Parasites as a Limiting Factor in Exploitation of Pacific Whiting, *Merluccius productus*

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Introduction

The parasite fauna of Pacific whiting, Merluccius productus, like that of most commercial fishes in the eastern North Pacific, have not been adequately studied. The extent of our knowledge is best exemplified by the fact that, while Margolis and Arthur (1979) listed 10 parasite species recorded for this fish in Canadian waters, a small-scale survey carried out fairly recently in the Strait of Georgia (Sankurathri et al., In press) augmented that list to 22 species. In view of the strong impact that some of these parasites exert on the Pacific whiting fishery, this lack of attention is regrettable.

The parasites of Pacific whiting on which attention has been focused recently belong to the protozoan phylum Myxosporea. Sankurathri (1977) described Conispora renalis from the renal tubules of the whiting in Georgia Strait. This species was found later to be identical with Myxoproteus meridionalis Evdokimova, 1977, discovered in the urinary bladder of Merluccius hubbsi Marini, 1933, on the Patagonian shelf. Evdokimova's (1977) description, chronologically before that of Sankurathri, was incorrect in placing that species in Myxoproteus. It was necessary to place it in Conispora, while retaining Evdokimova's original specific name. It is now known as

The authors are with the Pacific Biological Station, Fisheries Research Branch, Department of Fisheries and Oceans, Nanaimo, B.C. V9R 5K6, Canada. *Conispora meridionalis* (Evdokimova, 1977) (Sankurathri et al., In press).

More important, however, are the parasites belonging to the genus Kudoa Meglitsch, 1947, which, because of their histozoic habits, are of direct concern to the fishing industry. Grabda and Grabda (1975), who examined whiting taken by the Polish fishing fleet off California, recorded two species of Kudoa which they found in the musculature: Kudoa clupeidae (Hahn, 1917) and Kudoa rosenbuschi (Gelormini, 1944). The former has never been previously found in the genus Merluccius, but the latter is known to occur in the muscle of Merluccius hubbsi on the Patagonian shelf. Kabata and Whitaker (1981) put the validity of these records in doubt, because of morphological differences and dissimilarity in the host-parasite relationships. However, further studies in Californian waters are needed to allow a definitive conclusion in this matter. According to Kabata and Whitaker (1981), the two species of Kudoa infecting Pacific whiting off North American shores are Kudoa thyrsitis (Gilchrist, 1924) and Kudoa paniformis (Kabata and Whitaker, 1981). This paper concerns these two species.

Morphology and Life Cycle of Kudoa

Only the spores have been described in detail for the two species of *Kudoa* parasitic in Pacific hake. *Kudoa thyrsitis* (Fig. 1A) is distinguished by stellate spores, with four valves of unequal sizes. The spores are subconical in lateral view, the posterior corners of the valves forming sharp processes. The surfaces of the valves are smooth and the suture lines very fine. The polar capsules are pyriform, of unequal sizes, one capsule being distinctly larger than the other three.

Kudoa paniformis (Fig. 1B) has spores subrectangular in polar view, with rounded valves and smooth surfaces. Suture lines are devoid of ridges and are often somewhat sinuous. Polar capsules are pyriform. Detailed descriptions and measurements of spores are given by Kabata and Whitaker (1981).

The spores of Kudoa are important not only as the best clues to the identity of the species; they also play a prominent role in the life cycle of these parasites. The spore is the stage that serves as the means of dispersal of the parasite and as the source of infection for new host individuals. Released from the musculature of dead fish, it must float in water and make contact with the fish it is to infect. The release could occur as the result of natural death of the host and subsequent decomposition. It is also likely that moribund fish would be disposed of by predators. The spores, with the digested remains of their host, would then be voided by the predator. Whatever the mode of release, being heavier than water, they gradually sink and are likely to descend to levels deeper than the habitat of their potential host. Kovaleva et al. (1979) pointed out that the distribution of the various Kudoa species in



Figure 1. – Unfixed spores in lateral and anterior view: (A) Kudoa thyrsitis; (B) Kudoa paniformis. (From Kabata and Whitaker 1981).

the Atlantic Ocean coincided with areas of upwelling, in which the spores can be maintained by the ascending currents at the depths inhabited by their host species. The exceptions to this rule are provided by *Kudoa* parasitizing bottom-dwelling species of fish. (*Atheresthes stomias* provides an example of such a demersal host along the Pacific coast of North America.) The Pacific whiting is cannibalistic and is often taken with the remains of its conspecifics in the alimentary canal. The latter way of

infection is more likely to deliver a concentrated dose of spores to the new host.

It is currently presumed that *Kudoa* reaches its target site within the host via the intestinal tract and the circulatory system, but evidence supporting this presumption is still circumstantial, at least for this particular myxosporean genus.

The earliest stage known in the life cycle of *Kudoa* parasitic in Pacific whiting is a large trophozoite filling a sometimes substantial portion of a muscle fiber. In some instances the entire fiber is filled by the parasite to the point of becoming visibly distended. Observation with the naked eye reveals these fibers, or pseudocysts, as white or black streaks. A new generation of spores develops within sporoblasts contained inside these relatively gigantic trophozoites.

The distribution of pseudocysts in an individual host is not uniform. There are no significant differences between the right and the left side of the fish, but the number of infected muscle fibers tends to diminish from the anterior end toward the tail of the fish. The area most heavily infected is the dorsal musculature immediately behind the head; the lightest infection is found in the caudal peduncle. In view of the life history of Kudoa, this type of distribution is not unexpected. The sporoplasms (the infective agents carried within the spore) are released in the intenstine, penetrate the gut wall, and enter the bloodstream. They are then carried by blood via the hepatic portal system, through the liver, heart, and gills, to the dorsal aorta. Along the latter they are transported in the posterior direction. The blood vessels branching off from the aorta near its origin have the greatest chance of receiving the protozoan intruder. The number of parasites dwindles with their transport towards the tail.

Effect of Infection on Muscle Tissue

Both species of *Kudoa* mentioned above penetrate individual muscle fibers. They do not appear to undergo

any division, once within these fibers. Judging from some very high intensities of infection, some division probably occurs after the sporoplasm enters the blood vessel. In consequence, a single sporoplasm could provide the means for infecting many muscle fibers. Within the confines of a fiber, the feeding stage (trophozoite) expands and its surface membrane develops countless irregular villosities. The normal structure of the fiber is disrupted, and its tissue gradually breaks up and is replaced by the parasite. The trophozoite gradually fills with spores of various stages of development. The parasite within the fiber is sufficiently isolated from the host to prevent its immediate defensive reaction. At this stage the term "pseudocyst" is properly applied to the infected fiber, to distinguish this condition from the true cysts which are much more disruptive to the tissues and are surrounded by connective tissue capsules deposited by the host. Each pseudocvst is a cylindrical, elongated structure, often apparent to the naked eye as a streak of color, distinguishing it from the surrounding, uninfected muscle fibers. The color of pseudocysts varies with the age of the infection. At the relatively early stage, when the trophozoite is still growing and filling with spores, the color of the fiber is opaque white. As the villosities of the trophozoites approach the sarcolemma of the muscle fiber, the enzymes produced by the parasite leak out and are detected by the host; the host's reaction becomes histologically evident. It consists of surrounding the infected fiber with histiocytes. Within the coating of these cells, the infected fiber gradually assumes a yellowish hue, passing into brown and eventually black. By a process as yet unknown the parasite is compressed, the spores progressively crumpled, and, in the end, destroyed. (Work on the reaction of whiting to K. thyrsitis is in progress.)

The three stages, from uninfected (N), through young, white pseudocyst (W), to old, black ones (B) are shown in Figure 2. In particularly heavy infections nearly 1,000 pseudocysts per



Figure 2. – Transverse section through musculature of hake, showing uninfected fibers (N); young, white pseudocysts (W); and old, black pseudocysts (B).

gram of muscle tissue have been found (Kabata and Whitaker, unpubl. data). The infected fibers obviously lose their contractility and can no longer participate in the locomotion of the fish. The fact that the fish, even when heavily infected, can still continue its locomotory activities, is understandable, when one takes into account that the white muscle, which constitutes the substrate of the parasite, is not extensively involved in the normal cruising movements. *Kudoa* has not been found in the dark muscle, the main natatory effector.

The infected fillet is streaked with distended, white or black (or both) fibers, depending on the intensity and age of the infection. Not unnaturally, its appearance markedly lowers the acceptance of the product by potential customers, even if infected fish is supplied to them in otherwise satisfactory condition. From the point of view of the fishing industry, however, much more important than any mechanical damage is the effect of the chemical substances produced by the parasite.

As demonstrated by Patashnik et al. (1982), the substances in question are proteolytic enzymes. During the life of the fish, the excretory system is efficient enough to prevent the accumulation of the enzyme in quantities sufficient to result in serious damage to the muscle tissue. The death of the host has a twofold effect: It terminates the functioning of the excretory mechanisms, while, at the same time, the production of the enzyme continues unabated. Facing biochemical changes induced by the death of the host, the parasite brings its development to the final process of sporulation, and formation of protective spores, over a period of 8-12 hours (Willis, 1949). No longer removed from the site, the enzyme accumulates there, with consequences discussed by Nelson et al. (1985).

Tsuyuki et al. (1982) discovered two temperature optima for the proteolytic activity of the enzyme produced by *Kudoa*, one at 35-40°C (pH 3.8), the other at 55-60°C (pH 6.7). It is possible that these optima correspond to the activities of two enzymes, produced by the two species of *Kudoa* examined. There are strong indications that the efffects these species exert on whiting differ in their magnitude. Although more work is required to arrive at definitive conclusions, it appears, in light of present evidence, that *K. thyrsitis* is less damaging to whiting flesh than *K. paniformis*. Some speculations on the reason for this difference are included below.

Prevalence and Intensity of Infection

In spite of its acknowledged importance to the fishing industry, the prevalence of the Kudoa infection of whiting has never been subjected to an adequate parasitological investigation. The work of Patashnik et al. (1982) is an example of the difficulties facing workers investigating a parasitological problem without appropriate input from parasitologists. Although Patashnik and his colleagues were aware of the existence of two species of Kudoa (which were referred to as "small" and "large" Kudoa), the infection was treated as a single phenomenon. Having examined samples of 10-15 fish, they found that the combined prevalence ranged from 20 to 40 percent. These figures are at odds with those obtained by Kabata and Whitaker (1981), who found much higher prevalence of Kudoa. In a sample of 322 fish taken in a single haul off the southwest coast of Vancouver I. in September 1980, the prevalence of infection was 89.5 percent. K. thyrsitis was found in 32.2 percent and K. paniformis in 38.8 percent of the fish examined. A further 18.3 percent were infected with both species. In the Strait of Georgia, where 100 fish were examined, only K. thyrsitis was found, parasitizing 99 percent of the sample. It is possible that a systematic survey will discover a middle ground between these two sets of data. However, the prevalence figures of Patashnik et al. (1982) are probably too low. This is suggested by the data obtained recently (Kabata and Whitaker, unpubl. data) from examination of a small sample (35 fish) collected off the mouth of Columbia River in June 1982. The overall prevalence was 94.3 percent with *K. thyrsitis* present in 42.9 percent of the sample, *K. paniformis* in 17 percent, and mixed infection in 34.3 percent.

The estimate of intensity of protozoan infections is notoriously difficult, exact counts being impossible for obvious reasons. It is fairly generally accepted that categorizing of infection into light, medium, and heavy is sufficient to express intensity. Kabata and Whitaker (1981) used this scale, having arbitrarily defined light as the presence of < 20 pseudocysts, medium as 21-100, and heavy as >100 per area. Counts of pseudocysts were made under a dissection microscope, the entire fillet being macerated in the process. A fillet was divided into six areas, horizontally by the lateral line and vertically by two lines marking off three parts of equal length. Patashnik et al. (1982) estimated the intensity of infection by "visual observation," presumably without any optical aids. Their scale of intensity was 0-5, with 0 denoting absence of observable parasites. It was based "on the percent of the area affected," 1 = trace (up to 5 percent); 2 =slight (5-20 percent); 3= moderate (20-30 percent); 4 =severe (30-50 percent); 5 = excessive (>50 percent). The precise definition of the "area affected" was not provided. The present authors, in work now in progress, have resorted to a more quantitative determination of the intensity of infection. They are using a number of pseudocysts (nearly or completely equivalent to the number of trophozoites) per gram of muscle tissue in six areas defined above.

Neither of the two sets of observations described above can be said to reflect the true prevalence and intensity of *Kudoa* in whiting flesh. As mentioned, the presence of this parasite in the fish is not easily detectable until the development of pseudocysts. (Stages prior to cyst formation have not yet been detected.) Some period, of still unknown duration, must elapse between the time of entry of the parasite and the formation of these aggregates of spores. That period must be characterized by the intensive activity of the parasite, passing through its successive stages of development. The existence of a "hidden increment" of infection can be confidently postulated. The size of that increment cannot be assessed on the basis of data available. Its assessment is, however, necessary, if the true effects of Kudoa on the flesh are to be correctly understood. Some ambiguous results of investigation of these effects are almost certainly due to the fact that of any two apparently uninfected fish one might harbour Kudoa in its "hidden" stage. Proposed future studies of the Kudoa problem must, therefore, include investigation of the origin and early stage of infection.

The distribution of the two Kudoa species and their effects offer grounds for some interesting speculations. K. thyrsitis, the less harmful species, is also the more widespread. It has been reported from several species of fish as far from the American Pacific as Australia and South Africa. In the latter part of the world it was recorded in Merluccius capensis by Priebe (1967). In the area inhabited by the Pacific whiting it has been found also in walleye pollock, Theragra chalcogramma, and some flatfish species. Both the distribution and the host range suggest an "old" species, well adjusted to its hosts and, consequently, not excessively harmful. In contrast, K. paniformis, widespread in the offshore whiting population, appears to be a relative newcomer. It does not occur in the Georgia Strait whiting stock or in a small inshore stock on the west coast of Vancouver I., both isolated from the main offshore population. It has not been found in any other fish species. These facts suggest that K. paniformis infected whiting subsequent to the separation of these stocks. As a "new" parasite, it has not yet attained a stable equilibrium with its host and is, therefore, much more virulent in its effects.

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