills (Fig. 6).

In 1998, fishes collected from other locations showed patterns of infestation similar to those at Varner Harbor, with one exception. In October, when *A. ocellatum* was not detected in Varner Harbor, it was found on 45% of fish from Bombay Beach (n=58), on 80% from Red Hill (n=45), and on 100% from Salton City (n=56). Intensity of infestation by this parasite was low in fish from two first locations, and high at the last one. In that same month, *A. ameiuri* infested 100% of these same fish from Bombay Beach and Red Hill. Only at Salton City were the prevalence and intensity of *A. ameiuri* very low.

In general, the dynamics of young tilapia infestation by *A. ocellatum* and A. *ameiuri* in 1999 were similar to those in 1998, with events delayed by a month, perhaps because 1999 was colder than 1998 (Fig. 14A). Young tilapia became available only in June when water temperature was 18°C. In Varner Harbor, only 15% of fish were infested by *A. ocellatum* and 100% by *A. ameiuri*. In July and August, the picture of infestation was changed. *A. ocellatum* prevalence and intensity of infestation were peaked, but only 23% of fish were low infested by *A. ameiuri*. In October (25°C), *A. ocellatum* and *A. ameiuri* were found on 60 and 100 percent of fish, respectively. Intensity of infestation was high for *A. ameiuri* and low for *A. ocellatum*. Similar patterns of infestations were found in fish from other sites, Bombay Beach, Red Hill, and Salton City.

In all cases, when *A. ocellatum* and *A. ameiuri* cooccurred on the epithelial tissues of infested fish, they occupied different sites. Gills were infested mainly by *A. ocellatum* while *A. ameiuri* were concentrated on the skin. Sometimes, fin and tail surfaces represented areas of common habitation, but with each species having its own microhabitat: *A. ocellatum* tended to be found on the margins and *A. ameiuri* on the central areas of the fins.

Infestation by *Cryptobia branchialis* was registered once, in September 1997, in a school of very young tilapia (1.0–1.2 cm) at Bombay Beach. At that time, 100% of the fish were heavily infected by *C. branchialis*, with thousands covering their gills (Fig. 11). This level of infestation is abnormally high for wild-living fish.

There was a marked difference between the two species of fish examined, longjaw mudsucker and tilapia, with respect to their *Gyrodactylus* infestations. In April–May, 1998, 75% (n= 26) of the mudsuckers from the Red Hill were infected by *G. olsoni*. Intensity of infestation varied from one to 50 specimens per fish, averaging 25. In Bombay Beach, 80% (n= 15) of mudsuckers examined in July were infected but intensity was lower, varying from two to 30 parasites per fish and averaging 12.

The degree of tilapia infestation by *G. imperialis* was significantly lower than that for mudsucker. Only two of 52 tilapia from the Bombay Beach examined in August 1998 were infected by gyrodactylids, and these had only one to two specimens per fish. In November, the degree of infestation was equally low. In December, only four fish were examined, and one of these was infected by *G. imperialis* with 30 parasites distributed on its fins and tail.

Pathogenicity

The nature and severity of pathological alterations in fish caused by ectoparasites varied widely. In summer and autumn months, fish from the Salton Sea heavily infected by *A. ocellatum* demonstrated extensive damage to organs affected, especially gills. Acute hyperplasia of epithelial cells resulted in partial or complete fusion of respiratory lamellae and clubbing of gill filaments (Fig. 3). Gill tissue surrounding pedunculae of numerous trophonts showed severe irritation, local erosion of gill epithelium and degeneration of epithelial cells (Fig. 15). Scar-like spots and lesions were revealed on the gill epithelium after trophont detachment (Fig. 16). In heavily infected fish, severe deterioration of skin and fins were also observed.

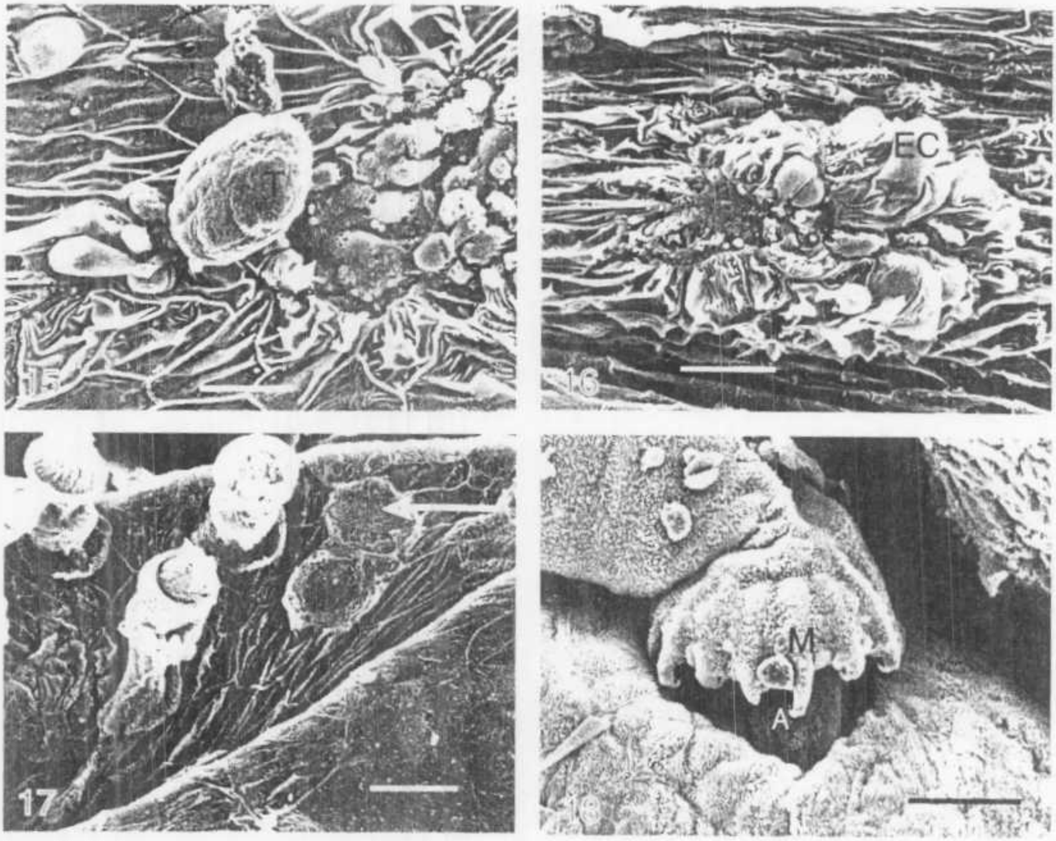
A. ameiuri that infected young fish in high numbers caused intensive damage to epithelial tissue. The skin was particularly affected (Fig. 17). Numerous impressions created by rims of the scopulae of *A. ameiuri* were found on the body surface after detachment of the peritrichs. Gradual dissolution of epithelial tissue under the scopulae caused lesions. Microfibrils and mucus patches were noted at detachment sites on the skin of heavily infested fish. We could not assess the direct effect of *A. ameiuri* on fish gills. These appeared more swollen than usual but the exact reason for this change was unclear.

Gills of fishes infected by *C. branchialis* were covered with a thick layer of mucus (Fig. 11). Severe swelling and subsequent fusion of lamellae transformed gill filaments into rod-like structures. However, at sites of parasite attachment to the gills, the surface of epithelial cells appeared normal (Fig. 6).

The pathogenicity of *G. olsoni* and *G. imperialis* arose from mechanical damage to fish gills, skin and fins caused by the opisthaptor. Fish gills were especially affected. Marginal hooks and anchors penetrated deeply into epithelial tissues and destroyed them (Fig. 18). Because of severe swelling of respiratory lamellae, the interlamellar spaces were greatly reduced (Figs 12 and 18). Affected skin and fins showed areas of tissue destruction at sites of gyrodactilid attachment.

Discussion

For the first time, ectoparasites are reported from fish of the Salton Sea. Parasitological monitoring carried



Figures 15–18. Damage to fish gills caused by ectoparasites. SEM. Figure 15. Erosion of gill epithelium of tilapia at site of attachment of *A. ocellatum* trophont. Figure 16. Degeneration of epithelial cells (EC) and lesions on the surface of gill epithelium after detachment of *A. ocellatum* trophont. Figure 17. Impressions and scars on skin of tilapia after *Ambiphrya ameiuri* detachment: Figure 18. *G. olsoni* on the surface of the gills of longjaw mudsucker, showing penetration of anchors into epithelial tissue. Scale bars: Figures 15–18 = 20 μm.

out in 1997–1999 revealed areas of persistent infestations around the perimeter of the Salton Sea. The diversity of fish parasites at the Salton Sea was limited. The five species found (*A. ocellatum*, *A. ameiuri*, *C. branchialis*, *G. olsoni* and *G. imperialis*) all have direct life cycles without involvement of intermediate hosts. This allows parasites to spread easily and widely. Endoparasites, which generally have more complex life cycles, were not detected at the Salton Sea. Two factors may explain this absence. First, there are a limited number of potential intermediate host species. In the Salton Sea there are only three species of copepods, which are the intermediate hosts of cestodes; two species of amphipods, the intermediate hosts of acanthocephalans; and no mollusks, the intermediate hosts of trematodes (Carpelan, 1961b; Dexter, 1993; Detwiler et al., 2002). Second, the free-living larval stages of parasitic helminthes with indirect life cycles are likely to have difficulty surviving in an environment with such high salinity and temperature (Dogiel et al., 1958).

Effects of environmental factors on parasites

The ectoparasites reported here are dangerous for cultivated fish (Bauer et al., 1969; Cone, 1995; Lom, 1995; Noga & Levy, 1995; Woo & Poynton, 1995). In densely stocked closed systems (fish hatcheries, farms, and aquaria) severe parasitic diseases are associated with poor environmental conditions such as lack of oxygen, alkalosis, acidosis, and water contamination (Khan & Thulin, 1991; Overstreet, 1993, MacKenzie et al., 1995). Environmental stress reduces fish immunity and facilitates infestation by ectoparasites. In natural ecosystems with minimal stress factors, fish infestation usually is low. In a stressed water body, infections can reach high levels, and fish stocks can be lost. The Salton Sea represents just this sort of ecosystem.

At the Salton Sea, levels of fish infestation by protozoan and metazoan parasites can be determined by critical combinations of pathogens, and such environmental factors as water temperature, salinity, oxygen tension, and sulfide levels. Temperature is among the most important regulatory factors for fish infection. It is especially influential on protozoan parasites and may account for much of the seasonal variation in degree of fish infestation by *A. ocellatum* and *A. ameiuri*. Both these parasites infect young tilapia from spring to fall but their peak infestations occur at different times. Reported thermal optima are 29–34°C for *A. ocellatum* (Paperna, 1980) and 22–24°C for *A. ameiuri* (Kuperman et al., 1994). At the Salton Sea, the peak infestations by *A ameiuri* and the lowest infestation by *A. ocellatum* occurred in spring and late autumn, when water temperature varied from 22 to 27°C. In contrast, in summer and early autumn, when collection water temperatures were 32°–40°C, prevalence and intensity of infestation by *A. ocellatum* were maximal and that by *A. ameiuri* were low.

Other parasites infesting fish in the Salton Sea also seem surprisingly tolerant of high water temperature. Neither *C. branchialis* nor *G. olsoni* and *G. imperialis* have been previously recorded from such warm waters. Generally, the preferred temperature range for *Cryptobia* spp. is 20–25°C (Burreson & Sypek, 1981; Diamant, 1990). The only heavy fish infestation by *C. branchialis* at the Salton Sea was recorded at a temperature of 30°C. Gyrodactylids are thought to have low tolerance for high temperatures. Their survival time increases with decreasing temperature especially in saline water (20 g/l; Soleng et al., 1998). Nevertheless, *G. olsoni* and *G. imperialis* seem to have adapted to temperatures of 22–38°C in the Salton Sea.

High levels of the infestation of fish from the Salton Sea may be explained not only by parasite preferences for high temperatures but also by condition of the fish hosts themselves. Even for thermophilic tilapia, water temperature in summer and early autumn months may be stressful. Thermal stress can affect fish by impairing their immune responses and predisposing them to severe infection (Overstreet, 1993).

High salinity is traditionally considered a stress factor but appears less important for parasites and fishes from the Salton Sea. The protozoan and metazoan parasites found seem more tolerant of high salinity that was earlier supposed. None of them has been previously reported from salinities of 41–45 g/. Even the resistant *A. ocellatum* which can survive salinities up to 70 g/l in short-term experiments, has not been found at salinities higher than 40 g/l (Paperna, 1980, 1984). Freshwater *A. ameiuri* and *C. branchialis*, as well as the brackish water gyrodactylids, *G. olsoni* and *G. imperialis*, have also successfully adapted to the Salton Sea environment. High salinity was not a barrier to the reproduction and distribution of these parasites. As for fishes, not only the salt tolerant tilapia, but also croaker, orangemouth corvina, and longjaw mudsucker are growing and reproducing in the Salton Sea. However, the combination of high water temperature and high salinity, along with other factors, may be weakening them and facilitating infestation by ectoparasites.

High intensity of fish infestation by parasitic or ectocommensal protozoans may be associated with eutrophication of the Salton Sea. In addition to whatever nutrients these protozoans may be obtaining directly from the fish, some may be able to use dissolved organic matter, and the dense free-living bacterial, protozoan and algal populations as food (Lom, 1984).

Effect of ectoparasites on fish respiration and osmoregulation

Young fishes from the Salton Sea infested by ectoparasites typically showed pathological alterations of organs responsible for respiration and osmoregulation. Extraordinary hyperplasia of gills with subsequent fusion of filaments and respiratory lamellae is common for fish that are heavy infected by *A. ocellatum*. In addition, parasitic trophonts destroy epithelial tissue. These changes in gill morphology result in dramatic decreases in respiratory surface and loss of the ion regulatory units, the chloride cells (Mallatt, 1985). Affected fishes can experience not only respiratory distress but ion regulatory failure and acid–base imbalance (Wendelaar Bonga, 1997). The gill alterations, caused by *C. branchialis* are histologically different, but may cause similar problems for fish. In contrast to *A. ocellatum, C. branchialis* causes severe swelling of gill filaments, reduction of respiratory lamellae, and overproduction of mucus. The latter forms an additional boundary layer hampering gas transfer (Shepard, 1994). As respiration and ionic exchange in fish gills are intricately related, both functions may be depressed.

Negative impacts of *A. ameiuri* are associated with the ability of these peritrichs to colonize the skin of the youngest fishes in the Salton Sea. Larval and postlarval fishes accomplish gas exchange mainly via cutaneous respiration (Rombourg & Ure, 1990). When present in massive numbers, *A. ameiuri* may be an additional burden to the host, impairing respiration and causing skin irritation or even damage. During heavy infestations of fishes in the Salton Sea, the tightly packed scopulae of *A. ameiuri* cover large areas of skin depressing its respiratory function. Even fins and tails, with blood vessels separated from the oxygen dissolved in water by a thin epithelium, are covered with peritrichs. After the detachment of parasites, damaged areas of epithelial tissue mark the attachment sites and have reduced capacity for gas exchange. In these conditions asphyxia of fish larvae may take place (Banina, 1981).

The major factor contributing to tissue changes is intensity of the infestation. Mild infection provokes minor tissue and cellular reaction. High parasitic load results in extensive histopathological changes. These can be influenced by environmental factors such as temperature extremes.

So, if present at high intensities, ectoparasites may be a substantial burden to their hosts, impairing respiration and causing surface tissue deterioration. Depression of respiratory functions is reinforced by the low oxygen tensions typical in the Salton Sea during summer (Carpelan, 1961b; Watts et al., 2001).

Ectoparasites and secondary infections

The various types of damage to epithelial tissues caused by ectoparasites create portals of entry for bacterial, viral and fungal infections. Fish with immune responses depressed by environmental stress may be more susceptible to these secondary infections. Sick and dead fish represent a source of disease for piscivorous birds though in the absence of pathogen transmission, they also can constitute an enhanced food supply for these birds.

From ectoparasites to ecosystem

The phenomena reported here may have consequences that go well beyond the physiological interactions between these tiny fish and their tiny parasites. Given the prevalence and intensity of infestations observed, especially during summer and fall months, it seems likely that they may be a major cause of juvenile fish mortality. If that is the case, these ectoparasites could play a large role in determining fish population dynamics in this lake. They could influence the number of fish that recruit each year into size classes utilized by other fish, e.g., corvina, by fish-eating birds, and by sports fishermen. They could influence total fish biomass in the lake as well as the relative abundance of the fish species. Given the strong influences that fish populations have on lacustrine foodwebs, water chemistry, and other ecosystem properties, the ectoparasites could be influencing these as well. An experiment using Salton Sea microecosystems to assess effects of tilapia (Gonzalez et al., 1998; Hart et al., 1998; Simpson et al., 1998) and an analysis of changes in plankton populations to following introduction of tilapia (Tiffany et al., 2002) demonstrates the types of influences that tilapia may be having on the Sea. The ultimate driving factor in these dynamics could be the oxygen, temperature and mixing regimes of the lake. These show large variations from one year to another (Watts et al., 2001), and parasite-fish interactions are likely to be sensitive to them.

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