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OFFSHORE PACIFIC WHITING: A PARASITE STUDY

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FINAL REPORT

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ABSTRACT

In this Final Report we describe the distribution of *Kudoa paniformis*, a parasite affecting fish muscle texture, in the Pacific whiting population, in samples obtained from 1986 to 1988. We identify age of the fish and geographic location in their summer feeding grounds as factors determining the distribution of the parasite. We determine that the parasite affects significantly whiting growth, and we quantify this effect. We propose that the parasite life cycle is direct, without requiring an intermediate invertebrate host, and that the parasite stays viable for several years within the host. We propose that the parasite problem ameliorates as harvest rates increase.

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EXECUTIVE SUMMARY

The Final Report of the project "Offshore Pacific Whiting: A Parasite Study" contains information related to the distribution, and factors determining the distribution, of the myxozoan parasite *Kudoa paniformis* within the offshore population of Pacific whiting. The distribution of the parasite is described in terms of its prevalence (percentage of parasitized fish) and intensity (parasite counts per gram of muscle tissue) based on a number of samples taken from the population. Results from this first part of the study indicate that the main factor affecting the distribution of the parasite in the whiting population is the host age. Accounting for age, significant differences in parasite characteristics were also found between whiting sampled in different geographical areas. This "area effect" is believed to be the result of the effect of the parasite on whiting migratory dynamics rather than the result of differences in the probability of whiting being infected in each area.

This study also includes an analysis of the effects of the parasite on Pacific whiting population dynamics. Specifically, the aspects analyzed include the host's individual growth and annual migration. Results showed that the parasite significantly affects both aspects of the host dynamics.

This report also presents findings concerning the life history of *Kudoa paniformis* relevant to the understanding of the dynamics of the host-parasite system. Aspects of the life history investigated include parasite transmission rate, and rates of the parasite developmental processes occurring within the host and parasite transmission mode. Results of this part of the study indicated that the life span of the parasite within the host is of the order of several years and that the host is infected directly from parasite spores in the water.

PURPOSE

The purpose of this study is to provide a basis for improving the quality of Pacific whiting catches affected by the presence of the parasite *Kudoa paniformis*.

DESCRIPTION OF THE PROBLEM TO THE FISHING INDUSTRY

The coastal stock of Pacific whiting *(Merluccius productus)* has been historically considered to be of low economic value because of the poor quality of its fish products. Even though interest in this stock is presently increasing because of the decreasing fishing quotas of traditionally harvested resources, the problem of low-quality still persists. The principal cause is that whiting flesh deteriorates rapidly after death, posing preservation limitations and rendering the products of low value for human consumption.

Whiting flesh deterioration results from muscle infection by a myxozoan species of the genus *Kudoa*. According to Kabata and Whitaker (1981), the species invading Pacific whiting are *K. paniformis* and *K. thyrsitis*. Of these two species, the former, which is the subject of this study, is the most virulent and has a severe effect on whiting flesh texture.

Because of the economic implications of the *Kudoa* infections in the offshore whiting population, several related studies have been performed in the last decade (Kabata and Whitaker 1981, 1985, 1986; Kudo et al.1985; Morado and Sparks 1986; Stehr 1986a, 1986b; Whitaker 1986). The emphasis of the research has been to determine the cause of the texture problems, describe the sporogenic process of the parasites within the fish host, and find technological alternatives for food processing to ameliorate the fish products.

OBJECTIVES OF THE PROJECT

The present study contributes to the understanding of the *Kudoa paniformis*-Pacific whiting interactions for practical fishery applications. The study investigates the distribution of the parasite within the host population and attempts to establish patterns that could provide a basis for selective fishing to alleviate the problem posed by the parasitic infection. The ultimate goal of the study is to help predict the parasite distribution within the whiting population, given a known host distribution, and propose fishing scenarios for minimizing the incidence of infected fish in whiting catches.

The study primarily investigates the distribution of the parasite and the factors that determine the distribution of the parasite within the Pacific whiting population, and the effects of the parasite on the host. It also explores fishing strategies for increasing the catch value. Finally, biological aspects of the host-parasite interaction are investigated to the extent that the data permit.

APPROACH

DESCRIPTION OF THE PERFORMED WORK

The following is a brief summary of the work that was performed. Details on the methods utilized during stages of the study are given in the pertinent sections. (The results of the modeling are still in preparation and will be reported in an addendum to this report.)

1. Collection of 1205 whiting muscle samples obtained during 1986 to 1988, along the distribution of the whiting population.
2. Parasitological analysis of the muscle samples under microscope.
3. Study of the data obtained to determine the distribution of the parasite.
4. Statistical analysis of the data to study the factors affecting the parasite distribution in the whiting population.
5. Statistical analysis to study the effect of the parasite in the fish growth.
6. Modelling of the host-parasite cycle.
7. Modelling of the whiting population dynamics, fishery and interactions with the parasite.

PROJECT MANAGEMENT

The study was performed by Sara Adlerstein and Robert Francis from the Fisheries Research Institute, University of Washington. The research was developped at the Fisheries Research Institute.

FINDINGS

This section begins with a summary of background information, on both the host and the parasite, essential for understanding the approaches followed during the study and necessary for interpreting the results. The section is then organized into four subsections: (1) description of the parasite distribution and analysis of its determining factors; (2) life history aspects of the parasite; (3) effects of the parasite in the host population dynamics; and 4) a host-parasite model.

I BACKGROUND INFORMATION

The Host: Offshore Pacific Whiting (*Merluccius productus*) Population

Distribution

The most recent and detailed species synopsis on Pacific whiting is Bailey et al. (1982). The offshore population of Pacific whiting, also called "the coastal stock," is distributed off the Pacific coast of North America from Baja California to Vancouver Island, British Columbia (Fig. 1). Whiting can best be described as a semi-pelagic species, even though its vertical distribution varies with age and with geographic location. Juvenile (ages 0 and 1) whiting are pelagic, inhabiting areas inshore of the 400-meter isobath (Stauffer 1985). Adults occur mostly in middle depths on the continental shelf in waters of less than 200 meters, and undergo diel migrations from near bottom during the day to near surface at night. According to Hollowed et al. (1988), these adults are more pelagic in Canadian waters than in the southern areas of their distribution.

Spawning and Migration

Pacific whiting mature between age 2 and age 4 and live up to around age 16. They spawn in the south end of their distribution between San Francisco and Punta Eugenio in Baja California. Spawning takes place during the winter, usually peaking during March. Annually, after spawning, a large part of the adult population migrates to northern areas. Juvenile whiting remain off the coast of California ranging as far north as Monterey.

The annual migration is described in detail in Alverson and Larkins (1989) and Bailey et al. (1982). The northward migration has been reported to occur in long, discontinuous, dense schools formed during daytime, moving at speeds of 5 to 11 km per day (Ermakov 1974). The extent of this migration is found to be correlated with an individual's age or size. Differences in the migration pattern between males and females exist because of differences in growth (Francis 1983). Thus, a higher proportion of females are found in northern areas. During the summer, adult fish remain in the feeding grounds where they are exploited by the trawl fishery. In early fall, the southerly migration starts and by October the fish disappear from their feeding grounds.

Recruitment

Pacific whiting normally recruit to the fishery at age 3 (when the fish start migrating to northern areas). Occasionally, age 2 fish can be numerous in commercial catches. Abundance of recruits is extremely variable between years. In general, the exploited population is dominated by a

small number of large year classes. Over the period of this study, the population was dominated by year classes spawned in 1977, 1980 and 1984. Information relating to Pacific whiting recruitment can be found in Bailey (1981), Bailey and Francis (1985), Hollowed and Bailey (1989), and Adlerstein et al. (in prep).

Fisheries

A complete description of the aspects of whiting fishery is given in Pacific Whiting Surimi Production Feasibility Study, a study prepared for the West Coast Fisheries Development by Beale and Jensen (1990) in partial fulfillment of Saltonstall-Kennedy Project #NA88-ABH-00014. Here, we will only give information that relates to the present study.

Historical reviews of the whiting fisheries are given in Francis and Hollowed (1985) and Nelson (1985). The resource has been exploited since 1900 by the United States. In 1966 the foreign fleet joined the fishery. Joint venture fisheries developed between the United States and Canada and foreign nations. Since 1980, joint venture operations have accounted for a large percentage of the whiting catch in U.S. and Canadian waters. In recent years, shore-based U.S. processors have been increasingly interested in processing whiting instead of more valuable but declining fish stocks. Acceptable biological catches (ABC's) for the whiting fishery are established annually and are split between the United States and Canada. Canadians, nevertheless, are not required to follow the U.S. recommendations.

Beale and Jensen (1990) analyzed technological and economic aspects of the Pacific whiting fisheries. The fish is marketed primarily in headed and gutted form. Although, it is a resource that could be used in products such as surimi and fillet blocks. U.S. processors have not used Pacific whiting in commercial production of surimi. The Japanese produced marketable quantities of surimi for the first time in 1988. Whiting is seldom used for fillet blocks because of limited markets.

The whiting fishery has taken place north of 43° N during late spring and summer, essentially following the northward fish migration in time and space. Catches are concentrated between May and October; in fact 95% of the landings occur in this period (Beale and Jensen, 1990).

The Parasite: *Kudoa paniformis*

General

Species of the genus *Kudoa* are obligate histozoic parasites (Myxozoa: Myxosporea) of fish muscle tissue. The only known phase of their life cycle, the sporogenic stage, is localized in the host. The *Kudoa* species parasitizing Pacific whiting, of which *K. paniformis* and *K. thyrsitis* are the most important, are localized within the fibers of the skeletal muscle. A muscle fiber and its parasite content are called a pseudocyst. This name is given to differentiate this type of infection from a cyst, in which a cell envelope surrounds the parasite.

Classification

Species determination of *Kudoa* is mainly based on morphology of the spores, which is well known since most of the biological studies of the species have focused on the sporogenetic process. *Kudoa paniformis* and *K. thyrsitis* can be easily differentiated since the spores of *K.*

thyrsitis are larger and more stellated in shape than the spores of *K. paniformis*. Figure 2 illustrates the characteristics of the spores of these two species.

Transmission

The general mode of transmission of *Kudoa* parasites in Pacific whiting is unclear. This is also the case for all species of the genus *Kudoa* and even for myxosporeans in general. Until recently, the phylum Myxozoa was divided into two classes: Actinosporea and Myxosporea. This classification was based on the nature of the host: Parasites of invertebrates were classified as actinosporean, while parasites of vertebrates were classified as myxosporean (Levine 1980). The transmission of the parasite in both cases was believed to be direct. The work of Markiw and Wolf (1983) left the classification under discussion. The authors reported that the life cycle of *Myxozoma cerebralis*, a myxosporean parasite of rainbow trout, requires a tubificid annelid as an intermediate host. The authors provided evidence that, at least in this particular case, organisms supposedly belonging to two classes of the phylum Myxozoa were actually different life stages of the same species. The authors' findings also opened the question about the transmission process. Thus, two alternative transmission hypotheses for *Kudoa* parasites exist at present. One hypothesis proposes that the parasite is transmitted directly from spores dispersed in the water; the other, that the transmission is indirect involving the presence of an intermediate host.

Regardless of the transmission mode, the spores pass from one host to another only upon the death of the first host. Once a fish dies, proteolitic enzymes produced by the parasite help degrade the fish muscle and set the spores free. More details on transmission aspects of the parasites will be given in the Life Cycle section of this report.

Processes Taking Place Within Host Fish

In general, *Kudoa* infective agents entering a new host, through either the digestive system or the gills, reach the circulatory system and from there the muscle tissue (Kabata and Whitaker 1985). The processes that take place before the settlement of these infective agents in the fish muscle fiber are unclear.

For *K. paniformis*, one general hypothesis proposes that each infected muscle fiber is the result of a single infective stage entering the host (Kabata and Whitaker 1986). An alternative hypothesis presented by the same authors considers division of the infective stage prior to the infection of the muscle fiber, subsequently resulting in multiple infections. The authors suggest that ". . . the sporoplasm of each ingested spore undergoes some kind of multiplicative process before establishment in the musculature, resulting in multiple infections." Once the infective stage is established in a muscle fiber, sporogenesis takes place.

Sporogenesis of *Kudoa* species in Pacific whiting has been studied in some detail. Among others, Morado and Sparks (1986) performed light microscopy observations of the sporogenic process of *K. thyrsitis* and *K. paniformis*, while Stehr (1986) and Stehr and Whitaker (1986) studied the sporogenesis of these species from an ultrastructural point of view.

The sporogenic process of *K. paniformis* can be summarized as follows. The earliest stage of the parasite that can be detected within the muscle cell contains the generative cells. Maturation of generative cells into spores is believed to occur by cytokinesis of a single generative cell initiating spore development. Mature spores are concentrated in the center of the infected muscle and, as their numbers increase, they expand into the fiber. As this occurs, the muscle is gradually replaced by the parasite. The parasite growth causes a breakdown of the fiber content without

immunological host reaction (Stehr 1986). The muscle fibers look white at this stage. As a result of the increase in spore numbers within the muscle fiber, the parasite comes into contact with the inner surface of the fiber sarcolema, and eventually the host immunological response is triggered (Stehr and Whitaker 1986). The host response consists of encapsulation of the pseudocysts, which causes parasite degradation and gradual destruction of the parasite. At this point, pseudocysts darken and gradually shrink.

The final stage as which the parasite can be observed occurs when the pseudocysts are reduced to strings of small black beads (Whitaker and Kabata 1987; Adlerstein, personal observation). This suggests that the signs of infection may eventually disappear. The time involved in each of the steps of the described processes is unknown.

In general, time of parasite development and host reaction depends on the *Kudoa* species involved and on the host species parasitized. Further, immunological responses toward parasites are highly variable even among individuals of the same fish species. Available information about immunological responses of whiting species to *Kudoa* parasites indicates a wide range of reaction time. Data presented by Whitaker and Kabata (1987) on *K. thyrsitis* in Pacific whiting in the Strait of Georgia show that the host immunological reaction can take place within one year from the onset of infection. On the other hand, in the case of the *Kudoa* parasite of the Argentinean blue whiting (*Micromesistius australis)*, the host reaction might be generated only after several years during which infections acquired in successive years are viable and accumulate up to a threshold level of parasite intensity (G. Tingley, Renewable Resources Assessment Group, Imperial College, pers. comm.; Sardella 1984). Other fish species are immunologically unable to generate a defensive reaction against *Kudoa* parasites (Kabata and Whitaker 1985).

Kudoa *Effects on Fish Texture*

In general, species of the genus *Kudoa* have been long associated with postmortem muscle tissue degradation. Several authors have suggested that increased proteolitic activity is associated with these infections. In the case of Pacific whiting, the adverse effects of *Kudoa* parasites have been established by Tsuyuki et al. (1982), who demonstrated proteolitic activity in fish infected with the parasites *K. paniformis* and *K. thyrsitis*. Furthermore, Patasnik et al. (1982) measured proteolitic activity in spore-filled pseudocysts, concluding that as the muscle cells break down after the host dies, an active proteolitic enzyme diffuses out of the pseudocysts. Finally, Kudo *et al.* (1985) found that the presence of *K. paniformis* correlates well with sensory texture of cooked Pacific whiting muscle.

The Hosts of Kudoa paniformis

Kudoa paniformis is a parasite specific to the offshore population of Pacific whiting; it is believed to have recently (in evolutionary sense) invaded this population (Kabata 1981). However, *K. thyrsitis*, the other *Kudoa* parasite of Pacific whiting, is also found in other Pacific whiting populations, such as in the Strait of Georgia (Kabata and Whitaker 1981) and in Puget Sound (S. Adlerstein, personal observation). Also, this parasite species is found among other fish species, such as walleye pollock (*Theragra chalcogramma)*, several flatfish species (*Microstomus pacificus, Lepidopsetta bilineata* and *Atheresthes stomias)* (Kabata and Whitaker 1987), Pacific halibut (*Hippoglossus stenolepis)*, and even in coho salmon *(Oncorhynchus kisutch)* (Kabata and Whitaker 1986). Because of the difference in host distribution and the difference in the level of

virulence between *K. paniformis* and *K. thyrsitis*, the latter is thought to be the older parasite of the offshore Pacific whiting population.

II DISTRIBUTION OF *KUDOA PANIFORMIS* IN THE OFFSHORE PACIFIC WHITING POPULATION

Introduction

In 1983, a cooperative research effort between the United States and Canada studied the coastal stock of Pacific whiting with regard to the presence of *Kudoa* parasites (*K. thyrsitis* and *K. paniformis*). The research focused on biological aspects of the whiting-*Kudoa* interactions as well as on impacts of the parasites on whiting flesh texture. The biological aspects studied mainly consisted of the parasite distribution within the whiting musculature, and the parasite's geographic distribution in the Pacific whiting population.

The biological aspects of the whiting-parasite interactions were studied by personnel of the Pacific Biological Station in Nanaimo, British Columbia. Mechanical property studies of the fish flesh were performed by personnel of the National Marine Fisheries Service (NMFS) Food Quality Laboratory, Seattle, Washington.

Results of the biological study relating to the parasite distribution are reported in Kabata and Whitaker (1986) and constitute the basis for the present study. The most important results were as follows:

1. Whiting of comparable age and size were twice as heavily infected (prevalence and intensity, defined later in this section) with *K. paniformis* off California as those harvested off Vancouver Island.
2. Whiting age 4 and older were more heavily infected with *K. paniformis* than whiting of age 3 and younger.

In their analysis, the authors categorized whiting that carried two parasites (*K. paniformis* and *K.thyrsitis*) into a "mixed infection" class and reported their results separately for each of the parasites and for the mixed infection category. This categorization somewhat confounds the interpretation of parasite distribution patterns. Nevertheless, the results show a geographical pattern in the distribution of *K. paniformis*, and these suggest that it is possible to identify geographic areas occupied by whiting with relatively low parasite loads, information that could be used in determining fishing strategies for maximizing harvest quality.

Kabata and Whitaker (1986) also indicate that the age of the host is an important factor in determining parasite load. Although the authors had no age information available for the specimens they analyzed, they were able to use an age-length key to infer not particular ages but ranges of ages for ranges of whiting sizes. Given this limitation, the authors could only discern between fish older than age 3 and fish age 3 and younger. Results based on this classification suggest that age or size are important factors determining parasite load.

Furthermore, the age structure of whiting population segments varies along its geographic distribution. Younger whiting occupy the southern areas, while only fish around age 4 and older reach the Canadian waters. Thus, if we want to predict the parasite distribution in the whiting population in a given year for different geographic areas, we are left with the following questions:

How much of the parasite's geographic distribution pattern is due to the age composition of the population components inhabiting different areas, and how much of the parasite distribution is due to some characteristic associated with each particular area? Further, what other factors related to the host affect the distribution of the parasite?

For example, if age is important in determining the parasite load of Pacific whiting, then the age-structure spatial dynamics of whiting should be analyzed. Specifically, fluctuation in whiting recruitment-t success causes large differences in abundance among year- classes. These year-classes occupy different areas along the coast as they grow older. Thus, the component of the population that inhabits a given latitude will vary depending on the age structure of the population in a given year.

On the basis of the above considerations, we have further sampled the whiting population to study the distribution of *K.paniformis* and to analyze factors responsible for that distribution. In particular, we studied the effect of the age structure of the Pacific whiting along their geographical range on the distribution of *K.paniformis*. Results will be the basis for a model, presented in the last section of this report, for possibly predicting the parasite distribution along the geographical range of the Pacific whiting population.

Materials and Methods

This section describes in detail the way the specimens used for the analysis were obtained and the procedures followed to obtain the parasitological information, and briefly touches on the data analysis procedures.

Sampling

A total of 1205 whiting was collected for parasitological analysis in a 3-year period. During summer 1986, 665 whiting specimens were collected, and 270 specimens during each of the summers of 1987 and 1988. Fish collected in 1986 were randomly sampled throughout the distribution of the Pacific whiting population. Figure 3 indicates the position of the sampling locations. Sampling in 1986 was performed by NMFS personnel during the 1986 Pacific Groundfish Triennial Survey. Fish were sampled by bottom trawling in U.S. waters and by midwater trawling in the Canadian zone. In 1987 and 1988, samples were collected only from the northern fraction of the whiting population distribution by joint venture fishery operations north of 41°N. These whiting specimens were collected by U.S. and Canadian observers from midwater trawl commercial catches. Fish were individually frozen within a couple of hours after capture. Table 1 summarizes the sampling information.

Only during 1986 was it possible to sample the full range of the Pacific whiting population distribution. Samples from 1987 and 1988 were collected to follow whiting cohorts in time, in order to study the parasite distribution in relation to age and size of the host. As mentioned previously, each year, the population of Pacific whiting is dominated by two or three large age classes. Thus, in order to sample representatively from host ages (around 15 age classes), either several years of sampling or a very large sample from one year is required. Also, samples from successive years were collected for studying short-term variations in parasite distribution.

Biological information such as sex and length was recorded every year for each specimen. Otoliths were collected for age determination. Otoliths collected in U.S. waters were processed by NMFS personnel at the Aging Unit of the Northwest and Alaska Fisheries Center in Seattle.

Otoliths of fish collected in Canadian waters were analyzed at the Pacific Biological Station in Nanaimo, British Columbia.

Parasitological Analysis

For each of the 1205 whiting specimens sampled, the parasitological analysis consisted of microscopic examination of subsamples of white muscle tissue. Prior to examination, fish were thawed and an approximately 2 cm^2 sample of white muscle tissue was removed from the antero-dorsal area. The dorsal area of the fish was selected for parasite examination following the method proposed by Kabata and Whitaker (1981, 1986). From these muscle tissue samples a subsample of 3 grams was studied for parasite analysis. Positive infection was detected by presence of parasite spores. Each 3-gram sample was inspected under a dissecting microscope, and preparations were obtained by setting monolayers of muscle fibers aligned on a microscope slide. These preparations were first scanned under the dissecting microscope, and later under a compound microscope, to detect and count the infected muscle fibers (pseudocysts). After determining parasite presence, the parasite species was identified by observing the spores under phase contrast. Figure 4a shows spores of *K. paniformis* as observed under phase contrast. Counts of the number of pseudocysts (infected fibers) per sample were performed until inspection of the 3-gram sample was completed. An average number of pseudocysts per gram of muscle was later obtained. Pseudocysts were categorized into three classes according to their developmental stages and counts were recorded separately for each class. These pseudocyst classes are as follows:

> Initial pseudocysts (Figure 4b): The parasites cannot be seen in the muscle cells under a dissecting microscope, and they are visible only with compound microscope. Relatively low numbers of spores are present.
> White pseudocysts (Figure 5a): The parasites can be easily detected under a dissecting microscope. High numbers of spores are present, to the point that the muscle fiber is distended and the pseudocysts look white in coloration.
> Black pseudocysts (Figure 5b): The parasites can be detected with the naked eye. The spores are destroyed or in the process of being destroyed. At this stage, identifying the parasite species might not be feasible. The pseudocyst is black as this point. Figure 5b shows the spore content in an advanced stage of reabsorption; thus, little parasite debris is present.

Kabata and Whitaker (1981, 1986) reported the intensity of the parasitic infection by counts of white and black pseudocysts per gram of fish tissue sampled. In this study the "initial stage" of pseudocyst development is added. Although subjective, this classification was adopted in an attempt to better understand the infection process. This initial stage category is assigned to pseudocysts containing a relatively small number of spores, implying that those fish have only recently been infected.

Average parasite prevalence and intensity per gram of whiting muscle tissue were calculated by year, age, sex and International North Pacific Fisheries Commission (INPFC) area. Relative abundance of the parasite was also calculated by year and INPFC area. Mean intensity and prevalence of the infection was calculated by pseudocyst class (initial, white and black) as well as for total infection (initial+white+black). In this study, prevalence, intensity and relative abundance are used in the context of the definition given by Margolis *et al.* (1982).

Prevalence: This term is usually expressed as a percentage. It is the ratio between the number of individuals of a host species infected with a particular parasite and the number of hosts examined. In this case prevalence was calculated as follows:

$$\frac{\text{Number of whiting with } \textit{K. paniformis}}{\text{Total number of whiting examined}}$$

Mean intensity: This term is usually expressed as counts. It is the total number of individuals of a particular parasite species in a sample of a host species. In the case of myxosporidean infections the parasite cannot be individualized (unlike an invertebrate parasite, for example); thus, the individual is the pseudocyst. Also, since the analysis was performed on a host subsample, the number of pseudocyts (individuals) was expressed in counts per gram of muscle instead of by the whole fish. In this case, mean intensity was calculated as follows:

$$\frac{\text{Sum of pseudocysts per gram among infected whiting}}{\text{Total number of infected whiting}}$$

Relative abundance: This term is also known as relative density. It is the ratio between total number of parasites in a sample of host species and the total specimens of the host species analyzed (infected and uninfected). It equals mean intensity x prevalence. In this case:

$$\frac{\text{Sum of pseudocysts per gram among infected whiting}}{\text{Total number of whiting analyzed}}$$

Some confusion exists in the literature over the use of these terms because their definitions vary with different authors. Also, there is no consensus as to which measure of central tendency best describes the intensity of parasitic infection. For example, Kabata and Whitaker (1986) expressed their results in terms of the median intensity of infection. This is probably because of the skewness of the data, in which case the median may be a good expression of central tendency. In this study, we express the distribution of the parasite intensity in terms of the arithmetic mean and use the normalized log transformed intensity data for statistical analysis which permits the use of parametric methods. In some cases, nevertheless, the median infection is also computed for comparative purposes.

Data Analysis

The particular methods of analysis used in different sections in this report will be described within the corresponding sections. In general, statistical analysis of the distribution of the parasite intensity consisted in multivariate analysis of variance using the SPSS/PC+ Version 3.1 software package for microcomputers. The analysis of factors determining the distribution of the parasite prevalence involved the use of generalized linear models using the Generalized Linear Interactive Modelling (GLIM) System, release 3.77 (Royal Statistical Society 1978). Other quantitative procedures used include parameter estimation of nonlinear functions and finding analytical solutions to systems of differential equations.

Results

The presentation of the results of the study is organized in the following way. First, we discuss the whiting sample characteristics, namely, the age composition of fish analyzed by INPFC area and by year. Next, we describe the distribution of the parasite, in terms of intensity and prevalence, and in some cases, relative abundance, in the whiting population by year, INPFC area, and by whiting age and sex. The parasite distribution is described by each single factor and also for factors combined. This is done to study the relationship between the parasite distribution

and the selected factors. Finally, we present results of analysis investigating which of these factors are statistically significant in determining the parasite distribution.

Sample Composition

As mentioned earlier, the coastal Pacific whiting population experiences highly variable recruitment success. Thus, the age structure of the population is annually dominated by only a couple of year-classes. Since the sampling was intended to be random, this population structure is reflected in the sample age structure. Table 2 and Figure 6 present the structure of the samples obtained in 1986, 1987, and 1988 by INPFC area.

In 1986, the population was dominated by ages 2, 6, 9 and 13 (1984, 1980, 1977 and 1973 year-classes, respectively). In 1987 and 1988, the population was dominated by the same cohorts growing older.

Distribution of Kudoa paniformis: *Single Factor Analysis*

In this section, we describe the distribution of the parasite (1) by INPFC areas covered by the distribution of the Pacific whiting population, and (2) by whiting age, and (3) for whiting sex. Interannual differences in the parasite distribution are also described.

Kudoa paniformis Distribution by INPFC Area. In general, results indicate that the intensity of the parasite are higher in the southern end of the Pacific whiting population distribution. Prevalence, however is higher in northern areas. The combination of the two, the parasite relative abundance, is higher in southern areas. Results of mean prevalence, intensity and relative abundance of the parasite in the Pacific whiting population in their final location of the feeding migration by INPFC area and by year are shown in Table 3 and in Figures 7-9; 1986 is the only year for which samples from the full range of the Pacific whiting population were available.

Parasite prevalence. Results of parasite prevalence (Table 3), indicate that the percentage of infected fish among INPFC areas and the three years of study ranged from around 30 to 70 (Figure 7). Prevalence of *K. paniformis* in samples collected in 1986 was highest in U.S. Vancouver, while the area with the lowest percentage of infected fish was Eureka. Actually, the percentage of infected fish in the samples was approximately constant around 50% across all geographical areas, with a deviation under the mean in Eureka and a deviation over the mean in U.S. Vancouver. In 1987, the prevalence of the infection increased slightly in Columbia and in Canada; however, the same overall pattern of 1986 continued (i.e., the area with highest infection was U.S. Vancouver and the lowest was Canada). In 1988, a latitudinal south-north trend of increasing infection prevalence was observed. In Columbia, only 36% of the fish were infected while in the Canadian zone this percentage increased by a factor of 2.

Parasite intensity. Results of *K. paniformis* intensity analysis indicated that the number of pseudocysts per gram of muscle tissue ranged from around 80 to 120 (Fig. 8, Table 3). The mean intensity of *K. paniformis* in samples collected in 1986 was highest in southern areas (Monterey and Eureka), where it reached counts of ~100 pseudocysts per gram of fish muscle. In Columbia, the infection intensity decreased, and towards the north it increased, with Canada values about halfway between Columbia and Monterey/Eureka.

The highest intensity among 1987 samples was found in Columbia, reaching almost double that observed the year before. Intensity was lowest in U.S. Vancouver and increased again in the Canadian zone.

In 1988, overall intensity increased once again. In that year, the area with the highest intensity was U.S. Vancouver, precisely the opposite of what was observed in the previous year.

Canada was the only area where the intensity level remained constant during the three years of this study. The other two areas (Columbia and U.S. Vancouver) increased in intensity by around 20% of the levels observed in 1986, but never reached values comparable to the intensities observed in Monterey and Eureka in samples from 1986.

Parasite relative abundance. Relative abundance combines infected and uninfected hosts and gives an integrated picture of the parasite distribution. Based on the results obtained, presented in Table 3, three areas can be defined in 1986 in relationship to *K. paniformis* relative abundance (Fig. 8):

a. high parasite relative abundance in the south,
b. low relative abundance in the center of the geographical distribution range, and
c. intermediate relative abundance in the north.

In 1987 the highest relative abundance was in Columbia and it decreased towards U.S.Vancouver and Canada. In 1988, the highest value was in U.S.Vancouver and Canada and the lowest was in Columbia.

Interpretation and discussion. In summary, the results presented above indicate that the distribution of *K. paniformis* along the geographical range of the coastal population of Pacific whiting is not uniform. In agreement with the results of Kabata and Whitaker (1981, 1986), we found that the parasite intensity was higher in southern areas. The results related to prevalence, however, were not similar. We found that prevalence was lowest in southern areas. Dissimilarity in the results can be due to differences in the age structure of the population (hence, in the samples) between the two studies.

In 1986, whiting sampled in Columbia and U.S. Vancouver had lower parasite intensity than the infected fish sampled in the other areas, but the area with the lowest percentage of infected fish was Eureka. The combined result, the relative abundance of the parasite, indicated that Eureka and Columbia had lower parasite abundance that year.

In 1987, relative abundance of the parasite in the Columbia area almost doubled, while the other areas remained near the same levels. In 1988,an increase was experienced farther north (U.S. Vancouver). Also, Canada experienced an increase, while Columbia returned to levels comparable those in 1986. The interannual differences observed in prevalence, intensity and relative parasite abundance were probably due to the whiting cohorts growing older and migrating according to their increase in age (or size) to areas further north.

The results presented above are for parasite prevalence, intensity, and relative abundance in the sample. The sample may not be representative of the latitudinal distribution of the parasite in the whiting population. For example, even though the sample was randomly selected, some whiting ages may not have been accurately represented; if age is important in determining the parasite characteristics, the results will be biased. A population estimate based on the results of all factors that determine the parasite characteristics is derived later in this report. It is also to be noticed that because the sampling scheme is considered only a "snapshot" (taken over a short time period) of the parasite distribution, and so the answers derived in this section and throughout this study are restricted to the time period in which the fish have already reached their final feeding locations.

Interpreting the patterns of intensity, prevalence and relative abundance of the parasite along the geographical distribution of the host population requires that all factors affecting the

parasite distribution be incorporated into the analysis. At this point of the study, three non-exclusive hypotheses are thought to explain the observed difference in parasite distribution between INPFC geographic areas:

a. The areas have unequal pools of parasite, hence probability of infection differs among areas.
b. The areas have the same pools of parasites, but parasite loads are dependent on the age of the host, which varies among areas.
c. The parasite load affects the swimming performance of infected Pacific whiting; thus, fish with different parasite infections migrate at different rates.

These hypotheses are elaborated upon later in this report.

Kudoa paniformis Distribution with Age of Pacific Whiting. *The results indicate that intensity and prevalence of the parasite increases with whiting age (or size).* Clarifying these relationships is fundamental for predicting the parasite characteristics of a particular geographical location since the whiting population is latitudinally stratified by age along its geographical range. Also, this information is critical for developing an understanding of the parasite life cycle. Results of intensity and prevalence of the parasite in relationship to whiting age are in Table 4.

Parasite intensity. *The results indicate that parasite intensity increases with age of the host.* The study of parasite intensity distribution with age of the host was based on different combinations of data from samples obtained during 1986, 1987 and 1988. Figure 10a shows the observed mean intensity of *K. paniformis* in Pacific whiting of different ages in samples collected in 1986 (Five INPFC areas). Unfortunately, only small sample sizes were available for ages derived from weak year-classes. Intensity ranged from around 40 to 120 pseudocysts per gram of muscle in age 2 and age 11 whiting, respectively. Clearly, intensity increases with the age of the host in the range of ages observed.

Figure 10b shows the observed mean intensity of *K. paniformis* in whiting of different ages during the three years of sampling. These means are from data from 1986, 1987 and 1988, from Columbia, U.S. Vancouver and Canada. Reasonable sample sizes for each age were available. Again, the number of pseudocysts per gram of sample increased with whiting age. Intensity ranged from around 10 to 140 counts per gram of muscle for age 2 and age 11 whiting, respectively.

Figure 11 represents the parasite intensity at whiting age when all the data available are combined. Data were from samples collected in all five INPFC areas in 1986 and in the three northern areas sampled in 1987 and 1988. The same pattern of increasing parasite intensity at age of the host can be observed.

Parasite prevalence. Results indicate that the percentage of infected fish increases with the age of the host. The study of the parasite prevalence distribution with whiting age is based on equivalent data combination as in the intensity case. Results are in Table 4. Figure 12a shows the observed parasite prevalence in whiting at age in the 1986 survey (five areas). Prevalence of the infection increased with age of the host from 20% to 70% in age 2 to 9, respectively. In whiting older than age 9, the percentage of infected fish decreased lightly.

Figure 12b presents the observed percentage of infected fish in 1986, 1987 and 1988 samples. Prevalence was calculated from data only from Columbia, U.S. Vancouver and Canada. The same pattern observed for 1986 was present: Prevalence increased with host age from ~10% to ~70% for whiting from age 2 to 8 (at which age it stabilized).

Figure 13 shows the mean prevalence in whiting at age based on all the data available. As in the two previous cases, there was an increase in parasite prevalence with host age. Clearly, the proportion of Pacific whiting carrying the parasite increases with age.

Interpretation and discussion. Unfortunately, it was impossible to obtain a random sample of the whiting population with reasonable sample sizes for all ages during one year; it was also impossible to sample all INPFC areas occupied by whiting in the three-year study in order to estimate the distribution of the parasite at age. When only data from 1986 are analyzed, not all ages are represented; when the data from 1986-1988 are combined, only a fraction of the population is considered; and when all data are pooled, samples from different geographical areas are combined. If the parasite distribution was affected by a spatial distribution of the host,or if the parasite abundance varied within the sampling period, combining data from different years and areas would bias the results.

Despite these difficulties, and regardless of how the data were combined, *parasite intensity and prevalence clearly increases with the age of the host.* Because the pattern resulting from combining intensity at age from consecutive years was smooth, it can be inferred that no significant changes in parasite abundance in the whiting population occurred during the time of the study. Statistical testing will be performed to validate this point. If we conclude that there was no inter-annual difference, then the data can be combined to produce estimates for parasite intensity in whiting at age, either by region (if region is found to be significant in determining the parasite load) or for the population as a whole .

Three non-exclusive hypotheses are thought to explain the pattern of increasing parasite intensity and prevalence with the age of the host:

a. The probability of infection increases with increasing host size.
b. The parasites accumulate with time.
c. Older fish occupy areas where parasites are more abundant.

These hypotheses will be analyzed after all factors affecting the parasite distribution are considered. An interesting feature in the relationship between intensity of the parasite and the age of the host was that the intensity reached an asymptote in whiting of older ages. This could be due to acquired immunity of the fish with age or to host mortality induced by the parasite. Another aspect of interest was that the increase in proportion of infected fish at age and the observed levels of the prevalence at age indicated that whiting are susceptible to acquiring the parasite at all ages. These aspects of the host-parasite relationship will be investigated further in the section entitled "Life Cycle of *K. paniformis*."

Kudoa paniformis Distribution with Sex of Pacific Whiting. *No differences are observed between female and male whiting either with respect to intensity or with respect to prevalence of the parasite.* The sex of the host was considered a potential factor determining the parasite distribution since female and male whiting experience different growth rates, which results in differences in size at age and different migration patterns. Male whiting reportedly migrate to the spawning areas later and also leave the spawning areas earlier than females. Thus, differences in parasite characteristics among sexes can be expected if the residence time in the spawning areas is related to parasite transmission.

Parasite intensity. *The mean parasite intensity for both sexes was around 80 counts/gram.* Table 5 summarizes the results of the analysis of *K. paniformis*. The table contains mean intensity for male and female Pacific whiting. These estimates were derived from data on

parasite intensity of whiting (all ages) from the five INPFC areas sampled in 1986, and from the three northern areas sampled in 1986 to 1988 ("all years").

The results in Table 5 indicate that mean parasite intensity is similar for male and female whiting. This is true both for estimates derived from the 1986 samples that representing the full range of the distribution of Pacific whiting, and for estimates derived from samples collected only in northern areas during the three-year study.

Parasite prevalence. *Prevalence for both sexes was around 50%.* Table 6 summarizes *K. paniformis* prevalence in female and male Pacific whiting. Estimates are derived from data from the five INPFC areas sampled in 1986, and from the three northern areas sampled in years 1986 to 1988.

The results in Table 6 indicate that there are no differences between sexes in the percentage of infected whiting, even though the percentage of infected female whiting was slightly higher in both cases.

Interpretation. Despite differences in size at age between female and male whiting, which also determine some differences in their relative latitudinal distribution, similar parasite intensity and prevalence was found among both sexes. Perhaps age was the most important factor in determining the parasite distribution, and size differences are not significant enough to cause noticeable dissimilarities in parasite characteristics. Alternatively, the effects caused by difference in size at age and by difference in latitudinal distribution could balance each other. In the next sections we examine the distribution of the parasite among sexes by introducing whiting age and whiting geographic distribution into the analysis.

Distribution of Kudoa paniformis: *Factorial Analyses*

The analyses performed previously indicated differences in parasitic infection in relationship to the area where the samples were collected as well as to the age of the host. No difference was found in relationship to the sex of the host. Here we analyze how these factors interact.

Kudoa paniformis Distribution with Age of Pacific Whiting by INPFC Area. *Results indicate that in all INPFC areas, both intensity and prevalence of the parasite increases with host age but at different rates.* Highest rates of increase were among the southern areas (Eureka and Monterey). The rates decreased towards the north.

Parasite intensity. *Parasite intensity increases with host age among all INPFC areas, but at different rates.* Results of intensity analysis in whiting at age by INPFC area by year are in the following table (Table 7).

Figure 14 shows the mean parasite intensity of whiting ages 2 to 13 by INPFC area for 1986, 1987 and 1988 combined. The relationship between whiting age and parasite intensity in the five areas follow a similar pattern, but with substantial differences. The area where whiting had the lowest intensity (in all ages except age 9) was Canada. The areas where intensity was the highest were Eureka and Monterey. Intermediate values were found in Columbia and Vancouver.

Parasite prevalence. *Parasite prevalence increases with age of the host in all INPFC areas, but at different rates.* Results of analyzing on prevalence in whiting at age by INPFC area by year are in Table 8.

Figure 15 shows the prevalence of parasite infection in whiting from age 2 to age 13 by INPFC area for 1986, 1987 and 1988 combined. Whiting ≤ 3 are absent from the northern areas. In general, prevalence of the infection increased with age, and the pattern of the relationship between whiting age and parasite prevalence was similar between areas, although absolute values

differed. The lowest percentage of infected fish among the full range of whiting ages was found in the Canadian zone. Highest prevalence was found in Monterey and Eureka. Prevalence curves for Columbia and U.S. Vancouver are similar, and their values are intermediate between curves for the southernmost areas and Canada.

Parasite relative abundance. As in the case of intensity and prevalence, relative abundance of the parasite increases with the age of the host among all INPFC areas, but the rates of increase are different between areas. Relative abundance in whiting at age by INPFC area are shown in Figure 16. This figure shows the parasite relative abundance among whiting of ages 2 to 13 by INPFC area. No separate table is given for the results since relative abundance is merely the product of intensity and prevalence, both of which are given in the two previous tables. Figure 16 clearly shows that the parasite was more abundant in the south, especially in Eureka, and decreased towards the north. Of note is that the curves for the three northern areas overlap up to age 9. At older ages, the curve for Canada stays stable while the curves for Columbia and Monterey increase significantly. The fact that relative abundance of the parasite was the same in different areas for one range of ages while being different for another range of ages suggests that the parasite load determines the area where a fish of a given age can go, instead of being the area that determines the parasite load. This is so because if the area determines the parasite load, all ages should have had different parasitic loads by area.

Interpretation and discussion. *The parasite distribution varies both with the area where whiting spend their summer and with whiting age.* This conclusion is derived from the fact that the relationship between parasite intensity and prevalence and host age showed differences between areas. This implies that the spatial dynamics of the host is integral to the distribution of the parasite.

The observed pattern of overall lower intensity of the parasite towards northerly locations among adult whiting could be the outcome of at least two situations:

a. Whiting that are heavily infected are not capable of swimming long distances and stay in the southern areas and the parasite is less abundant in the north. Thus, whiting that swim north are not exposed to the parasite during the rest of the feeding season to the extent these whiting are exposed in southern areas.
b. Whiting that stay (not limited by the parasite but by preference) in the southern areas are more exposed to the parasite than whiting that migrate further north.

The opposite pattern (increasing parasite intensity towards northerly locations) in the parasite intensity distribution among younger whiting (mainly age 2) probably has a different origin. Whiting of young ages are probably less affected in their swimming abilities than older whiting, since the intensity of the parasite is low and also because young fish do not migrate long distances; thus, the situations proposed above are not likely to apply. The pattern of the distribution among these whiting could be associated with the fact that young fish found in the northern range of their distribution are larger (they are either stronger swimmers or better fed). The probability of these larger fish acquiring infection is higher than that of small fish. This is so because the transmission relates either to whiting gill surface or to the body surface, depending on the mode of the transmission. Thus, larger two-year old fish found further north are bound to acquire larger loads of parasite.

Kudoa paniformis Distribution with Sex and Age of Pacific Whiting. Previous results indicated no differences between female and male whiting parasite loads when the population as a whole was analyzed. *Results in this section indicate that prevalence and intensity of the parasite among female and male whiting at age are slightly different.*

The comparison between parasite intensity and prevalence in female and male whiting at age was based on the samples from 1986, 1987 and 1988 and from Columbia, U.S. Vancouver and Canada. These data were selected instead of 1986 or "all the years all areas" data as a compromise between having a reasonable sample size of whiting at age and not mixing data from different geographic locations.

Parasite intensity. *Results suggest that there are differences between parasite loads of female and male whiting of same age, at least north of the Monterey area.* Intensity among female and male whiting at age are presented in Table 9. Figure 17 shows the parasite intensity in relationship to age among female and male Pacific whiting. In female whiting ages 2 to 11, intensity increased almost linearly from around 10 to 140 counts per gram of muscle tissue, and decreased at age 13. In males, the pattern was similar except that the increase was up to age 8, from ~10 to 100 counts per gram, and after that age the intensity dropped steadily to ~40 counts per grams. Female whiting tended to be more heavily infected than males at ages >10. At those ages, females are larger than males. This could be one reason for the observed difference. It could also be that mortality rates among males are higher than among females, and finally, it is also possible that the more heavily infected male whiting are more seriously affected in their swimming abilities than females and are not able to migrate to the northern areas (it should be kept in mind that this analysis omits the southern areas Eureka, and Monterey).

Parasite prevalence. *Prevalence increases with the age of the host among both female and male whiting.* Results of prevalence in male and female whiting are in Table 10. Figure 18 shows the relationship between prevalence of the parasite and whiting age among females and males. The only noticeable difference in prevalence among sexes was that the prevalence was higher for female whiting between ages 3 and 7. This is the period in which females experience higher growth rates than males.

Interpretation. In summary, some differences between parasite infection in female and male whiting could be observed. These differences were, however, not consistent across ages. Thus, no real pattern emerged. For example, parasite prevalence among females younger than age 5 was higher than among males of similar ages, but intensity levels were higher in three year old males and lower at age 4. With increasing age, the percentage of infected females and males became similar, but at the oldest ages females were more heavily infected than males.

Kudoa paniformis Distribution with Area and Age and Sex of Pacific Whiting. *The results show no clear pattern in the distribution of the parasite when analyzed according to age, sex of the host and geographical area simultaneously.* In the previous sections, the distribution of the parasite by single factor and pairs of factors was presented. In this section all three factors are studied simultaneously.

Parasite intensity. *No general pattern in the distribution of the parasite intensity emerges when analyzed by age and sex of the host by area simultaneously.* Figures 19 through 21 show the intensity of *K. paniformis* in samples from 1986, 1987 and 1988 by INPFC areas, and by age and sex of the host.

In 1986, high intensity was found in southern areas in female and male whiting in ages 6 and older. Intensity dropped in Columbia to a minimum and increased steadily towards Canada. The highest parasite intensity was found among age 9 female and male whiting in Monterey, followed by age 6 male whiting in Eureka. The lowest parasite intensity was found among age 2 female and male whiting in Monterey. In general, whiting aged ≥6 in southern areas were heavily infected, while younger whiting are more infected in the northern end of their geographical range.

Whiting older than age 9 were not included in these figures because the sample size was too small when broken down into these categories.

In 1987 the highest intensity was found among 10-year old female and male whiting in Columbia, and the lowest intensity among three-year old in the same area. In 1988, the highest intensity was found among 11-year old females and males in Columbia, and the lowest intensity among 11-year old males in Canada.

Parasite prevalence. *No general pattern in the distribution of parasite prevalence emerges when analyzed by age and sex of the host and area simultaneously.* Figures 22 to 24 show the prevalence of the parasite in samples from 1986, 1987, and 1988 by INPFC area, and by age and sex of the host. In 1986, the highest prevalence of parasite infection occurred in age 9 female and male whiting in U.S. Vancouver and Columbia. The lowest percentage of infected whiting was found in age 2 females and males in Columbia. Age 2 whiting showed a pattern of decreasing prevalence with increasing latitude in their range of distribution. The same pattern was true for age 9 males and females in the northern areas. But in general, prevalence in fish of the same age varied little between regions, except in the Eureka region where only ~20% of the age 9 females were infected. One intriguing aspect of the parasite distribution was the equivalent parasite prevalence among age 6 and 9 male whiting and also in the same age range of female whiting found in the Canadian area. The average prevalence for female whiting of those ages was around 50%, while for males it was around 30%.

In 1987, the highest parasite prevalence was found among 10-year old female and male whiting in Columbia and the lowest among age 3 males in the same area. Parasite prevalence among age 10 fish of both sexes decreased with increasing latitude. Also in both sexes, prevalence in age 7 fish attained maximum in U.S.Vancouver, a minimum in Canada, and was intermediate in Columbia. In 1988, the highest prevalence was found among age 8 females in Canada and in same age males in Columbia. Lowest prevalence was found among age 4 males. Prevalence was fairly constant among age 8 females and males. Among both sexes in whiting age 4, prevalence increased with increasing latitude.

Interpretation. Here again, we note that the pattern of parasite intensity was different in whiting of different ages in different regions. Some differences were observed between male and female infection, but no definite pattern was evident. The results show that no significant differences in parasite characteristics are expected to be found based on host sex. The main differences in both intensity and prevalence of the parasite were observed among whiting ages.

Analysis of factors affecting K.paniformis *distribution.*

The results from this exploratory analysis are in agreement with Kabata and Whitaker's results since they indicate that at least two main factors are responsible for the distribution of *K. paniformis* within the Pacific whiting population:

a. the age of the host. This factor seems to be the strongest determinant of the parasitic load of a fish.
b. the area where the host is located in the feeding grounds.

In this section are presented the results of statistical analysis of parasite intensity and prevalence data to identify the factors that significantly relate to the parasite distribution in the whiting population.

Factorial Analysis of Parasite Intensity

Age, area and sex. *The results from this analysis corroborate previously presented observations on the distribution of parasite intensity, in the sense that age of host and distribution of the host in their terminal location in the feeding migration are factors that significantly relate to the intensity.* A multifactorial analysis of variance was performed to evaluate the significance of the previously described factors (age,sex and area) in determining the distribution of *K.paniformis* intensity in the Pacific whiting population. Data incorporated in this analysis were from samples collected in 1986 only, because including the three years of study in this analysis would have implied to create several empty cells. Comparison between years will be performed in a separate analysis.

Figure 25 shows the frequency distribution of the intensity data. The distribution of the data is skewed. Hence, the analysis of variance was performed on log transformed intensity data as the dependent variable. Figure 21b shows the log transformed intensity data. Equality of variances was tested with Cochran's C Test (Cochran 1947) (C(25,10) = Maximum variance/Sum of variances = 0.13669, P = 0.933). Small values of α (Probability of Type I error) indicate that the hypothesis that the populations have the same variance is rejected. Age of the host was incorporated as a covariate. Area and sex, the other two independent variables, were incorporated as factors. The log transformed intensity varied linearly with age, which allowed it to be used as a covariate. The analysis was a multivariate analysis of variance, performed using the MANOVA option in the SPSS/PC+ software package. The method of estimating parameters for the model assumes that the design is unbalanced; thus, it handles unequal sample sizes per cell. The covariate is entered first in the analysis. Table 11 presents the results.

Inspection of the Pearson residuals indicates that a linear regression model with normal error distribution was appropriate. *The results from the analysis indicate that significant factors determining the intensity of the parasite in Pacific whiting are the age of the host, and the area where the host was sampled. Also, the results indicate that the difference in mean parasite intensity in male and female whiting was not statistically significant (95% confidence level).* Thus, sex of the host is not important in determining parasite intensity.

Size, area and sex. *The results from the analysis indicate that size of the host is a significant factor determining parasite distribution.* A similar analysis was performed using the 1986 parasite intensity data to investigate the significance of host length in determining its parasitic load. Host length was incorporated in the analysis as a covariate. As in the case of the age-based analysis, the dependent variable was the log transformed intensity data. Inspection of residuals and results of Cochran's C test indicated appropriate use of the linear regression model. The results, shown in Table 12, indicate that length is significant in determining the parasitic load of the host. As in the results of the previous analysis area is significant and sex is not. The effect of the age and of the size of the host cannot be separated based on these results since age and length are correlated.

Contrast Analysis of Intensity Between Areas. These results indicate that parasite mean intensity among whiting are significantly different among INPFC areas. In this section, we perform a forward step towards determining which areas were significantly different (in 1986). The analysis uses the "Contrast" option in the MANOVA section of SPSS/PC+. This contrast analysis was adjusted for age as a covariate, and performed under the "Special" option that makes individual contrasts possible. Table 13 summarizes the results. The results indicate that whiting

sampled in the following areas were significantly different from each other in terms of intensity of parasitic infection:

a. Monterey and Eureka from Columbia
b. Eureka from U.S. Vancouver

In fact, these results suggest that there was a breaking point in parasite intensity between Eureka and Columbia. The parasite intensity in Monterey and Eureka in 1986 was around 100 counts per gram, while intensity in Columbia was less than half of that. The analysis indicates that as regards the differences in intensity derived from the age composition (the covariate), the difference among these particular areas was significant. The highest intensity was found among whiting in Eureka, and this intensity was significantly different from the intensity in U.S. Vancouver (79.8). The difference between Eureka and Canada, although apparently larger, was not significant. Thus, the difference in this case was due to differences in the age distribution. Also, the apparently large difference in intensity northern areas (with values ranging from 47.5 to 79.8#/gram) is not explained by an area affect. This difference is probably the result of the whiting population age structure in those areas. For example, the intensity in Vancouver was high because the samples from that area are mainly from fish older than age 6.

Interannual Variation in Parasite Intensity. *No significant differences were observed among years in parasite intensity during the period of the study.* An analysis of variance incorporating year as a factor was performed to investigate the variation of the parasite intensity between 1986, 1987, and 1988. Data analysis was limited to Columbia, U.S. Vancouver and Canada, the areas sampled in all that three years. Again, age was introduced as a covariate in the analysis. In this particular case, the representation of the ages was more complete than in the cases where only one year of data was analyzed. Table 14 summarizes the results, which indicate that no significant differences exist between parasite intensities in the three year-study, taking into account the fact that the fish are growing older (age used as a covariate). Also, the results indicate that interaction between the factors was not significant, and neither is the sex of the host. As previously found, age of the host is significant in determining parasite intensity. In this particular case, the results indicate that area is also significant, even though this data set considered samples only from the three northern areas. This last result differs from the previous where only data for 1986 were considered. Previously, the results indicated that these three areas were not significantly different. Further analysis will investigate these areas to determine significant difference by year. That no significant differences exist between years is probably because whiting population abundance fluctuated little during the years of the study, and because the rate of parasite transmission depends on the population dynamics of the host. Specifically, it depends on the number of infected whiting dying every year.

The lack of variation in parasite intensity among years precluded the study of the relationship between parasite abundance and whiting population abundance. The same fact made possible to study the relationship between parasite characteristics and host age by following whiting cohorts across years. This is elaborated upon later in this study.

Interannual Variation Among the Three INPFC Northern Areas. The results indicate that 1988 was the year when differences in parasite intensity between the three northern areas occurred. The following analyses were done to determine in which year(s) the distribution of parasite intensity was significantly different in the three northern INPFC areas. The results are shown in Table 15 and indicate that during 1988 the intensity of the parasite differed among areas ($\alpha = 0.06$). As described earlier, the mean intensity in the three northern areas was as follows:

Area	Counts per gram
Columbia	84.9
U.S. Vancouver	96.2
Canada	74.8

Since this difference is not explained by differences in the age composition, a real dissimilarity among areas exists. Perhaps this areal difference is the result of differential migration of the more infected fish, only less infected whiting are able to attain the most northern areas.

Factorial Analysis of Parasite Prevalence.

Age, area and sex. *As in the analysis of factors involved in the distribution of parasite intensity, results indicate that age of the host as well as their final location in the feeding migration determines the distribution of parasite prevalence.* Figure 14 shows the relationship between *K.paniformis* prevalence and Pacific whiting age by INPFC area. Prevalence increased with host age, but with some differences between areas. The following analysis of deviance investigates the statistical significance of the factors age, sex and area in determining parasite prevalence in Pacific whiting. The analysis was performed using the General Linear Interactive Modelling (GLIM) system as defined in Materials and Methods. Parasite prevalence has a binomial probability distribution. Thus, logistic regression was used to model this binomial response variable. This was achieved by using the link function LOGIT, available in the GLIM system package.

Initially, the analysis was performed incorporating age of the host as a covariate and area and sex as factors. Observation of the Pearson residuals from the model fit showed a negative trend when plotted against age. This is because prevalence increases with whiting age in a nonlinear way. Thus, the analysis was repeated with age incorporated as a factor instead of as a covariate, which eliminates the need for a linear relationship between age of the host and prevalence of the parasite. This analysis used ages for which sufficient data were available (ages 2, 6, 9, 11, and 13). Table 16 summarizes the results.

Model comparison is based on deviances, i.e., the difference between deviances follows a chi-squared distribution with difference between the two model df's as its degrees-of-freedom parameter. Thus, in this case the results indicate that the main factors determining parasite prevalence are age and area. This is since chi-square for 4 df at $\alpha = 0.05$ is 9.4, and the change in deviance when age is incorporated in the model is 83.1 and when area is incorporated is 15.6. The area-age interaction was also significant since α for 13 df is 22.36. Sex is not a significant factor since the chi-square for one df is 3.841 and the change in deviance when sex is incorporated is only 0.2. Parameter estimates of the model, including the factors of age, area and interaction age-area are given in Table 17.

Parameter 1 represents the mean prevalence in the logistic scale among age 2 whiting in the Monterey area, including the age(2).Monterey area interaction. The other parameters represent differences between each of the corresponding factor levels and the mean parameter.

The parameter estimates for the age factor show increasing values with age, indicating higher prevalence with increasing host age. First, the increase was from age 2 to ages 6 and 9, and then there was a greater increase to ages 11 and 13. The parameter estimates for the area factor showed a decrease as the hosts move in a northerly direction from Monterey to U.S. Vancouver, indicating lower prevalence in northern areas. Canada, the northern-most area is similar to U.S.

Vancouver. Beyond this point, interpreting the parameter estimates in this complex model is not practical.

The overall results of this analysis indicate that age of the host and area where the host is located in the summer grounds are significant factors in determining the prevalence of *K. paniformis*. Also, the analysis indicates a significant interaction between age and area, which could be real or due to unrepresented ages in some areas.

Interannual variation in prevalence. *Results indicate that no significant differences in parasite prevalence occurred in the years of the study.* The following analysis investigates interannual variation in the prevalence of *K. paniformis* in the Pacific whiting population during the three-year study. The comparison includes prevalence data from Columbia, US Vancouver and Canada, the areas sampled over the entire time period. The analysis was performed with GLIM, as in the previous section (fitting a logistic regression model). In this case, age was incorporated as a covariate instead of as a factor. This is so because whiting ages in the sample varied over the years of the study, making the factor analysis unsuitable. Area and year are incorporated as factors, with three levels each.

Results of the analysis of deviance and parameter estimates are in Table 18. Fitting of a model that includes year, area and age as independent variables determining infection prevalence resulted in a scaled deviance of 1215 with 923 df. The chi-square value for $\alpha = 0.05$ and 923 df is 41100. This value is well over the calculated deviance, which indicates no evidence that the effects of the factors were non-additive on the logistic scale, and hence the appropriateness of the use of the logistic model.

These parameter estimates indicate that whiting samples from the Vancouver area were more infected than samples from Columbia, while samples from Canada were less infected. In terms of interannual differences, 1987 samples had a lower prevalence of infection than 1986, whereas prevalence in 1988 was greater. These differences, nevertheless, are not significant at $\alpha = 0.05$.

Observation of the Pearson residuals from the model showed only two relatively high values around 2, and plotting of the residuals against the independent variables did not show any trend, which indicates appropriateness of the selected model.

From this analysis we conclude that there was no significant difference in prevalence of the parasitic infection over the range of years in the study. This result indicates that the three years of data obtained can be combined to estimate the relationship between parasite prevalence and whiting age. This relationship will be analyzed in the Life Cycle section, later in this study, and will be used in a fishery model representing the the dynamics of the Pacific whiting and the *Kudoa* parasite interaction.

III DISTRIBUTION OF *KUDOA PANIFORMIS* PSEUDOCYST STAGES IN THE PACIFIC WHITING POPULATION

Different stages of *K. paniformis* pseudocyst affect the texture of parasitized whiting muscle differently. Black pseudocysts have been described as affecting the fish quality more in aesthetics than in texture. White pseudocysts, on the other hand, have been associated with serious texture damage. Initial pseudocysts, although never considered a separate stage, can be thought to produce damage equivalent to, although less dramatic than, the damage imposed by white pseudocysts.

Figure 26 presents intensity of initial, white and black pseudocysts of *K. paniformis* in Pacific whiting at age by INPFC area in 1986 samples. Pseudocyst stages are as previously defined in Material and Methods. Results are as follows:

Initial Pseudocysts:

The range of initial pseudocyst counts in Columbia was from 0 to 300 pseudocysts per gram of fish muscle for age 2 and 13 whiting, respectively. In all areas, the number of pseudocysts increased with age except in U.S. Vancouver where age 11 and 13 were less infected than age 6 and 9 whiting. Initial pseudocysts were not found among whiting of any age in Canada. Within host age, mean initial pseudocyst intensity decreased in whiting occupying northerly locations.

White Pseudocysts

In general, the number of white pseudocysts per gram of fish was higher than the number of initial pseudocysts. The range of white pseudocyst intensity was from 0 pseudocysts per gram of fish muscle in age 11 whiting in Eureka, to over 200 in the same age fish in Canadian waters. No definite pattern of intensity at age appears among areas. In Monterey, the number of infections per gram increased linearly with increasing whiting ages. In U.S. Vancouver, the pseudocyst numbers in all ages were approximately constant. In the three remaining areas, intensity increased to a plateau and then decreased. In Eureka, the maxima were at age 6, whereas in Columbia and Canada there were at age 11. Also, no pattern is evident within whiting ages in different areas. Overall, the area having fish with the highest mean white pseudocyst intensity was Canada.

Black Pseudocysts

In Monterey, the range of black pseudocyst intensity was narrower than the range for initial or white pseudocyst intensity, running from 0 to 100 counts per gram of muscle in age 2 and 9 whiting, respectively. No black pseudocysts were present in age 2 whiting in any area. No increasing pattern of pseudocyst counts at age was apparent in any area, nor did a definite pattern exist among whiting ages across areas. The area with highest overall intensity was Monterey.

The interpretation of these results poses some problems that should be pointed out. The first, and most important problem is that the results were obtained from whiting sampled from California to Canada in a period of ~3 months. Since the transitional times between pseudocyst stages are unknown, the distribution of the pseudocyst stages could be changing during the survey period. This fact could introduce bias into the interpretation of the results depending on various aspects of their parasite dynamics. Also, it should be kept in mind that the results obtained in the south represent the distribution of the parasite at the beginning of the summer, whereas the results obtained in the north represent the distribution of the parasite at the end of the season.

With the above consideration in mind, one possible interpretation of the observed decrease of the counts of initial pseudocysts towards northern areas is that the parasite is acquired in the south and by the time whiting attain northern locations the initial stages have already become white stages. An alternative hypothesis is that parasites are acquired in the full geographic range of the distribution but only during a certain period of time; therefore, sampling in northern areas occurring later in the season results in absence of initial stages in the samples. The fact that both initial as well as white pseudocysts were present in the southern areas weakens this second hypothesis.

An interesting aspect of the results was the relatively higher black pseudocyst intensity in Monterey, the most southern area. This fact can be considered the effect of the parasite on whiting swimming performance; fish with a high number of old parasitized muscle fibers, already dysfunctional, cannot swim long distances, and so they stay in the south. Alternatively, relatively higher black pseudocyst intensity in the south can be the result of parasite-induced mortality associated with high parasite infection occurring between sampling took place in the southern and northern areas. Lack of a negative trend in mean pseudocyst intensity with northerly direction weakens this second hypothesis. These results of parasite distribution by pseudocyst stages will be incorporated into the study of the parasite life cycle.

IV EFFECTS OF *KUDOA PANIFORMIS* ON GROWTH AND MIGRATION OF PACIFIC WHITING

The role of predators in controlling natural populations has been extensively studied by ecologists. Nevertheless, the influences of pathogens on the dynamics of their host populations are poorly understood. This is in part because pathogens are not easily detectable and also because the effects of these pathogens are difficult to quantify. Anderson and May (1981) showed that "parameters characterizing the interaction between pathogens and their host populations are often such as to make pathogens as important as the more commonly studied predators in constraining growth of host populations." In general, host population growth can be constrained by pathogens through decreasing their host birth or increasing their host death rates. Paul Smith (NMFS, Southwest Fisheries Center, pers. comm.) proposes that observed long-term fluctuations in the abundance of the offshore population of Pacific whiting could be related to biological interactions such as diseases. Theoretically, an increase in whiting population abundance should be accompanied by an increase in transmission rate of the *Kudoa* parasite. Further, this increase could produce higher whiting mortality rates and lower birth rates, resulting in reduction in fish abundance. Lower fish abundance would result in lower parasite transmission rates, and the overall outcome would be long-term oscillations in whiting abundance.

This section of the study focuses on:

1. The effect of the parasite on individual growth of Pacific whiting,
2. The effect of the parasite on fish migration.

Effect of *Kudoa paniformis* on Pacific Whiting Growth

Introduction

As stated in the General Introduction, one goal of this research is to explore fishery scenarios for minimizing the number of infected fish in the catch. In order to perform this analysis, it is necessary to model the population dynamics of the host, the host-parasite interactions and the host fishery. One aspect to be included in the modelling is whiting growth. This section is to determine wether the parasite significantly affects the host individual growth. If the parasite has an effect in growth then whiting growth has to be modelled independently for infected and uninfected fish.

Materials and Methods

In this study, the effect of *K.paniformis* on whiting growth is investigated in two steps. The first step is to test the hypothesis of parasite effect on whiting growth by whiting cohort. In the first step the intensity of the parasite is considered in the analysis. The second step makes an overall comparison of growth of infected and uninfected fish (without consideration of the parasite intensity) and produces estimates of the parameters for a von Bertalanffy growth model. These estimates will be included in a whiting model in the last chapter of this study. Because Francis (1983) found differences between female and male growth, the analyses take into consideration this factor. These analyses are as follows:

First, whiting length data were subjected to analysis of variance using the following linear model:

$$\text{Length} = a + (b1)\ \text{Sex} + (b2)\ \text{Age} + (b3)\ \text{Parasite Intensity} + \text{Error}$$

Also, a similar model with slope and intercept for female and male whiting was considered, which would allow for separate effects in growth in both sexes. The analyses were done individually by cohort. The youngest cohort corresponded to the 1984 year class. Three ages were available in this case: ages 2, 3 and 4. The intermediate cohort corresponded to the 1980 year class with ages 6, 7 and 8. The oldest cohort was the 1977 year-class with ages 9, 10 and 11. This third data set also incorporates 13-year olds. The analyses were done by cohort to avoid confounding year effects. Whiting age and parasite intensity were included as covariates.

The effect of the parasite on whiting growth can be determined by the degree of parasitism or by the period of time that the fish has been infected. Here we test wether the parasite affects the growth of whiting irrespective of the time of the infection. Thus, the parasite intensity is included in the analysis without consideration of the stage of development of the infection (which gives an indication of the time the fish has been infected). The relationship between whiting length and age is in general nonlinear, but within the limited range of ages it is considered linear. Whiting sex was included as a two-level factor. The analyses were done with the Generalized Interactive Modelling (GLIM) system, release 2.7.

Second, overall comparison of growth of infected and uninfected male and female whiting was performed. Whiting growth in length is well defined by a von Bertalanffy (1938) growth curve (Francis 1983). Here, von Bertalanffy growth curves were fitted with length-at-age data on female and male infected and uninfected fish. The von Bertalanffy model parameters (L_{inf}, k, t_o and variance) were estimated using the method of maximum likelihood. The estimation was done using the nonlinear gradient search algorithm subroutine FLETCH (Wassen 1978), written in BASIC programming language. Three variance scenarios were explored: a normally distributed (1) constant variance across the range of fish ages, (2) linearly increasing variance proportional to age, and (3) increasing variance with the square of age. Then, the growth curves for infected and uninfected whiting were compared using a likelihood ratio (LR) test (Kimura 1980, 1990). LR tests provide a general method for the statistical comparison of growth curves. In this particular case the use of an LR test allows us to test the hypothesis that a more complex model (that includes different parameters for infected and uninfected whiting) significantly explains more variation in the data than a simpler model.

A total of 1210 samples collected during 1986, 1987, and 1988 was available. Ages for both infected and uninfected fish ranged from 2 to 16. Parasitological analysis was performed as described previously.

As shown previously, age of the host is the major determinant of the intensity and prevalence of the parasite. Thus, older ages are more infected, and consequently should be more affected by the parasite. If the parasite affects growth, we expect that this feature will be captured both in the analysis of variance and when fitting the von Bertalanffy model.

Results

The results of both analyses indicate that accounting for differences in host sex the parasite significantly affects whiting growth. First, we present the results of the analysis of variance. The results from the analysis based on the comparison of von Bertalanffy growth curves for infected and uninfected fish are presented next.

Tables 19-21 present the result of the analyses of variance performed on the whiting length data. As indicated previously, data are analyzed by whiting cohorts and two models are considered for the analysis. The results are presented first for the model with common intercept and different slopes for female and male whiting, and second for the model with separate intercept and slopes. The significance of the effect of the parasite is tested by a F statistics based on the comparison between models with and without parasite intensity as a independent variable [(Change in MS /Change in df)/(MS of the larger model/df)]. Significance of the independent variables can, in general, be assessed also by dividing the corresponding parameter estimates (slopes) by their standard error. A ratio of 2 or greater indicates significance of the variable.

The results from both models in Table 19 indicate that the parasite does not affect the growth of Pacific whiting in the range of ages considered ($P > 0.25$). On the contrary, the coefficients for infection were positive, which indicates that parasitized fish are longer at age than unparasitized fish. This was true for female and male whiting. These results are not surprising and actually do not reflect the effect of the parasite on the fish growth. This result is because larger whiting at age have a greater chance of becoming infected. The effect of the parasite is not dramatic at these ages since intensities are low, and no effect is detected.

Table 20 presents the results of the analyses for older fish. These results indicate that parasite infection significantly affects whiting growth ($P < 0.01$). The same conclusion is reached from the analyses from both models. Both male and female whiting are significantly affected by the parasite. This conclusion is derived from the fact that both parameter estimates divided by their standard error were higher than 2. Also, higher negative values of the contribution in slope of males (-.00764), indicate that male whiting are more affected by the parasite in the age range considered. Table 21 present the results for older whiting. These results indicate that, overall, the negative effect of the parasite in whiting growth is significant ($P < 0.05$). Nevertheless, inspection of parameter estimates from the second analyses indicated that only the females are significantly affected by the parasite. This conclusion is reached because the parameter estimate of the contribution of the effect of the parasite on female growth divided by its standard error is higher than 2, which is not the case for males.

From these results we can conclude that the parasite affects the host growth and also that growth is significantly different between female and male whiting. In the next analysis we perform an overall comparison that includes data from all three cohorts previously analyzed individually and that permits comparison of growth of infected and uninfected fish and estimation of growth parameters for future computations.

This second section presents the results of the comparison of von Bertalanffy growth curves for female and male infected and uninfected whiting. Figure 27 shows length-at-age data for infected and uninfected whiting in the comparative analysis. Table 22 presents the mean length-at-age for infected and uninfected fish in the sample. The results in Tables 22 and 23 allow for statistical comparison of growth of infected and uninfected female and male whiting, and also for definition of the structure of the error that best fits the data. Likelihood values for the parameters of the von Bertalanffy growth model fitted with combined and separate data for each sex and under different assumptions about the error distribution are presented in Table 23.

These results indicate that the best representation of the error in whiting growth was that it varies proportionally with age (Cte*age). Based on the likelihood of the model that incorporates this type of error the LR test was performed.

-2LR = -2((ln(likld of model from all data)-(ln(likld of model for infected whiting)+(ln(likld of the model for uninfected whiting))

-2 LR (Females)= -2(2,493.3-(1283.19+1193.72) = 32.8

-2 LR (Males) = -2(3,405.99-(160.809+1,797.57) = 13.2

with -2LR is chi-square distributed with degrees of freedom equal to the difference in the number of parameters between the compared models. Chi-square for 4df (the change of the number of parameters between the models) = 9.408. Thus, LR test indicates that the difference between infected and uninfected female and male whiting growth is significant.

Table 24 shows the results of an analysis similar to the previously performed, but this time data from male and female whiting are combined. A model for sexes combined is derived for future use in the last chapter of this study. Since the sex ratio in the Pacific whiting population is 50/50, the use of a model for sexes combined is equivalent to the use of two separate models.

Figure 28 shows the von Bertalanffy growth model fits for infected and uninfected whiting. This figure shows an overall difference between the two curves where growth of infected and uninfected fish age <4 is similar, but infected fish at age 2 have a slightly longer curve than uninfected fish. The shape of the curves also shows that infected whiting at age ≥5 are smaller at age than uninfected fish. The significance of these differences are tested below.

Again, on the basis of these results, the best assumption about the error variance, among the options explored, is that it varied proportionally with the age of the host . Once the variance structure was chosen, comparison between the two growth curves was performed based on a LR test as follows :

-2LR = -2 [ln(liklhd of all the data) - (ln(liklhd infected) + ln(liklhd non infected)]

= 2(6,009-(2,926+3,073)) = 23

with -2LR being distributed as a Chi-square with degrees of freedom equal to the difference in the number of parameters between the two models, in this case 4. At an alpha level of 0.05 this value equals 9.488. Thus we reject the null hypothesis that having separate models for infected and uninfected fish does not improve significantly the overall fit. Hence, the result shows that the parasite significantly affects the host growth. Given this result, the model representing whiting population dynamics in the last chapter of this study will include separate representation for infected and uninfected fish using the parameters given in Table 25.

Conclusions

These analyses indicate that K. paniformis *significantly affects the individual growth of Pacific whiting, individuals of intermediate ages being more affected.* The fact that lengths of age 2 infected and uninfected whiting is not different probably relates to the fact that whiting are not heavily infected at that age. The mean intensity of age 2 whiting was only around 40 pseudocysts per gram of muscle, while intensity at age 11 was about three times that level. The reason for the smaller difference between infected and uninfected male whiting older than 8 years old is probably that the fish at that advanced age that tested negative for parasite presence probably had the infection in the past and had experienced the effect of the parasite at some point in time. Alternately, only fish that had not been severely affected by the parasite are able to survive until older ages; thus, the effect of the parasite in these fish would not be important. In summary, the effect follows the pattern of parasite intensity with host age. Thus, as intensity increases with whiting age, the effect of the parasite becomes more severe but decreases at the oldest host ages.

One problem brought out by this analysis is the impossibility of obtaining complete information on the life history of parasite infection of a host. Specifically, whiting that tested negative for infection could have been infected in the past, but the parasite could have been reabsorbed. Thus, the differences in whiting growth due to the parasite are potentially much higher.

Effect of *Kudoa paniformis* on Whiting Migration

Throughout this study, we have pointed out that characteristics of the parasite distribution in the whiting population suggest that the parasite affects fish migration. Unfortunately, our results do not clearly differentiate between cause and effect of the distribution. For example, that fish of the same age were found to be more infected in the southern areas could be the result of the parasite having affected in their swimming performance; thus, only less infected fish could swim to northern areas. Alternately, fish were more infected because they stay in the southern areas where the parasite was more abundant. Also, both processes may be occurring simultaneously, potentially causing higher parasite infection in fish remaining in the south. The following is a summary of the information indicating that the parasite affects whiting migration.

1. Fish of the same age were more infected (higher intensity and prevalence) in the southern areas than in the northern areas. This "area effect" is believed to operate in the following way:

   Fish acquire the infection off the California coast prior to their northerly migration (only adults migrate). At that point, heavily infected fish are unable to migrate as far as the less infected fish. Because these more infected fish stay in areas where parasites are more abundant, they become even more infected, dying eventually and contributing high numbers of parasite spores to the area.
2. All fish age >9 found in southern areas were highly parasitized. In particular, the intensity of black pseudocysts (old infections) was high in those cases.
3. Intensity of black pseudocysts was highest in Monterey, the most southernmost area.
4. Intensity (and prevalence) of the parasite in the areas to which fish migrated (Columbia, U.S. Vancouver and Canada) steadily increased similarly with age up to around age 9. Whiting infection kept increasing in Columbia and U.S. Vancouver, while in Canada the levels remained relatively consistent. Around age 10, the infection peaked and later decreased.

The above observations bring up several questions: If the parasite did not affect the fish migration, and since infection increases with age, why would age 10 whiting in Columbia and U.S. Vancouver be more infected than older ages? Also, why did the infection not increase with age in the northernmost area? If the fish were acquiring their parasite loads in the areas where they were sampled, the parasite intensity would be expected to increase with age in each region and this increase would be expected to be consistently proportional to their parasite pool.

One auxiliary piece of information that supports the hypothesis that the parasite affects whiting migration is our novel finding of infected muscle fibers in the red muscle of Pacific whiting. The literature describes the presence of *Kudoa* parasites of Pacific whiting in white muscle tissue only. White muscle is known to be used by fish for rapid movements such as escape from predators, while red muscle is involved in sustained swimming activities such as migratory movement. Thus it is expected that the swimming performance of infected whiting will be affected, and by extension the migratory pattern of those infected fish.

The finding of parasitized muscle fibers in red muscle was accidental and occurred when samples collected in 1987 were analyzed; hence, at that point it was impossible to perform systematic analysis to address this aspect of the parasite biology. Nevertheless, qualitative results indicate that in every observed specimen where white muscle was parasitized, the red muscle was also infected. On the other hand, some specimens with uninfected white muscle had infected red muscles. In all specimens where red muscle was infected, only black pseudocysts were observed. Potentially, immunological reaction of the host occurs faster in red muscle fibers than in white muscle: Since fibers are smaller, the parasite would replace the fibers and trigger the host response sooner. However, it is possible that other pseudocyst stages, harder to see, were overlooked.

As a final remark, in relation to the effect of *Kudoa* on their hosts, it is hard to imagine that fish with a high parasite infection would be unaffected in their swimming abilities. Muscle serves fish as their major protein storage, from which they can satisfy energy needs not only during starvation but also during migratory swimming and for reproductive functions. Although Weatherly and Gill (1985) postulate that fast-growing fish such as Pacific whiting retain the capability for recruiting new muscle fibers (myogenesis) for a long time period, the fibers that are replaced with the parasite are not functional and recruitment of new fibers has a high energy cost. For the Argentinean hake, *Merluccius hubbsi*, a species similar to the Pacific whiting in growth characteristics. Calvo (1989) reported that recruitment of new fibers stops in females of approximately 52 cm in length (around 70% of the maximum length observed for this species) and at smaller sizes in males. Thus, on one hand, the parasite consumes the protein reserves of the fish, and at some point it also destroys the muscle to the extent that the tissue can no longer be regenerated.

V LIFE CYCLE ASPECTS OF *KUDOA PANIFORMIS*

The life cycle of *Kudoa paniformis* is largely unknown. Information available on the subject is scarce and mainly relates to the parasite sporogenetic process. Sporogenesis takes place in the whiting muscle fibers. Other stages of the life cycle, which take place outside of whiting fibers, are unknown, and several alternative hypotheses have been presented concerning the main processes involved. In this section of the study we investigate two main aspects of the parasite life cycle. We will discuss each aspect separately. These aspects are as follows:

1. dynamics of the infective process in Pacific whiting (parasite transmission and development of pseudocyst stages); and

2. mode of transmission of the parasite.

Available information about the parasite life cycle was summarized in the general introduction to this study. Pertinent information to this section is recapitulated to give a frame of reference: it is currently believed that after *Kudoa* infective stages succeed in establishing themselves in a whiting muscle fiber, the sporogenetic process begins. This stage of development corresponds to what we called in this study initial pseudocyst. Sporogenesis takes place without recognition of the parasite presence by the host. Eventually, fiber content is consumed and replaced by the parasite. This stage is known as white pseudocyst. Finally, an immune reaction takes place and destroys the parasite, leading to the formation of the black pseudocyst stage. If the host dies before this destruction occurs, spores are released and are able to infect a new host. Alternatively, the spore content is destroyed and the cell debris is eventually reabsorbed by the muscle tissue. The slower the immune reaction, the longer is the viability of the spores in the host. These processes can operate simultaneously in a fish muscle fibers.

Figure 29 shows alternative pathways of *Kudoa paniformis* life cycle. The figure summarizes what is known and what has been hypothesized about parasite life cycle and puts in perspective the processes under study within the general picture. The processes investigated are highlighted. Information used to generate this chart is mainly drown from Kabata and Whitaker (1981, 1986).

Dynamics of the Infective Process in Pacific Whiting

Introduction

In this first section, we investigate the rate of transmission of the parasite among the whiting population as well as the rate of parasite development from initial to white to black pseudocyst stages and also the rate of black pseudocyst reabsorption. The rate of transmission of the parasite determines the percentage of newly infected fish in the population. The rates of pseudocyst development determine the life expectancy of the parasite, or the viability of the parasite once it invades a new host. Finally, the reabsorption rate determines the time necessary for the host to lose signs of infection. Information on this latter aspect is of primary importance for subsequent studies of this parasite-host interaction. If the rate of reabsorption is high, then infected whiting quickly lose signs of the infection, making the study of effects of the parasite in the host virtually impossible.

No information exists in the literature about *Kudoa* transmission rate or about rate of reabsorption of black pseudocysts. Some information about the host immune reaction time is available. Based on what is known about other *Kudoa* parasite species, a single infection of *K. paniformis* could be viable in the host (equivalent to its life expectancy in the new host) for a period ranging from several months to a host's lifetime. Extreme cases have been described for *Kudoa thyrsites* and for the *Kudoa* species parasitizing the Argentinean blue whiting. In the case of *K. thyrsites*, which parasitizes whiting in the Strait of Georgia, the time elapsing between the moment the parasite invades the host and the time at which juvenile whiting (4 to 12 months old) develop an immune reaction is relatively short. The parasite can be destroyed in a matter of a few months (Whitaker and Kabata, 1986). In the case of the *Kudoa* parasite of the Argentinean blue whiting (*Micromesistius australis)*, for which the species has not been determined, the host is not capable of generating much of an immune reaction. Thus, the parasite stays viable during most of the host's lifespan (Tingley, personal communication, Imperial College, London; Sardella 1984).

Materials and Methods

Procedures. The dynamics of the infective process of *K.paniformis* taking place in whiting muscle fibers are investigated in two steps, which form separate units of this section on the dynamics of the infective process in whiting:

In the first unit of this section, we investigated wether the period of parasite viability in the muscle fibers is shorter or longer than a year. To address this aspect of the study, we asked wether the parasite prevalence depends only on whiting size or on whiting size and age. If prevalence is only size dependent it implies that parasite viability within the host is one year or less. Otherwise infections should accumulate in time and the older host should be more infected. On the other hand, if prevalence is both size- and age- dependent, it implies that the period is longer than a year because for that to happen pseudocyst should have accumulate for more than a year. In order to carry out this investigation (if parasite prevalence is dependent on age or size of the host), we compared parasite prevalence among whiting 6 and 9 years old of similar sizes. The size range was from 47 to 58 cm. As indicated, similar prevalence among 6- and 9-year olds indicates the period is one year or less, higher prevalence at age 9 indicates the period is longer than a year.

The answer from this part of the study determined the next step to follow. If the answer turns out to be that parasite viability period is shorter than a year, only the parasite transmission rate can be derived based on current year total parasite prevalence. But, pseudocyst developmental and reabsorption rates cannot be estimated. This is because available data have a time resolution of a year. If the viability is longer than one year, parasite transmission rate and rates at which pseudocyst stages generate can be determined.

In the second unit of this section on the dynamics of the infective process, we investigated further the dynamics of the infective process based on results in the previous section which indicated that the viability of the parasite in the muscle fibers is longer than a year. The method of investigating these processes involved modelling. We first proposed a system of first-order differential equations representing the infection processes, and we found an analytical solution for the host-parasite model. Then, from data on parasite prevalence by pseudocyst stage in whiting at age, we estimated the model parameters. The estimation used the nonlinear gradient search algorithm Fletch (Wassen 1978) written in Basic programming language. Details of the method used are given, together with the results of the corresponding analysis.

Data. Data used in both units of this section are from the 665 specimens collected during summer 1986 from the full range of whiting distribution. Also, a sample of 50 juveniles of about two to four months old was analyzed. This latter sample was collected in the Monterey area by personnel of the NMFS Tiburon Laboratories. For this juvenile sample, parasitological analysis was done for the whole fish. For the other 665 specimens, parasitological analysis was done on 3-gram sub-samples of fish muscle dissected from the antero-dorsal area of the whiting specimens as described earlier in this report. Except for the 50-juvenile sample, information concerning age and length was available for each whiting analyzed.

Data on parasite prevalence in whiting at age for the first unit of this section were calculated as defined previously in the section concerning the distribution of the parasite. Namely, parasite prevalence corresponds to the ratio between number of infected whiting and the total number of whiting of each age analyzed.

Data on parasite prevalence by pseudocyst stage in whiting at age used for parameter estimation in the second unit of this section were calculated as the ratio between the number of whiting with one particular pseudocyst stage and the total number of whiting at each age analyzed.

The pseudocyst stages considered were: 1) initial pseudocyst in which whiting muscle fibers had few parasite spores; 2) white pseudocysts in which muscle fibers were filled with spores; and 3) black pseudocysts in which muscle fibers spores are destroyed by whiting immune reaction or in the process of being destroyed. If a muscle sample had the three kinds of pseudocysts, then the presence of each pseudocyst stage was registered. The same was done for the presence of two stages or one stage. Thus, one individual whiting was involved in the calculations three times if it had the three pseudocyst stages. Consequently, the sum of the prevalence of initial, white and black pseudocysts does not correspond to the prevalence at age obtained in the previous section unit .

Results

The results from the analysis in the first part of this section indicate that parasite life cycle processes occurring in whiting muscle fibers take more than one year. This is indicated by prevalence among whiting of a common size range at age 9 being around 20% higher than among whiting age 6. This higher prevalence occurs because the parasite accumulates in the host for more than one year. Parasite prevalence among whiting ages 6 and 9 in a size range from 47 to 58 cm is presented in Table 26 and shown in Figure 30.

Mean prevalence among whiting age 6 was 40%, whereas at age 9 already 62% of the fish carried the parasite. Clearly, parasite prevalence increases with age at a given host size range. This result clearly shows that the part of the life cycle of the parasite that takes place within the host is longer than one year. Thus, the parasitic load of whiting in a given year is the product of more than the current year's transmission rate.

The result of this second section is a model that describes the host-parasite dynamics. As mentioned before, we are interested in investigating the parasite transmission rate, the developmental rates from one pseudocyst stage to the next stage, and also the parasite reabsorption rate. We will start this section by describing the steps for carrying out such an analysis, and then present the results.

The rates of parasite development taking place within the host were investigated by modelling the life cycle processes as a system of first-order differential equations. This procedure was based on the assumption that a first approximation to model the change of each parasite stage by a first order rate process is appropriate. The approach was to model the system as simply as possible to unravel the basis of the parasite cycle. Thus, we assumed that we could study the development of parasite in time by analyzing parasite distribution across whiting ages. In other words, we modelled the population dynamics of the host-parasite interaction by following one host cohort. We assume that a sample of the host population of fish of different ages taken in one year is representative of a fish cohort growing old. We also assumed that parasite development is independent of the age of the host; thus, development between pseudocyst stages is a function of time only and not of the age of the host. Finally, we assumed that the development of the infection occurs in the following sequence: (1) initial pseudocyst, (2) white pseudocyst, (3) black pseudocyst, and (4) black pseudocyst reabsorption.

The system of equations is composed of four first order equations. The first equation (1) describes the rate of change of one host population cohort declining over time as product of natural and fishing mortality. Mortality was assumed to be constant at age.

$$\frac{dn(t)}{dt} = -a\ n(t) \qquad (1)$$

where n(t) represents the number of whiting at time t and a the mortality rate derived from both natural and fishing sources of mortality. The second equation (2) describes the rate of change of initial pseudocysts as the balance between increments due to new parasite infections and losses as initial pseudocyst stages become white pseudocyst stages and also as the host cohort declines.

$$\frac{dn_1(t)}{dt} = b\, n(t) - \phi_1 n_1(t) - a\, n_1(t) \qquad (2)$$

where $\phi 1$ is the rate of development from initial to white pseudocysts and n1(t) the number of whiting with initial pseudocysts at time t. The third equation (3) describes the rate of change of white pseudocysts. This rate is the balance between the rate at which initial pseudocysts mature and the rate at which white pseudocysts are destroyed by the host immune system. Again, host mortality was considered as a source of white pseudocyst loss. All three parameters were assumed to be constant at age.

$$\frac{dn_2(t)}{dt} = \phi_1 n_1(t) - \phi_2 n_2(t) - a n_2(t) \qquad (3)$$

where $\phi 2$ is the rate of development from white to black pseudocysts and n2(t) the number of whiting with white pseudocysts at time t. The last equation (4) describes the rate of change of black pseudocysts which is the balance between formation of these pseudocysts and reabsorption of the cell debris by the host and host mortality.

$$\frac{dn_3(t)}{dt} = \phi_2 n_2(t) - \phi_3 n_3(t) - a n_3(t) \qquad (4)$$

where $\phi 3$ is the rate of reabsorption of black pseudocysts and n3(t) the number of whiting with black pseudocysts at time t. To recapitulate, the symbol in the equations are as follows:

$n(t)$	=	number of whiting at time t
$n_1(t)$	=	number of whiting with initial pseudocysts at time t
$n_2(t)$	=	number of whiting with white pseudocysts at time t
$n_3(t)$	=	number of whiting with black pseudocysts at time t
a	=	mortality rate (natural and fishing mortality)
b	=	infection rate
f_1	=	of development from initial to white pseudocysts.
f_2	=	rate of development from white to black pseudocysts.
f_3	=	rate of reabsorption of black pseudocysts

The next step in the analysis was to find a general analytical solution for the system of equations. This was obtained by solving the Eigen system associated with equations 1 through 4 following the approach outlined by Boyce and DiPrima (1976). Utilizing the initial conditions given below, the specific solution to the problem was found by determining the constants C1 through C4. Initial conditions at time zero, equivalent to whiting age 0, are as follows:

n	=	n_o
n_1	=	0

$$n_2 = 0$$
$$n_3 = 0$$

Solution to the System of Differential Equations. The solutions to the system of first-order differential equations for describing the relationship between parasite prevalence by pseudocyst stage in time are as follows:

$$n(t) = C_1 \frac{\phi_3}{b} e^{-at} = n_o e^{-at} \quad (1)$$

$$n_1(t) = C_1 \frac{\phi_3}{\phi_1} e^{-at} + C_2 \frac{(\phi_1-\phi_2)(\phi_1-\phi_3)}{\phi_1-\phi_2} e^{-(a+\phi_1)t} \quad (2)$$

$$n_2(t) = C_1 \frac{f_3}{\phi_2} e^{-at} + C_2 \frac{(\phi_3-\phi_1)}{\phi_2} e^{-(a+\phi_1)t} + C_3 \frac{(\phi_3-\phi_2)}{\phi_2} e^{-(a+\phi_2)t} \quad (3)$$

$$n_3(t) = C_1 e^{-at} + C_2 e^{-(a+\phi_1)t} + C_3 e^{-(a+\phi_1)t} + C_4 e^{-(a+\phi_1)t} \quad (4)$$

where

$$C_1 = \frac{n_o b}{\phi_3}$$

$$C_2 = \frac{n_o b \phi_2}{(\phi_1-\phi_2)(\phi_1-\phi_3)}$$

$$C_3 = \frac{n_o b}{(\phi_2-\phi_3)}$$

$$C_4 = -C_1 - C_2 - C_3$$

Parameter Estimation. From the above solutions, we estimated the parameters of the model. These parameters are the parasite transmission rate (b), white pseudocyst developmental rate (ϕ1), black pseudocyst developmental rate (ϕ2) and rate of black pseudocyst reabsorption (ϕ3).

Parameter estimates were obtained by fitting data on prevalence by pseudocyst stage in whiting at age to the model. Since prevalence by pseudocyst stage was from specimens collected in 1986, and in that year whiting of ages 2, 6, 9 and 13 were predominant in the population and also in the sample, only estimates for those ages could be obtained (table 27). These data were assumed to represent a whiting cohort. Parameter estimation used the routine Fletch written in Basic. Data for parameter estimation are in Table 27 and represented in Figure 31; they are parasite pseudocyst stage prevalence by whiting age.

No infection was detected in 2-4 month old whiting. Prevalence of initial pseudocysts was constant at age. Prevalence of white pseudocysts increased with age up to age 9. Prevalence of black pseudocysts increases up to age 9 and then decreased.

Whiting mortality rate (a) was not estimated in this study; rather, it was assumed constant at age with a value of 0.3. This value represents the sum of natural and fishing mortality. Whiting

natural mortality, although known to decrease with age, was estimated as constant by Francis (1983) as 0.2. Since natural mortality decreases with whiting age and fishing mortality does the opposite, a constant mortality of 0.3 was considered appropriate. Also, mortality among infected and uninfected whiting was assumed equal.

Parameter values were estimated using the search algorithm Fletch. The estimation was based on the criteria of minimizing the sums of squares between the data in table 27 and the model prediction. The results are follows:

$$b = 0.13020$$
$$\phi_1 = 1.10305$$
$$\phi_2 = 0.26440$$
$$\phi_3 = 0.24795$$

Prevalence of pseudocyst stages at whiting age predicted from the model are presented in Figure 31. The model prediction reproduces the data closely, which indicates that the simple model we proposed is appropriate to describe the host-parasite dynamics. From the parameters, we can estimate T, the time constant of the transition processes as the inverse of the corresponding parameters. Thus, T for initial pseudocysts changing into white pseudocysts ($T= 1/\phi 1$) was 0.965 years. Thus, the characteristic time by which this process takes place was nearly one year. The time constant for the transitional process between white and black pseudocyst was 3.788 years. The time constant for black pseudocyst reabsorption was 4.0339 years. Note that by definition within one time constant (T) 36% of the population is still in their original stages (i.e., initial, white and black, respectively), while 64% of the population is already in the next stage.

Conclusions and Discussion

On the basis of the results obtained in this section of the study we propose that the period that elapses between the parasite spores being detected in muscle fibers (initial pseudocysts) and the destruction of the parasite content by the host's immune reaction, takes an average of 4 to 5 years. This result is supported by the fact that three-year old whiting are the youngest fish in which black pseudocysts were observed and in very low percentage. Whiting are probably infected in their first year at low rates and with low parasite loads (less than 5% prevalence). White pseudocysts develop in whiting aged 2 and black pseudocysts appear for the first time in their third year.

The value obtained for the transmission rate of the parasite (at the level of whiting population observed) was low (0.1302) which translates into a time constant for the process of 7.63 years. By definition this means that if the parasite did not accumulate in time, only 36% of the population would be infected in this time period. As mentioned earlier, this transmission rate is the probability of infection of a fish conditional to the exposure time to the parasite. Thus, even though the probability of infection of an individual increases with its size, the time exposed to infection decreases as it spends less time in contact with the infection, since bigger fish migrate to northern "cleaner" areas.

The timing of the described processes is probably highly variable among whiting. Since in general, immune responses at the individual level are diverse. Also, another potential source of variation is the difference in growth rate among hosts. This should influence the timing for these processes, since as the muscle fiber grows, the current capacity for the parasite expands. Likewise, the age at which the host is infected probably influences the timing of the immune response, since

rates of pseudocyst development depend both on the rate of the parasite spore production and the host reaction time.

The rate of black pseudocyst reabsorption is slower than the other rates of pseudocyst development. The time constant (T) of the rate process is 4.039 years. Thus, it takes that much time for only 36% of the black fibers to be reabsorbed. Therefore, even though the parasite is neutralized, its presence can be detected for a number of years in the muscle fiber. This presence is desirable to study the effect of the parasite in individual hosts.

For comparative purposes, we present a qualitative analysis based on the parasite intensity by pseudocyst stages at whiting age rather than on the parasite prevalence. This analysis allowed the study of the timing of the processes taking place between initial and black pseudocysts stages only. Thus, parasite transmission and black pseudocyst reabsorption rates could not be estimated from this procedure. The approach here was to graphically analyze the relationship between intensity of the parasite by pseudocyst stage and whiting age. The average time elapsing between stages was estimated from the distance in the x axis between the corresponding curves representing the variation of pseudocyst numbers by stage in time (age of the host). This analysis is presented for comparative purpose only and does not pretend to have the same depth as the previous modelling exercise. It is rather a conceptual model supported by limited data. The basic assumptions of this approach was essentially the same as in the previous analyses.

The intensity of infection, defined as pseudocyst counts by gram of fish muscle, is a good measure of the parasite intensity for the purpose of the previously performed analysis since it relates directly to the quality of fish muscle. However, this measure is not a fully appropriate intensity index for the purpose of studying the life cycle. For example, suppose that a host is infected only once in its life, and that the infection occurs during its second year of life with an intensity of 10 pseudocysts per gram. At age 13, the same fish will have grown to about four times its age2 volume. Fish growth occurs mainly by increasing the size of the muscle fibers (there is also a marginal growth due to recruitment of new fibers, but only for reduced number of years). Thus, even though no changes in the initial number of infected fibers occurs, the same fish at 13 years of age will have about four times fewer pseudocysts per gram of muscle (if the parasite has not been reabsorbed). To account for the host growth process, an intensity index, which represents the total parasite load of a fish, was calculated by multiplying the average intensity of pseudocyst stages at whiting age by a scaling factor that accounts for the relative volume of whiting muscle fibers at age. Conversion factors are in Table 28.

The volume of a muscle fiber of a 2-year-old whiting was used as a reference point; for example, the conversion factor for 3-year-old whiting indicates that the fiber volume at that age is 1.52 larger than a fiber of a 2-year-old. Figure 32 represents intensity index for year 1986 for the three kinds of pseudocysts. Results are in Table 29. Whiting a few months old did not present signs of parasite infection.

Initial pseudocyst intensity increased with host age for the age range analyzed. White and black pseudocyst intensity increased up to age 9 and later decreased. The curves of initial and white pseudocysts are similar but only up to age 9. From the shape of the curves we can infer the following conceptual model: at age 2, white pseudocyst intensity is lower than initial pseudocyst intensity because it corresponds to initial intensity in the previous year(s) decreased by whiting mortality. In whiting aged 3, white pseudocyst intensity has increased as the sum of the previous year's initial pseudocysts and remaining white pseudocysts. At that age, some of the last year's white pseudocysts become black pseudocysts and a certain quantity is lost by whiting mortality.

The initial pseudocysts accumulate in only a short time but their intensity increases as whiting body size increases.

The average time elapsing between white pseudocysts becoming black pseudocysts, estimated from the distance between the corresponding curves in the x axis suggests a period of 3 to 4 years. This estimate is close to the 3.788 years characteristic time estimated from the prevalence data. The decreasing trend of white and black pseudocyst intensity after age 9 could represent increased whiting mortality induced by high parasite intensity.

In terms of potential problems with both of the analyses presented, the first point we want to make is that, even though this study was concerned fundamentally with mechanistic aspects of the life cycle, it was based on observational analysis of the parasite distribution in the whiting population. Unfortunately, the study lacks experimentation to provide particular answers, since experiments with whiting in captivity are not practical. Given this limitation, the results cannot be independently tested. Nevertheless, features of the cycle can be better understood in the light of the results obtained, and directions for future research can be identified.

The second point we want to stress is that the value of transmission rate (b parameter) of the parasitic infection derived in this study (0.1), is valid only for population levels of the host observed during the years of the study. Theoretically, parasite transmission rates fluctuate with host population abundance. The rest of the parameters should not fluctuate with population abundance directly, even though density-dependent factors could influence those processes by changing the host immunological time response to the parasite.

The third aspect that should be pointed out is that the prevalence distribution in whiting at age used in parameter estimating was derived from samples taken only during summer. Also, samples were collected by a survey moving north during a two-month period. Thus, samples from Monterey were taken in August, whereas samples from Canadian waters were taken at the end of September. This "survey effect" could introduce bias in the results.

Other potential sources of bias are errors in aging the fish, missing the presence of pseudocyst stages, and misclassification of pseudocyst stages. This last factor is likely to occur since the classification is very subjective. Finally, the results are sensitive to the chosen value of mortality. If the population experienced higher mortality rates during the time of the study, the rate estimates obtained would be underestimated. Also, the fact that mortality was considered constant at age is likely to introduce bias in the results. The rationale behind making this assumption is that including further details in the model precludes capturing the basic dynamics of the parasite cycle.

Overall, we believe that despite the problems involved in the analysis, we have contributed significantly to the understanding of the host-parasite interactions. The strongest result derived from the study is that the parasite cycle takes longer than a year. This result is not affected by the assumptions made and has profound consequences in the study of the relationship between host population abundance and parasite abundance. Before this information was available to us, we had contemplated deriving a model to help predict parasite abundance in a given year based on, among other factors, the host population abundance. The appropriate data for estimating the model parameters were thought to be the host population abundance during the years of the study and the annual parasite prevalence during those years, plus the 1983 parasite data obtained by Kabata and Whitaker (1986). It turns out that from our results the only infections that can be assumed to be originated in a current year are the initial infections, and the Kabata and Whitaker data set does not have those counts. This precludes further study and indicates that future research intended to determine the relationship between host population abundance and parasite transmission rates should consider obtaining initial pseudocyst counts.

Mode of Transmission of *Kudoa paniformis*

As depicted in the parasite life cycle chart in this section's Introduction, several pathways for the parasite transmission are possible. Two main hypotheses exist at present:

1. Direct transmission: Spores, freed from a dead host, by floating in the water column, reach the next host through its gills. If the host is preyed upon, spores are dispersed into the water with the feces. If the predator is also a whiting, spores can infect the new host directly.
2. Indirect transmission: The spores floating in the water column are ingested by a filter-feeding invertebrate (intermediate host) which is later eaten by whiting. Euphausiids are the most likely intermediate host since they constitute the highest proportion of invertebrates in the whiting diet at all fish ages.

Kabata and Whitaker (1981, 1983) leaned towards the indirect transmission hypothesis arguing that parasite intensities observed among Pacific whiting are too high to be caused by a transmission mode that requires each muscle fiber to be infected by one spore. The authors thought that transmission through an intermediate host was more likely to produce the high intensities observed. In this section of the study, we investigate the parasite transmission mode by comparing the potential intensity outcome of these hypotheses.

Materials and Methods

Mode of transmission of *Kudoa paniformis* was studied by comparing the relationship between parasite intensity in Pacific whiting at age and whiting food consumption. If transmission of the parasite is indirect (acquired through an invertebrate as intermediate host), intensity of initial pseudocyst stages should fluctuate with invertebrate consumption. The proportion of invertebrates in whiting diet decreases with increasing whiting age (Livingston 1983; Livingston and Alton 1982; Rextad and Pikitch 1986). Thus, if the transmission is indirect, intensity should decrease with age. On the other hand, fish of increasing size (age) have increasing respiratory requirements with water circulating through the gills. Thus, if transmission is direct (acquired through the gills), parasite intensity should increase with whiting respiratory requirements, and hence, with body size or equivalently with total food consumption.

Parasite intensity data for this analysis were initial pseudocyst intensity indices in Pacific whiting at age from Monterey, 1986. These intensity indices were calculated as shown in the previous section. The initial pseudocyst data were selected for the analysis instead of total intensity because, based on results obtained in the previous section, only initial pseudocysts correspond to the current year infections, and we wanted to compare food consumption information from 1986 with the infections acquired in the same year. Data from Monterey were selected because it is the southern most area of whiting distribution. Thus, fish collected there did not inhabit other areas during the current year (the fish migrate in a northerly direction). Consequently, whiting consumption rates for that area could be compared with parasite infection indices from the same area without introducing confounding effects due to fish migration.

Invertebrate and total food consumption were estimated from unpublished data provided by P. Livingston (NMFS, Seattle). These were estimates of proportion of prey items in the diet of Pacific whiting at age during summer 1986 in Monterey. The food consumption estimation also included information on Pacific whiting daily ration from Francis (1983).

Results

Results from this section indicate that parasite intensity correlates better with total food consumption than with invertebrate consumption. From on this result, we propose that transmission rate is direct. Table 30 summarizes the information on euphausiid prey content in whiting diet in Monterey. Up to age 4, whiting diet consisted of 100% euphausiids. This percentage decreased with age; among whiting 8-year-old and older, only 16% of the diet was euphausiids. Total amount of euphausiids consumed in one day was calculated by multiplying the percentage of euphausiids in the diet by whiting daily ration. The total amount of euphausiids consumed daily increased up to age 4 and then decreased. Figure 33 shows the daily total consumption and the daily euphausiid consumption of whiting at age.

As mentioned earlier, if the mode of transmission of the parasite necessitates an invertebrate intermediate host, intensity of initial pseudocysts at whiting age should correlate with the amount of invertebrates in the diet. If the parasite has a direct cycle, then the intensity of initial pseudocysts should correlate with the host's total daily consumption. This is so because the daily ration is a measure of the metabolism of the fish which is a measure of oxygen consumption and thus, a measurement of the water exchange through the fish gills. Table 31 presents whiting initial pseudocyst intensity at age in Monterey, 1986.

From the results in Tables 30 and 31, represented in Figure 34, it is clear that initial pseudocyst intensity index is an increasing function of age. Total food consumption is also an increasing function of age for the range of ages considered; whereas daily invertebrate consumption increased only up to age 6 and then decreased. Figure 35 shows the natural logarithm of intensity index and both total daily ration and invertebrate consumption ration. Again it is clear that the intensity index fluctuations correlates better with total daily consumption than with invertebrate consumption.

Conclusions and Discussion

Results suggest that mode of transmission of the parasite is direct, with no intermediate host involved. This result is in agreement with conclusions reached by Sardella (1984) for *Kudoa sp.* parasitizing the Argentinean whiting and also with the theory about myxozoan transmission prior to the work of Markiw and Wolf (1983).

We believe that, even though the method to investigate the parasite transmission process was not optimal, the result provided good evidence supporting one of the alternative hypotheses concerning parasite transmission. Laboratory work, which could have provided definite answers, are impractical, but following the intensity and prevalence of pseudocyst stages in one whiting cohort from age 0 for several years could also be an appropriate approach to study the process more adequately.

Given the results, cannibalism can be thought to be the cause for the highly parasitized fish observed. Coincidentally, cannibalism is reported to be common in whiting sampled off the Californian coast where high parasite intensity is also found (Livingston 1983).

EVALUATION

WHERE THE GOALS AND OBJECTIVES OF THE PROJECT ATTAINED?

Yes, the study contributes to the understanding of the Pacific whiting-*Kudoa paniformis* distribution. Results of the study serve to identify the factors that determine the parasite distribution. Also, on the basis of our results our understanding of many aspects related to the host-parasite interaction was improved. Finally, we developed a computer model that can be used to explore the effect of fishing strategies in the distribution of the parasite in the catch.

WERE MODIFICATIONS MADE TO PROJECT GOALS AND OBJECTIVES?

No, but a particular result obtained during the development of the project precluded developing a whiting-parasite model that enabled prediction of parasite transmission rate based on whiting abundance. This limited the proposed whiting-parasite fishery model to levels of Pacific whiting abundance to the range observed during 1986-1988. The result we are alluding to was that the parasite cycle within the host is longer than a year. Given this circunstance, no data was available to investigate the relationship between parasite and host abundance.

WHAT ARE THE SPECIFIC ECONOMIC OR OTHER BENEFITS ACCRUING FROM THE RESEARCH RESULTS?

The benefits are hard to evaluate since they depend on several aspects. First, the validity of the results hinge on the characteristics of the fishery in the future. If fishing effort shifts to the beginning of the summer, our results might not fully apply. Second, if the population levels of the whiting population vary significantly, our results might not be appropiate. In addition to the above-mentioned problems, if fisherman make use of our results (e.g., target on smaller fish, or concentrate the effort in Columbia), the quality of the parasite-related catch will be improved.

TO WHAT EXTENT ARE BENEFITS MEASURABLE VS. INTANGIBLE?

Benefits can be measured if a comparison of fish quality between catch in different areas is conducted.

ARE BENEFITS ONE-TIME OR CONTINUING?

Continuing benefits obtained by using absolute results from this study are only resticted by significant variation in whiting population abundance. However, even under those circunstances we believe the relative distribution of the parasite would be the same. Thus, using the results would still lead to a continuing benefit.

ARE BENEFITS THE RESULT OF A "NEGATIVE FINDING"?

No, results are not from negative findings.

TO WHAT EXTENT DID AND/OR WILL THE PUBLIC HAVE ACCESS TO THE PRODUCTS OR SERVICES PRODUCED BY THE PROJECT?

The public will have access to the generated information to the extent that the contractor of the project disseminates the information. Sara Adlerstein has agreed to give an oral presentation of the results in a place and time considered convenient to the contractors. She has also been in contact with the Pacific Whiting Management group, which is aware of the progress of the project.

TO WHAT EXTENT DID AND/OR WILL THE PUBLIC USE THE PROJECT'S PRODUCTS OR SERVICES TO SATISFY A NEED OR LESSEN BUSINESS OR OTHER RISKS?

In recent years, the interest for Pacific whiting fishing has been is increasing. We believe that if the fishing industry is aware of the study they will make extensive use of the results. We have had several requests already for a Final Report of the study.

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FIGURES

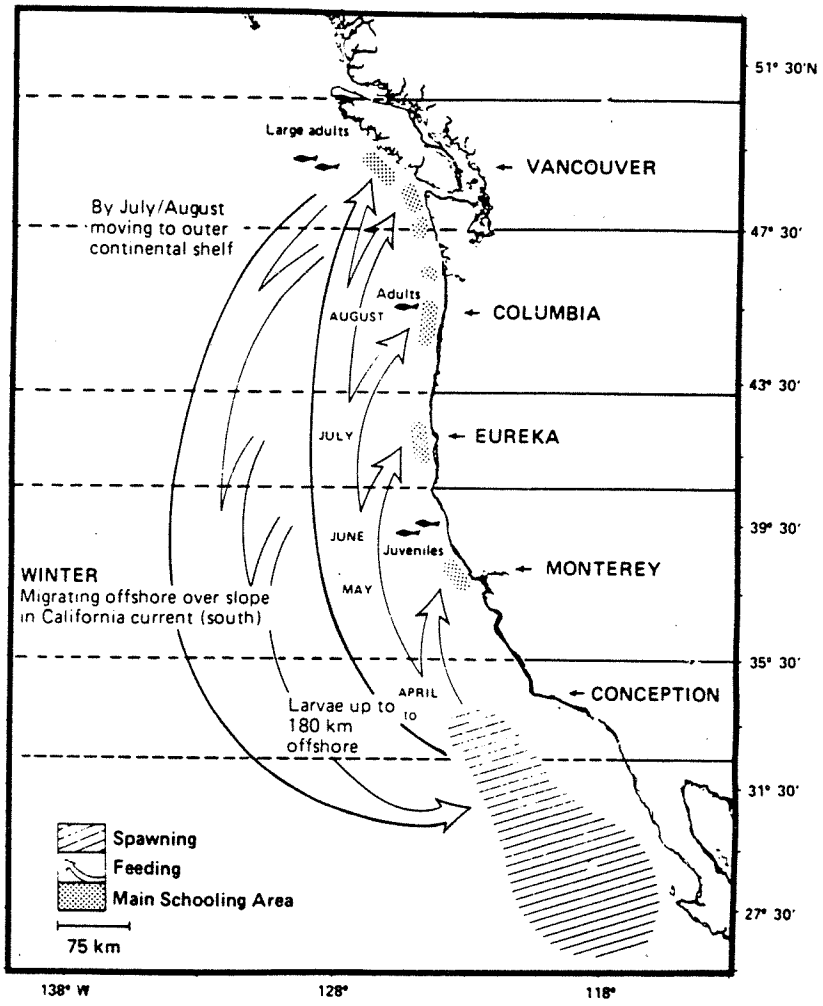


Figure 1. Distribution and migration of Pacific whiting.

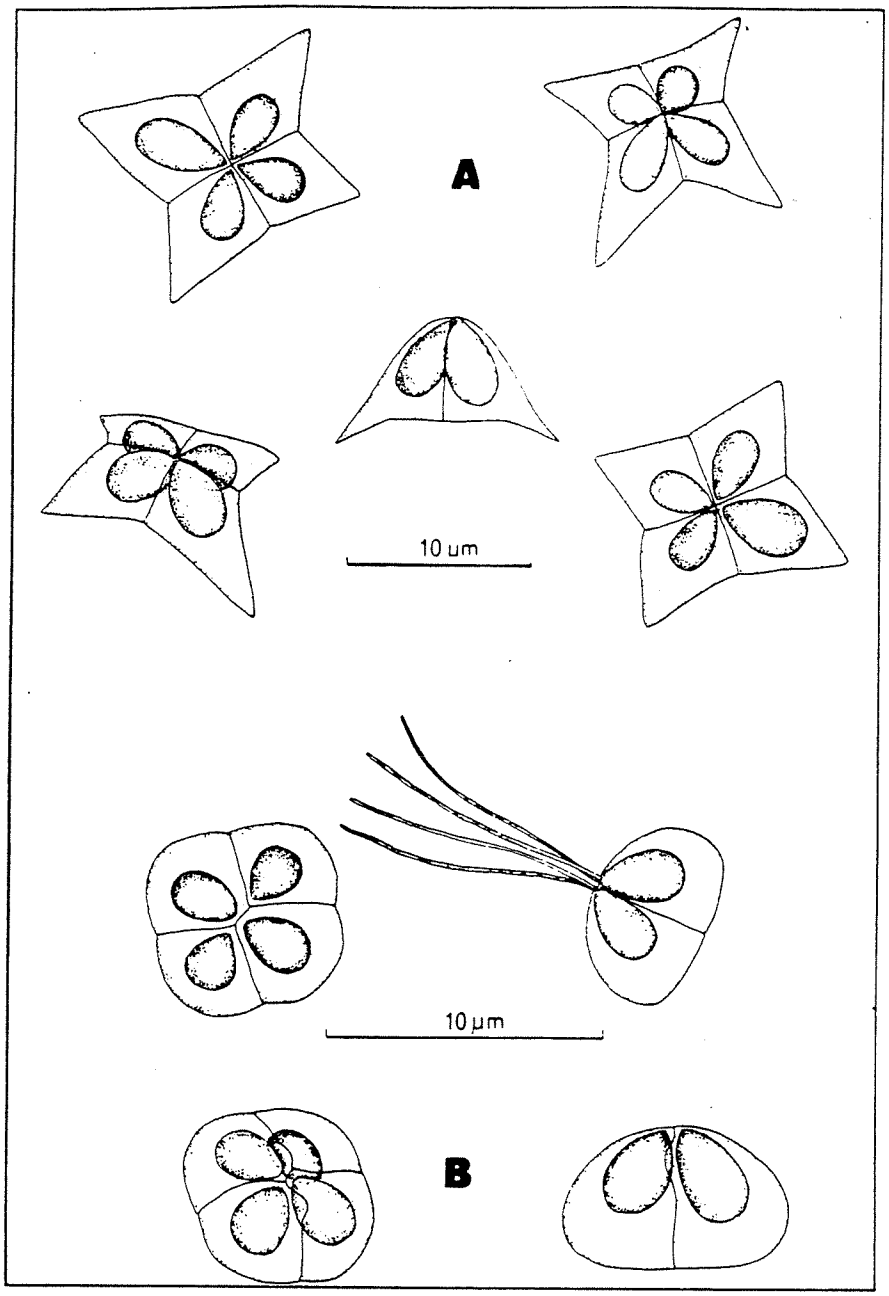


Figure 2. *Kudoa paniformis* and *Kudoa thyrsites* spore morphology.

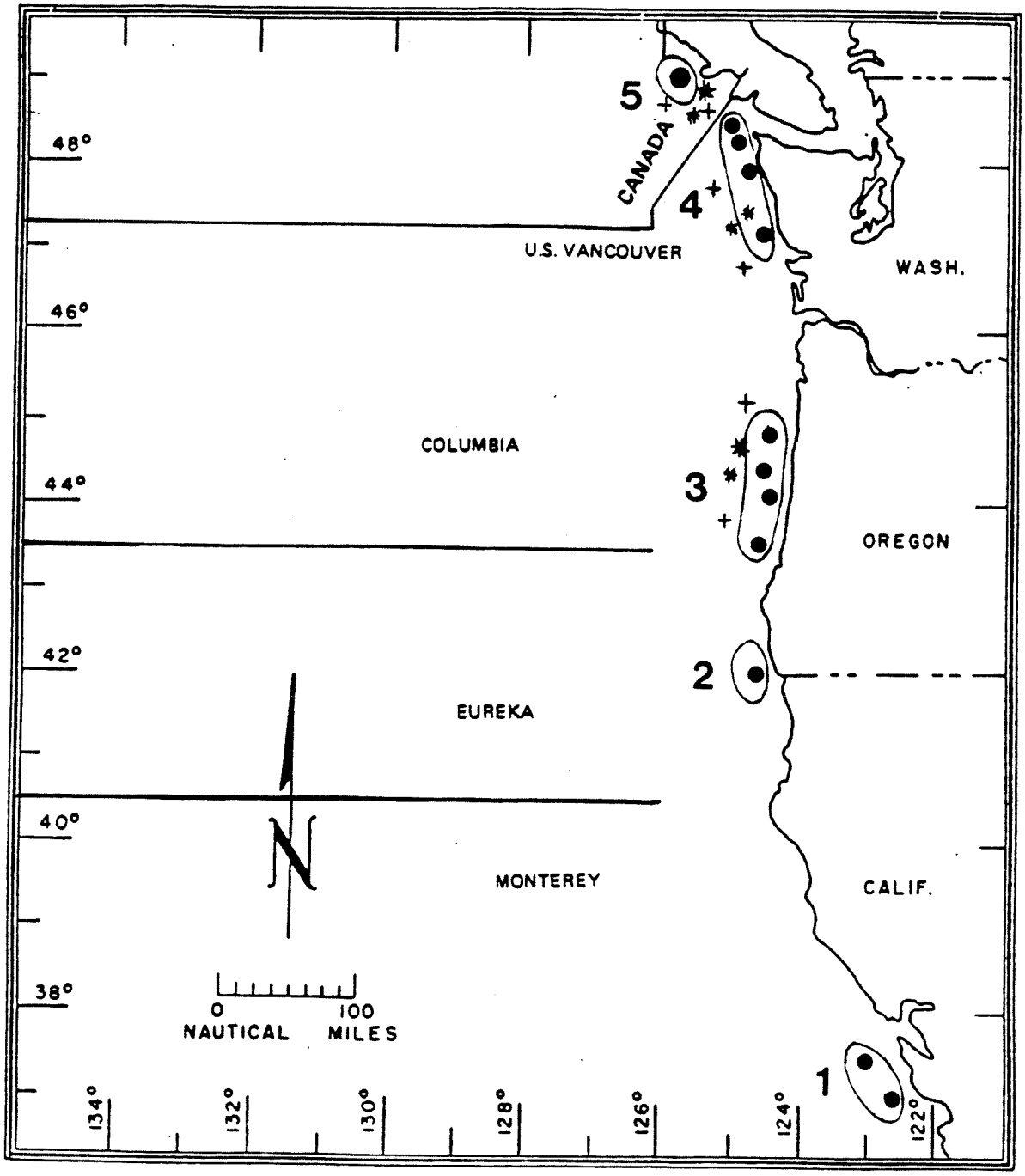
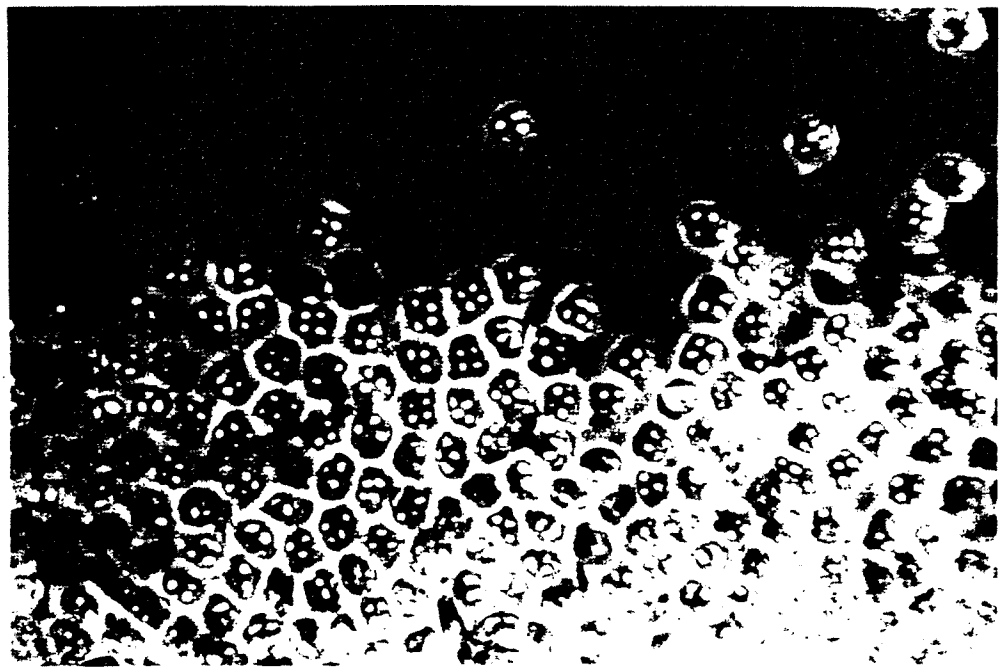


Figure 3. Sampling locations: ● = 1986, ✱ = 1987, + = 1988.

(a)



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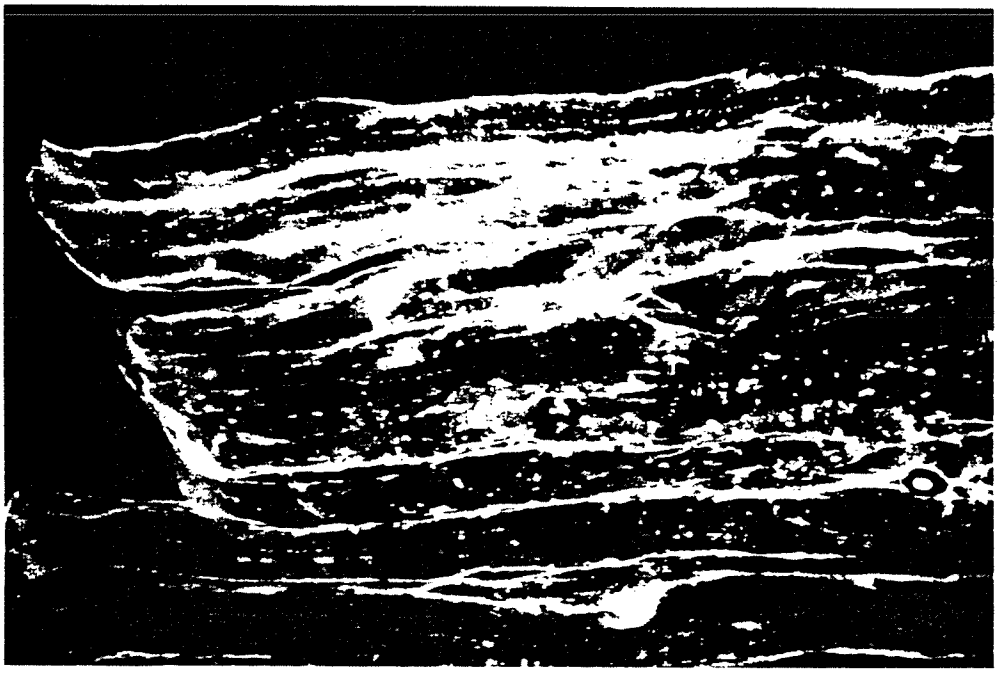
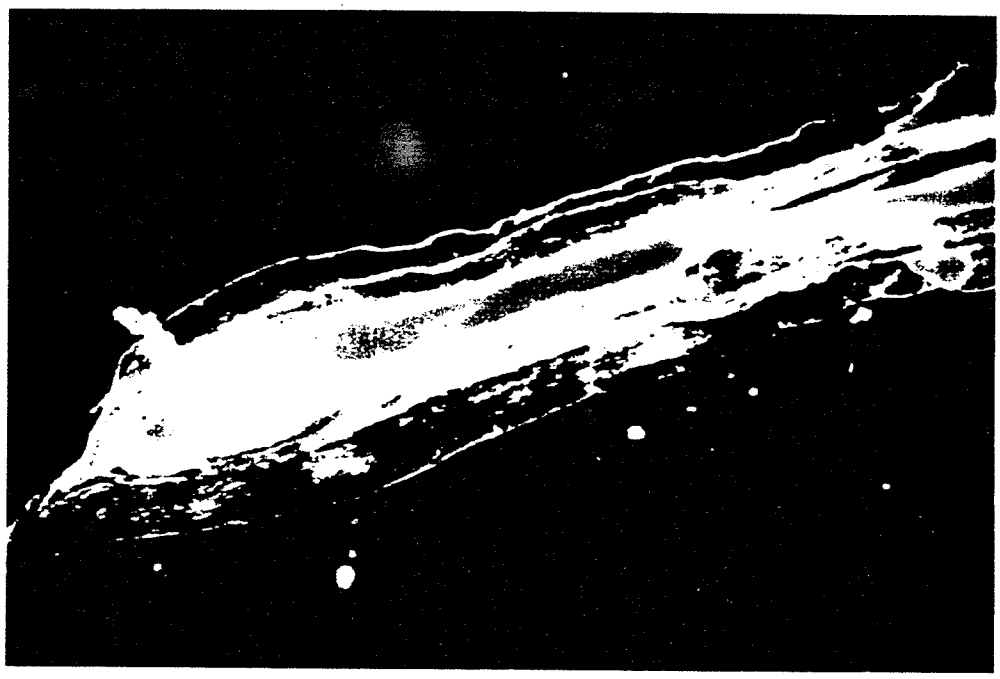


Figure 4. *Kudoa paniformis* (a) spores and (b) initial pseudocysts.

(a)



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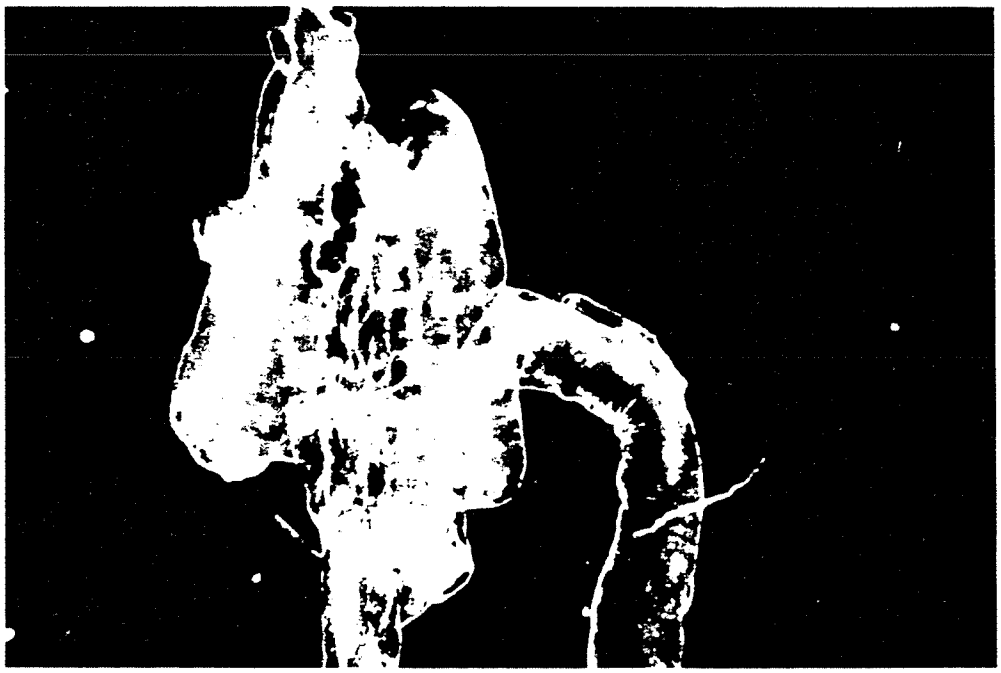


Figure 5. Pseudocyst stages (a) white, and (b) black.

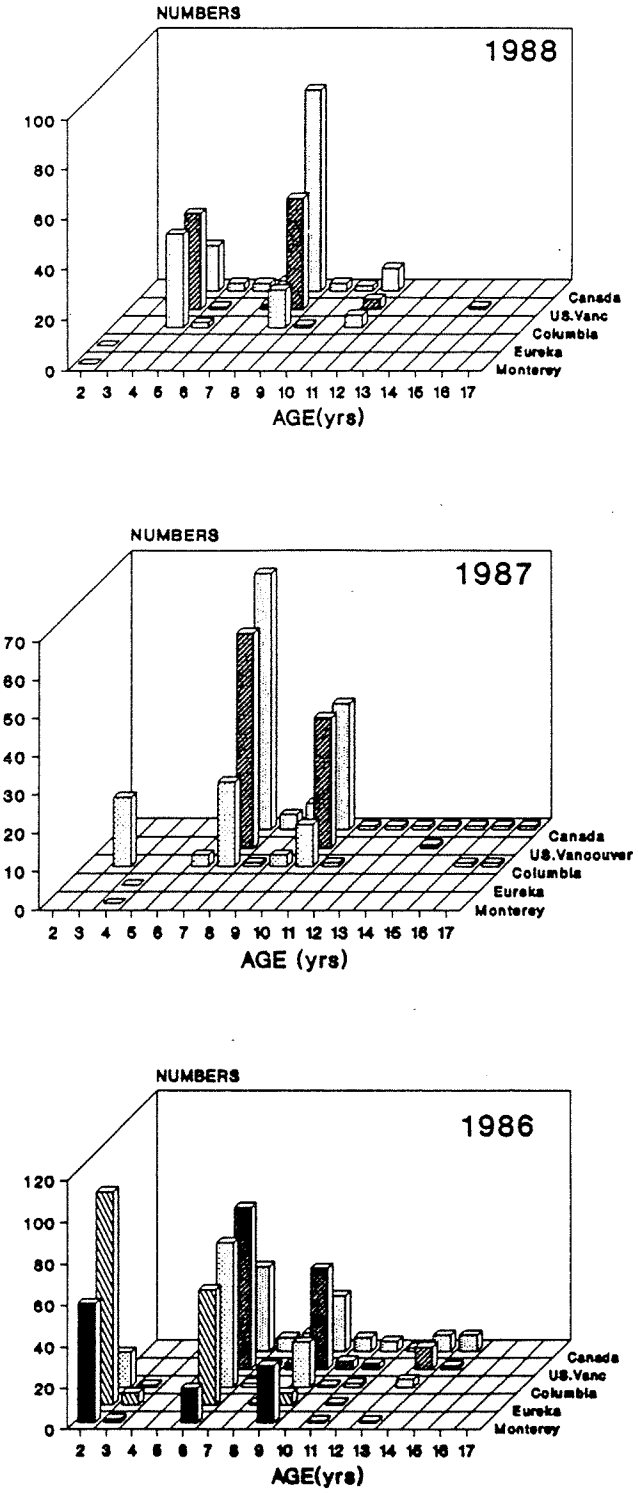


Figure 6. Age composition of the sample (a) 1986, (b) 1987, and (c) 1988.

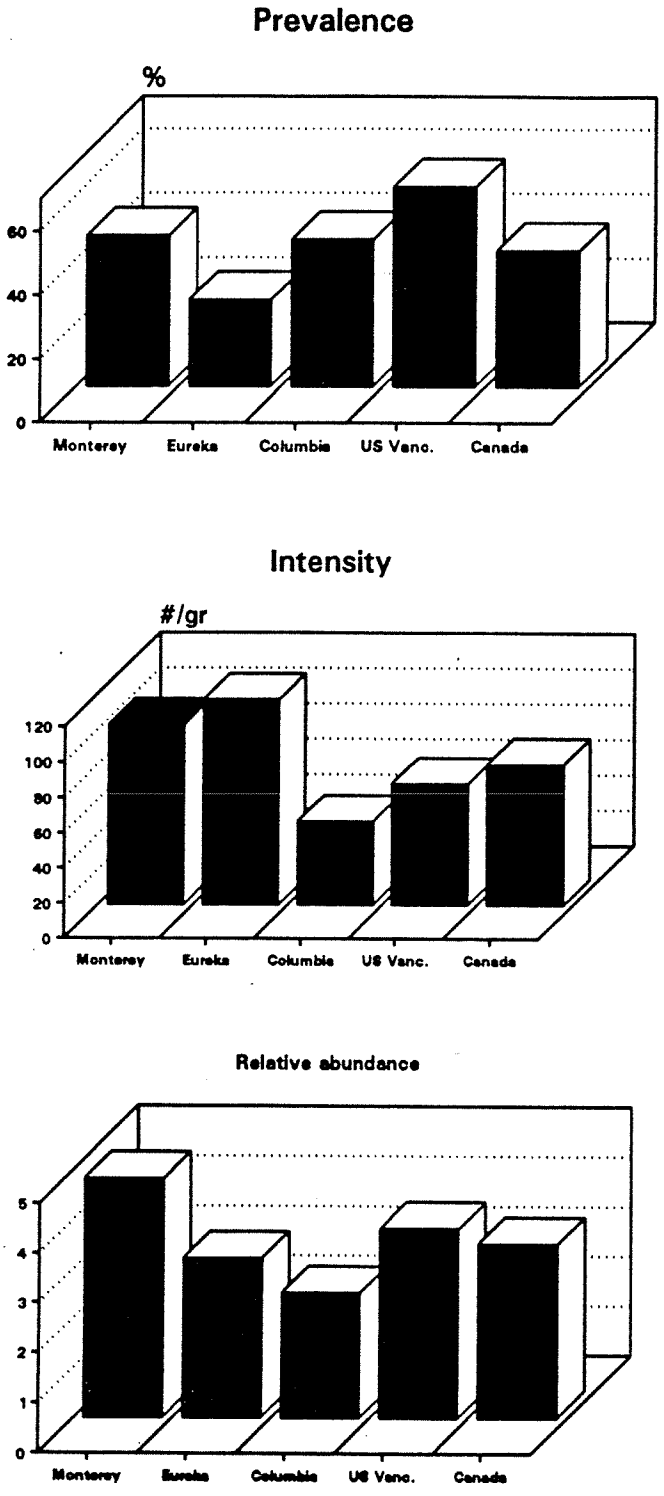


Figure 7. *Kudoa paniformis* distribution by area, 1986.

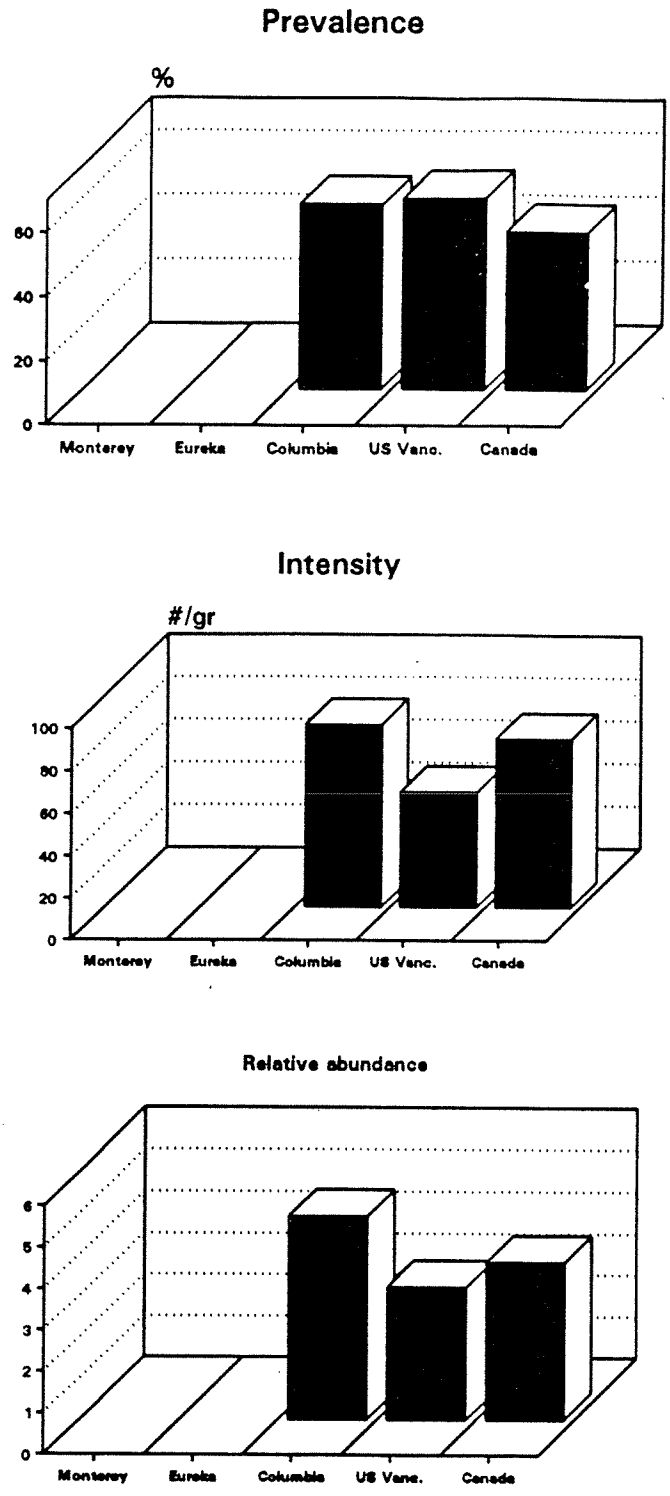


Figure 8. *Kudoa paniformis* distribution by area, 1987.

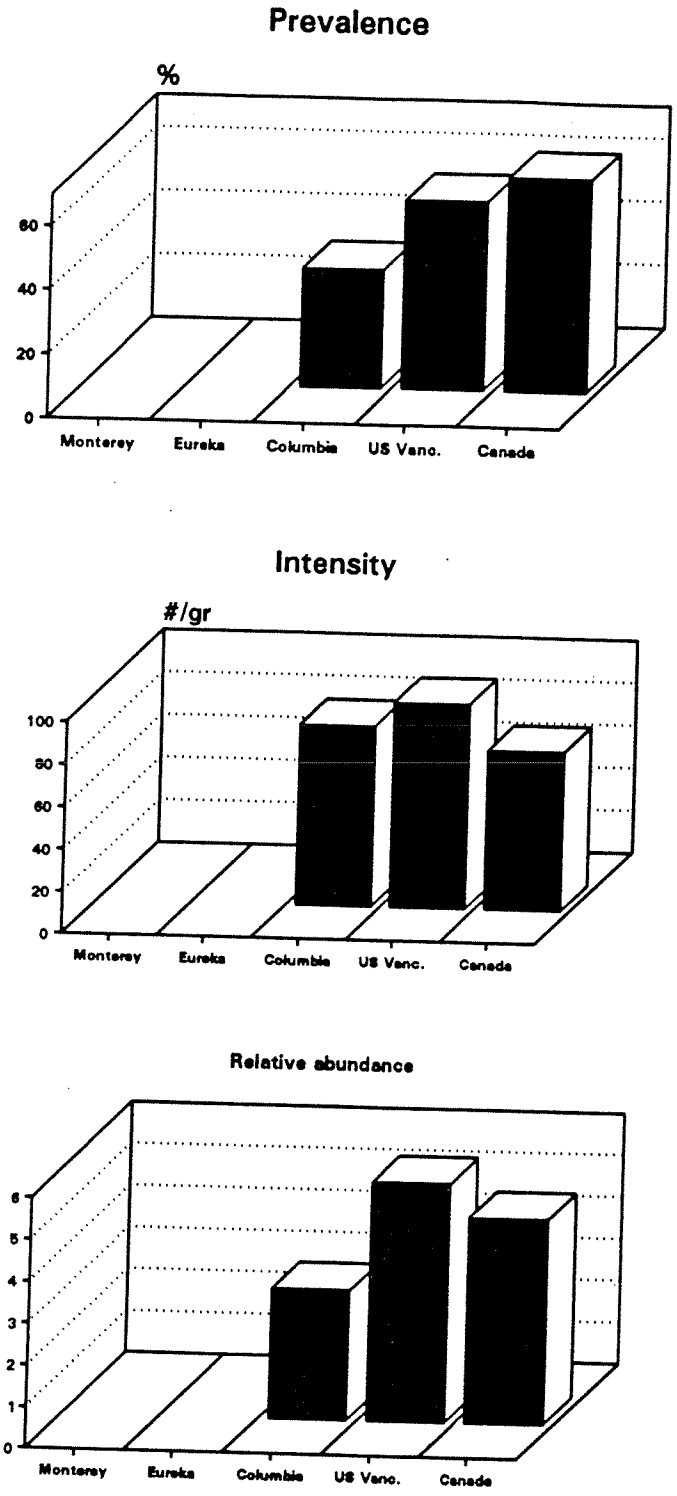
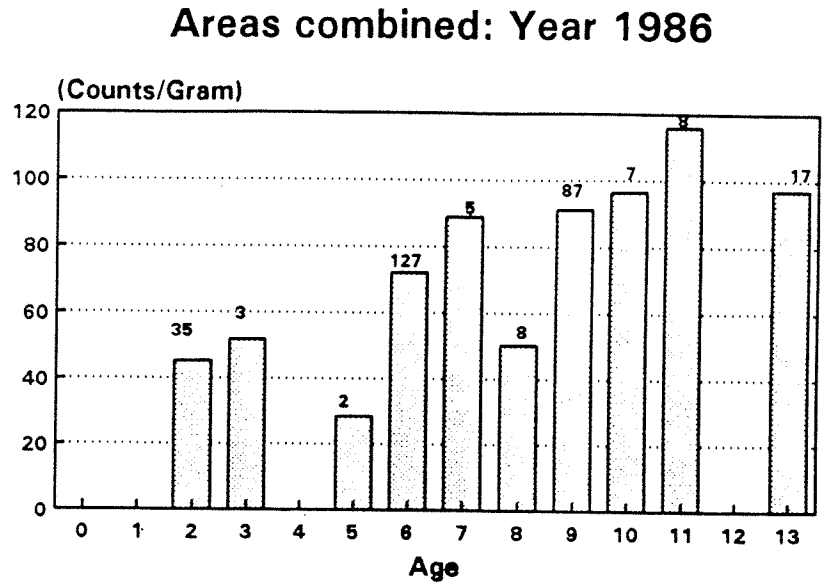


Figure 9. *Kudoa paniformis* distribution by area, 1988.



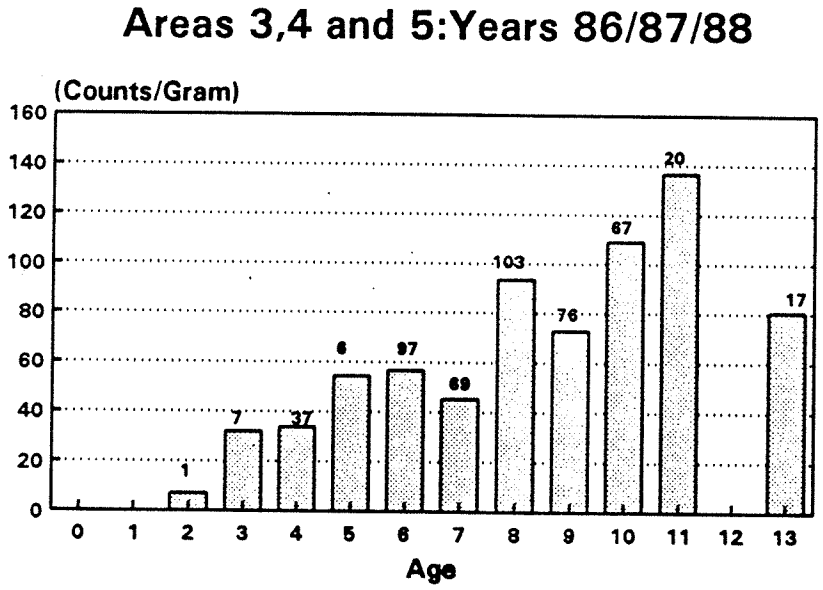


Figure 10. *Kudoa paniformis* mean intensity at whiting age (a) 1986, (b) 1986, 1987 and 1988 combined for Columbia, U.S. Vancouver and Canada.

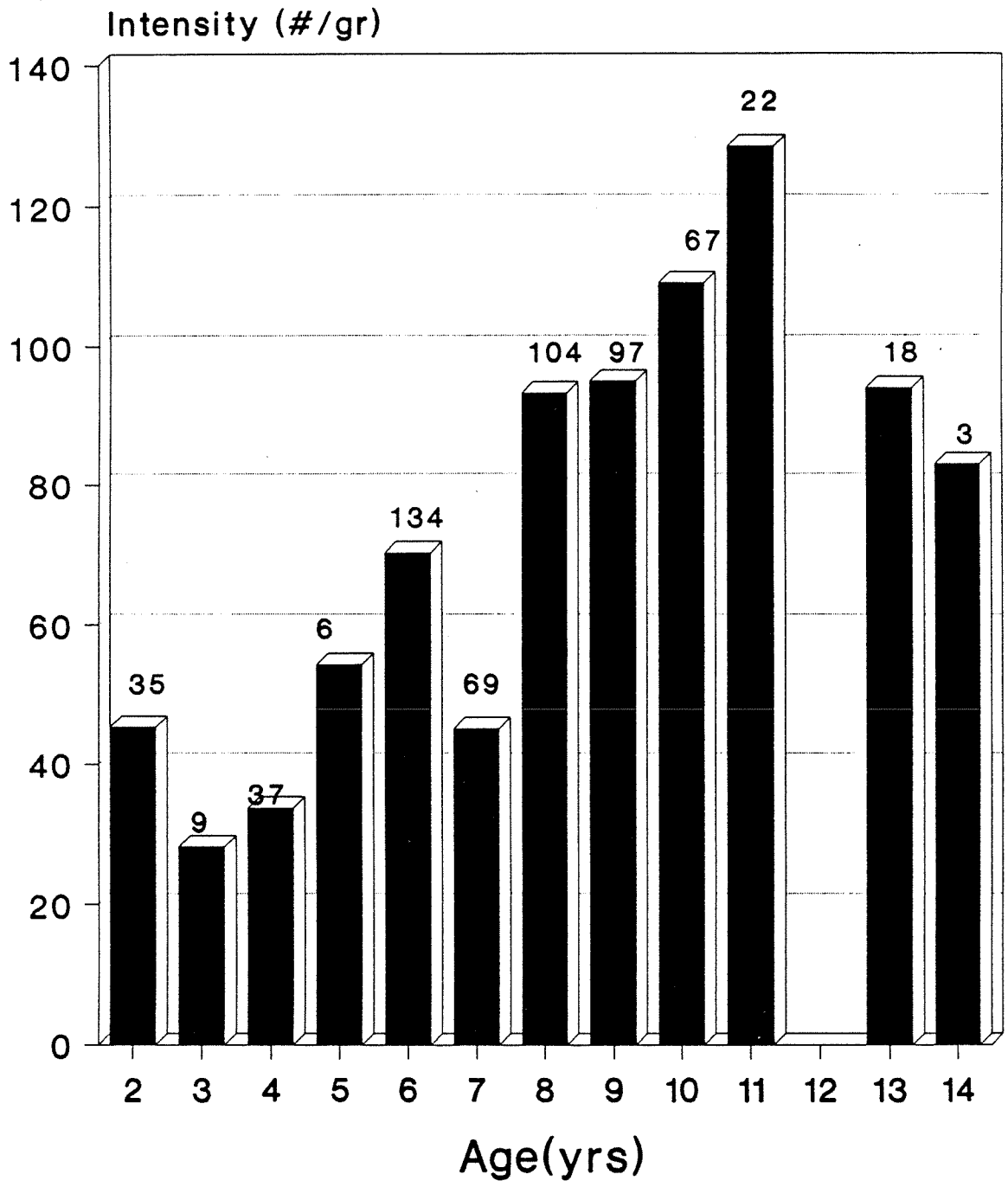


Figure 11. *Kudoa paniformis* mean intensity at whiting age, 1986, 1987 and 1988 combined.

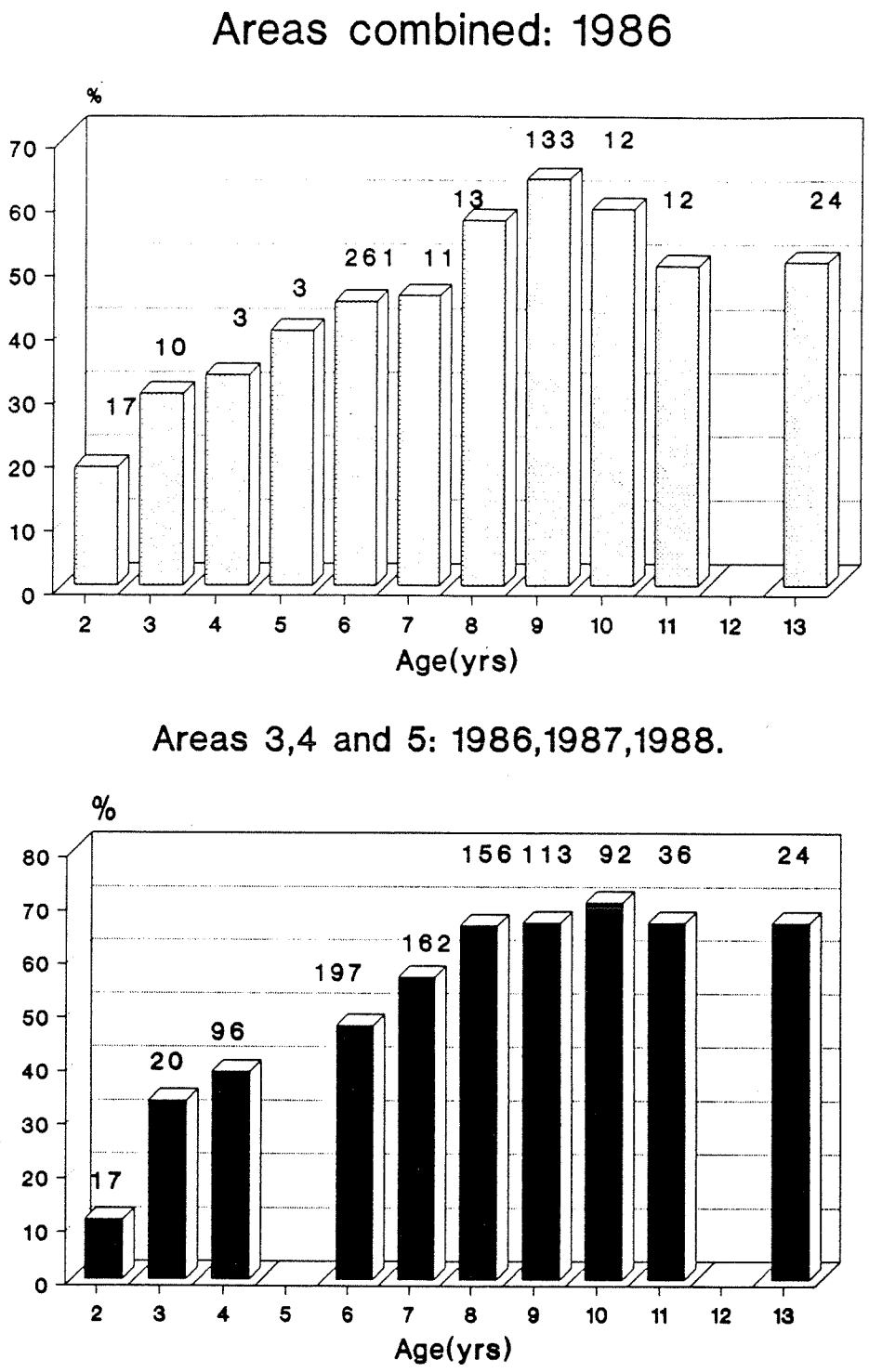


Figure 12. *Kudoa paniformis* prevalence at whiting age (a) 1986, (b) 1986, 1987 and 1988 combined for Columbia, U.S. Vancouver and Canada.

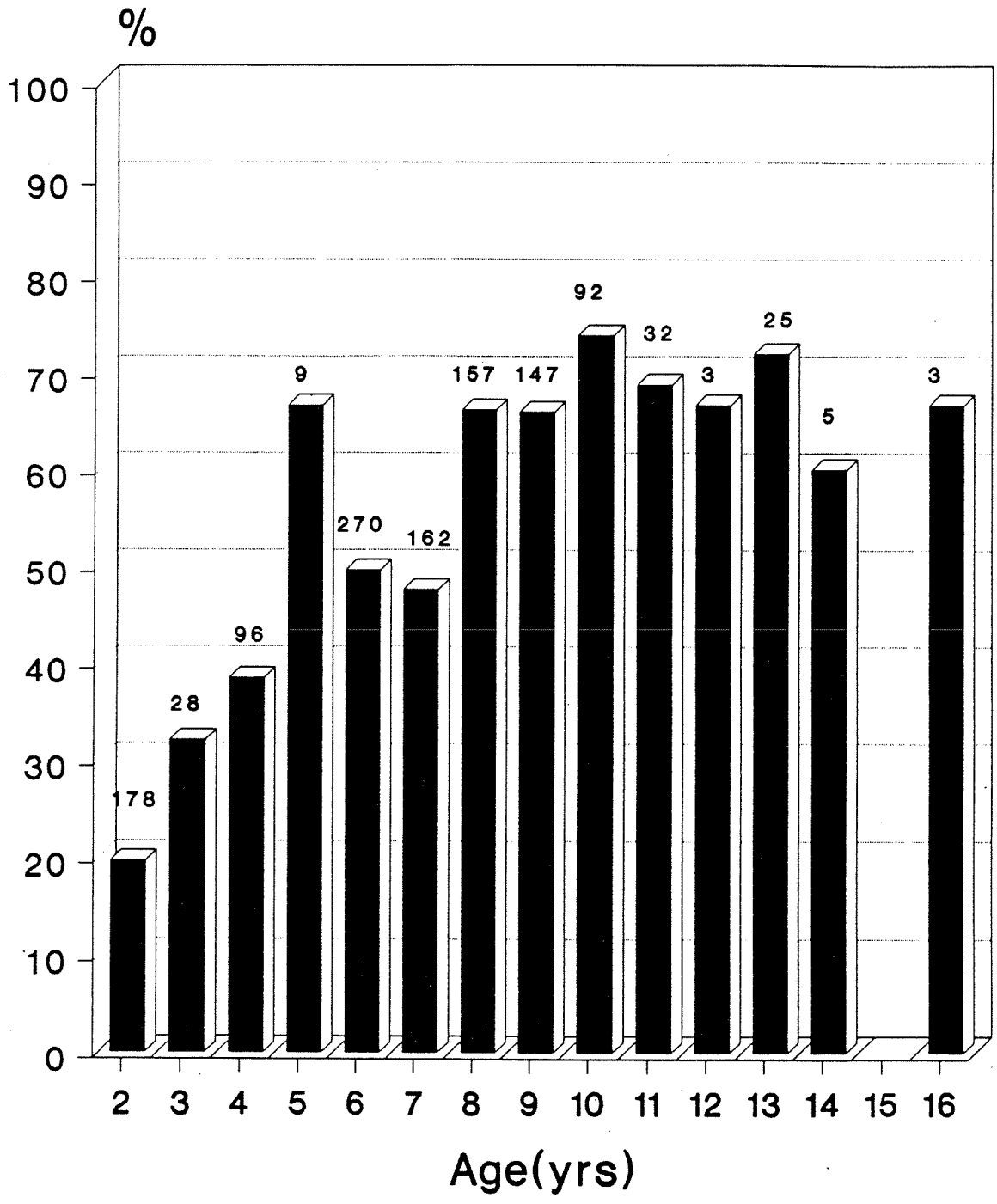


Figure 13. *Kudoa paniformis* prevalence at whiting age, 1986-88 combined.

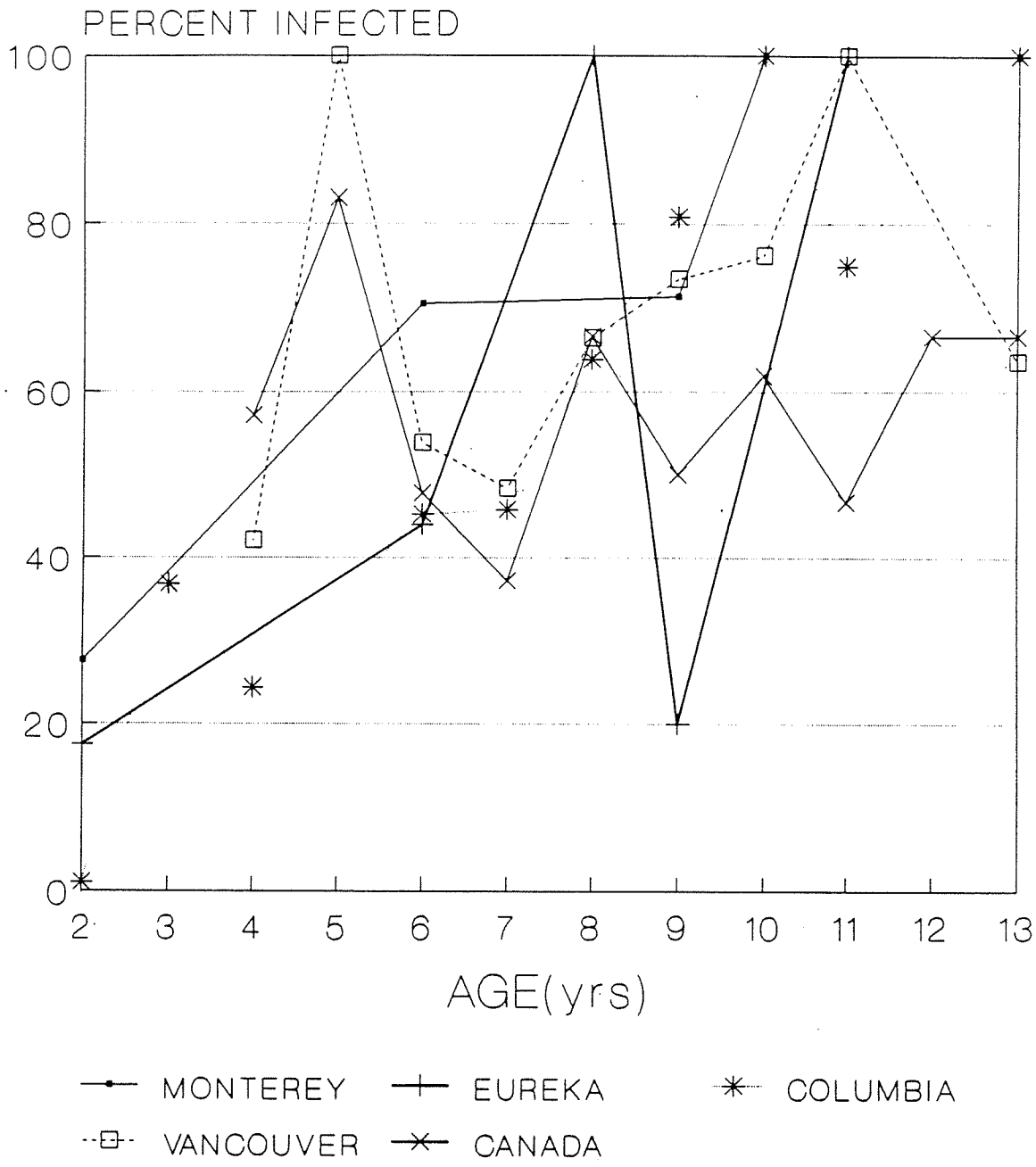


Figure 14. *Kudoa paniformis* prevalence by area, 1986-88 combined.

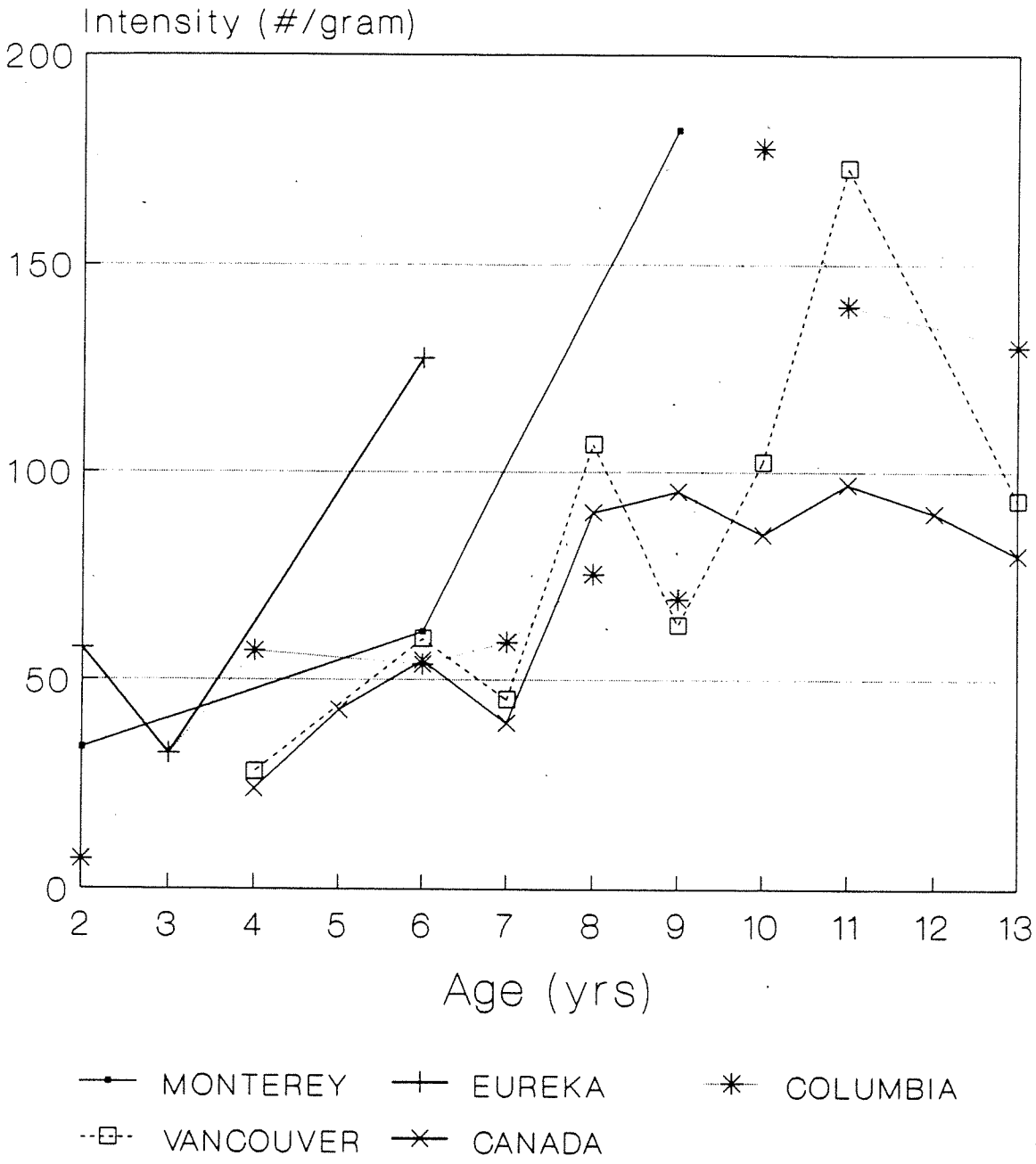


Figure 15. *Kudoa paniformis* mean intensity by area 1986-88 combined.

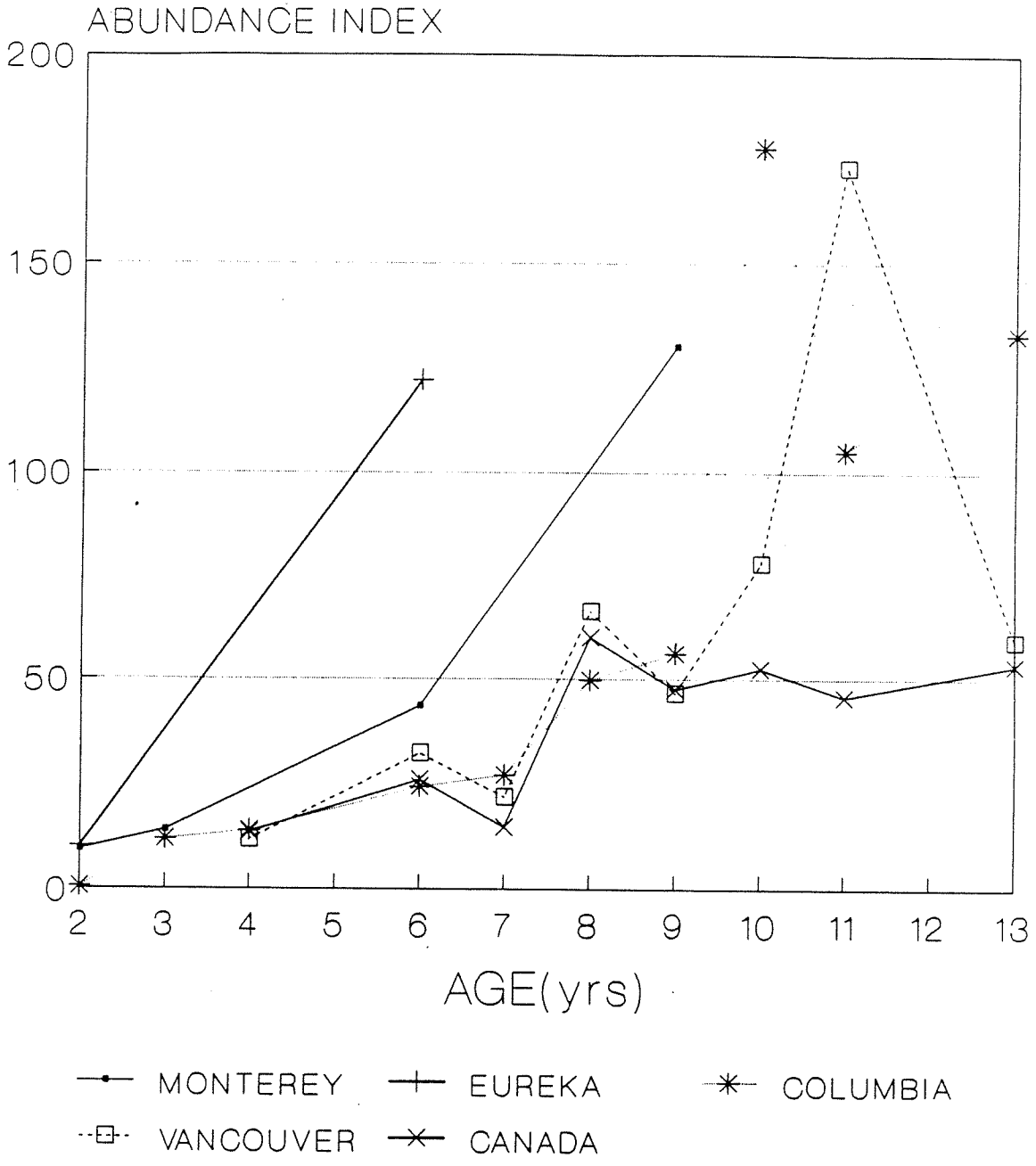


Figure 16. *Kudoa paniformis* relative abundance, 1986-88 combined.

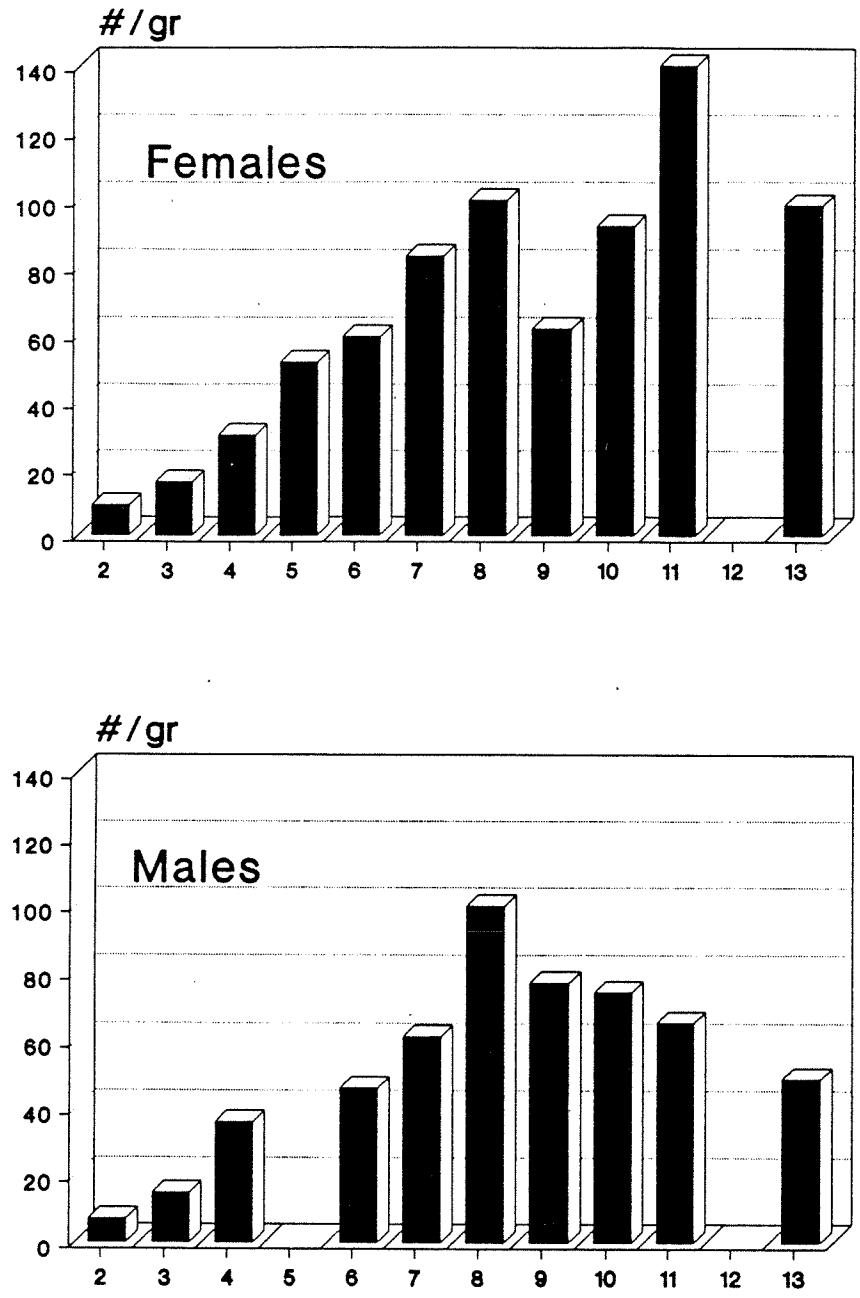


Figure 17. *Kudoa paniformis* intensity with whiting sex and age.

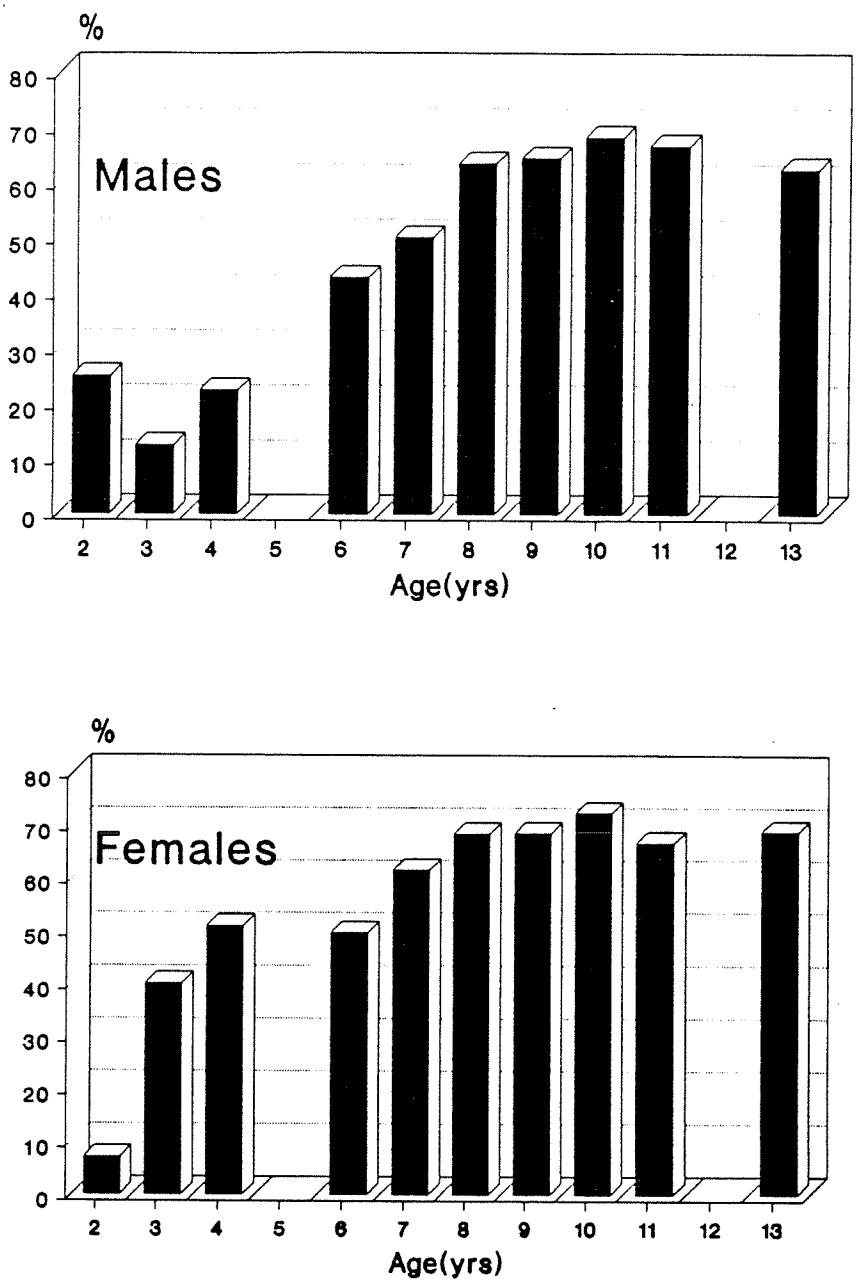


Figure 18. *Kudoa paniformis* prevalence with whiting sex and age.

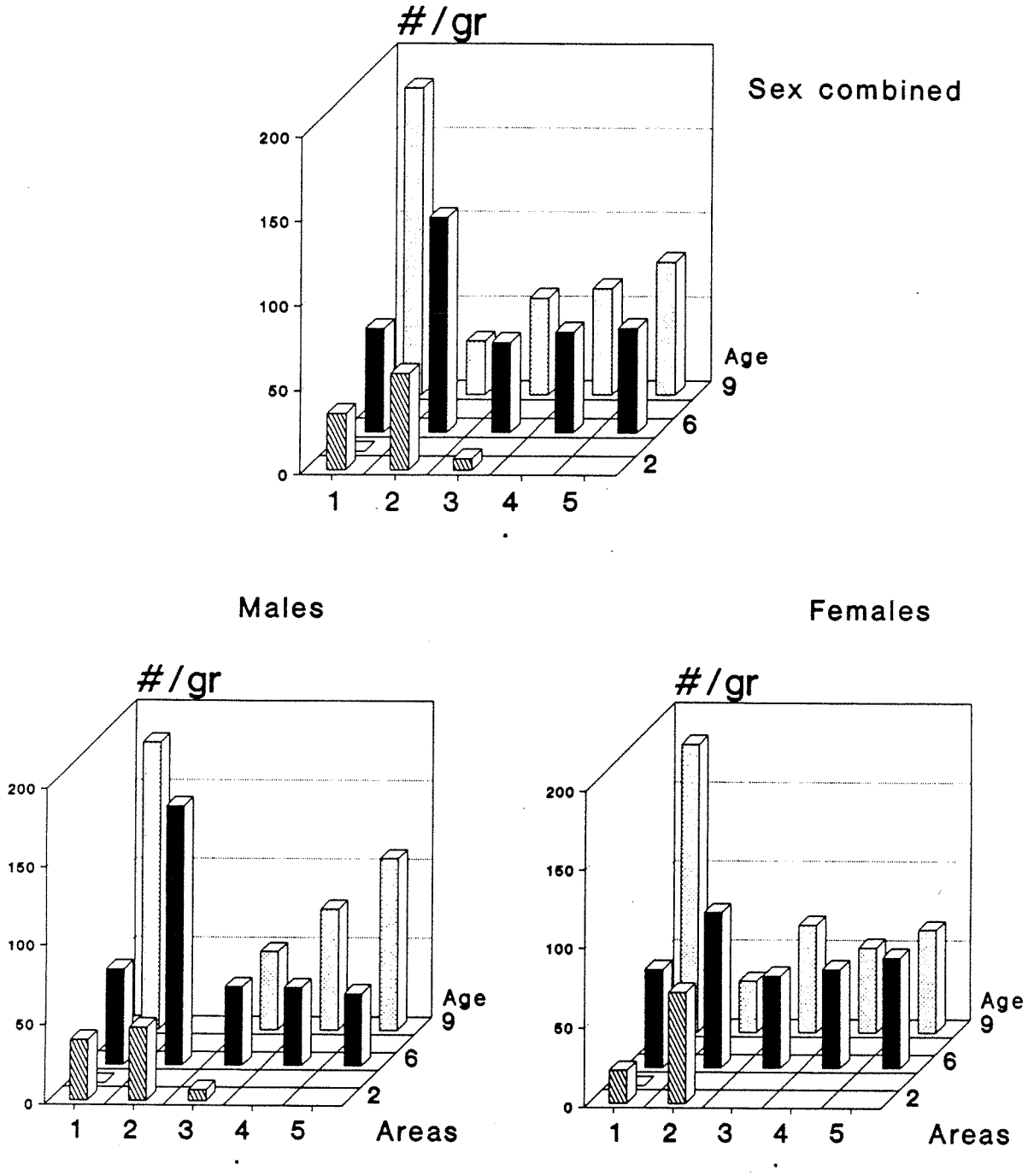


Figure 19. *K.paniformis* intensity by area and whiting age and sex for 1986.

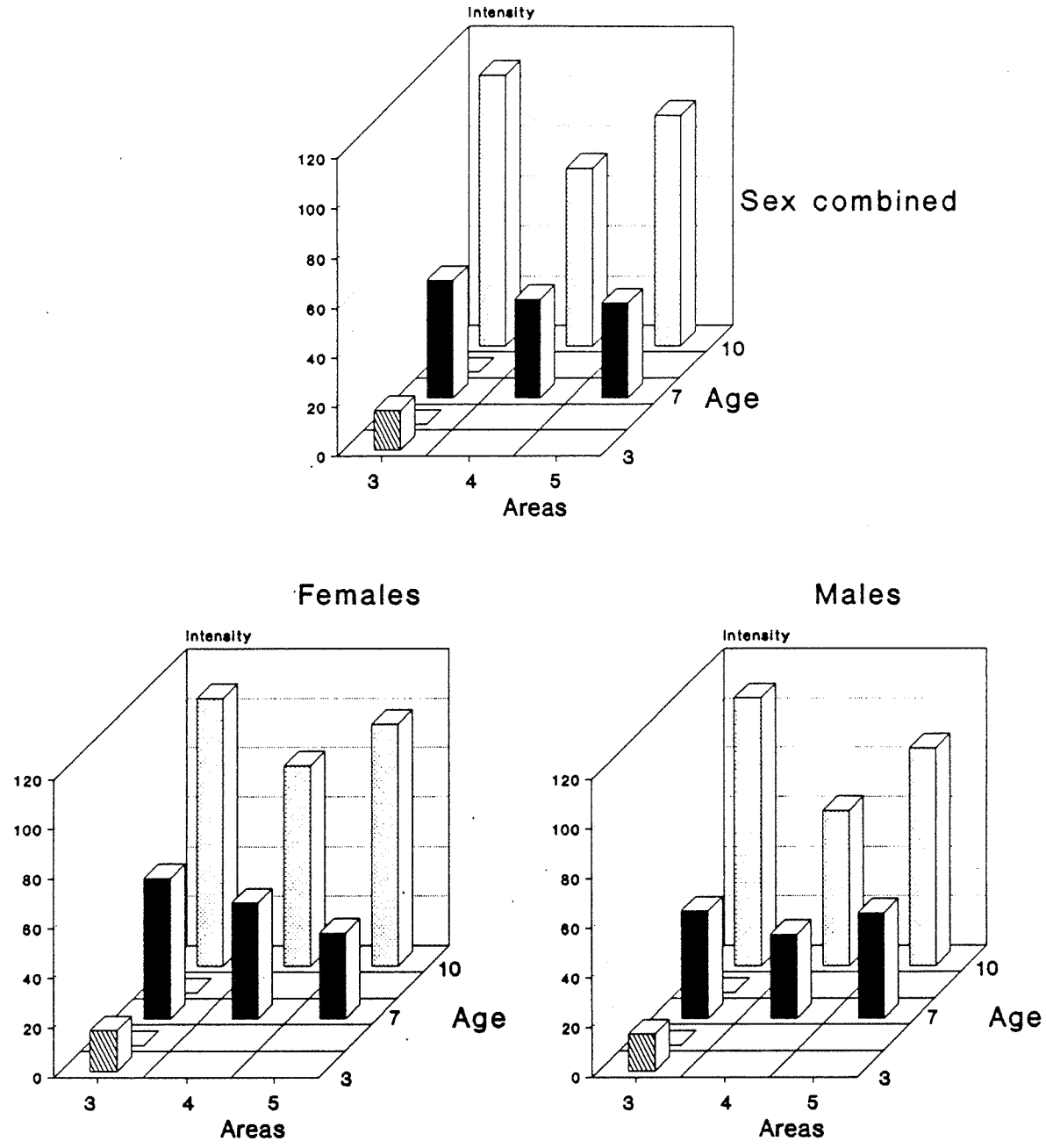


Figure 20. *K. paniformis* intensity by area and whiting age and sex for 1987.

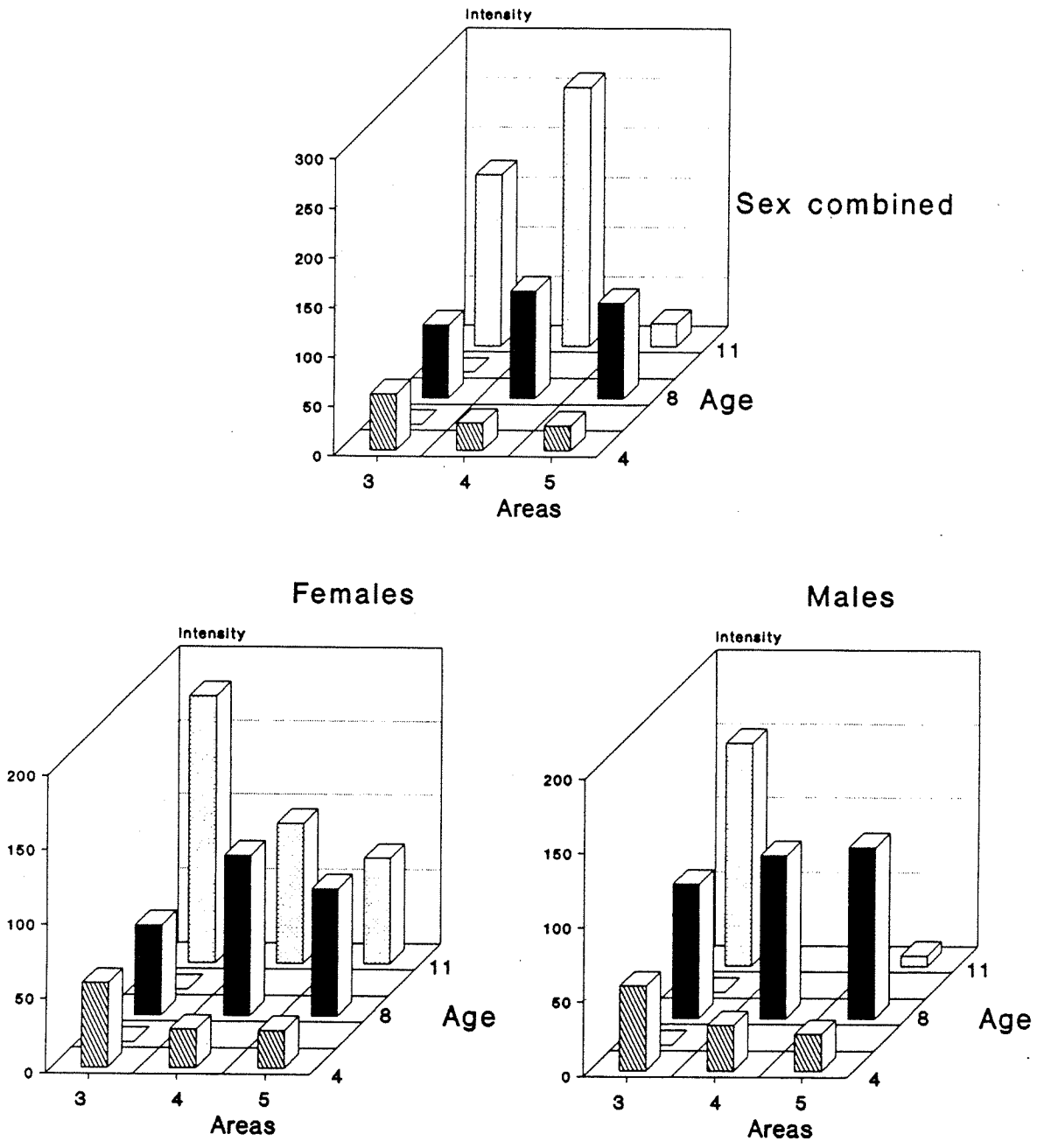


Figure 21. *K. paniformis* intensity by area and whiting age and sex for 1988.

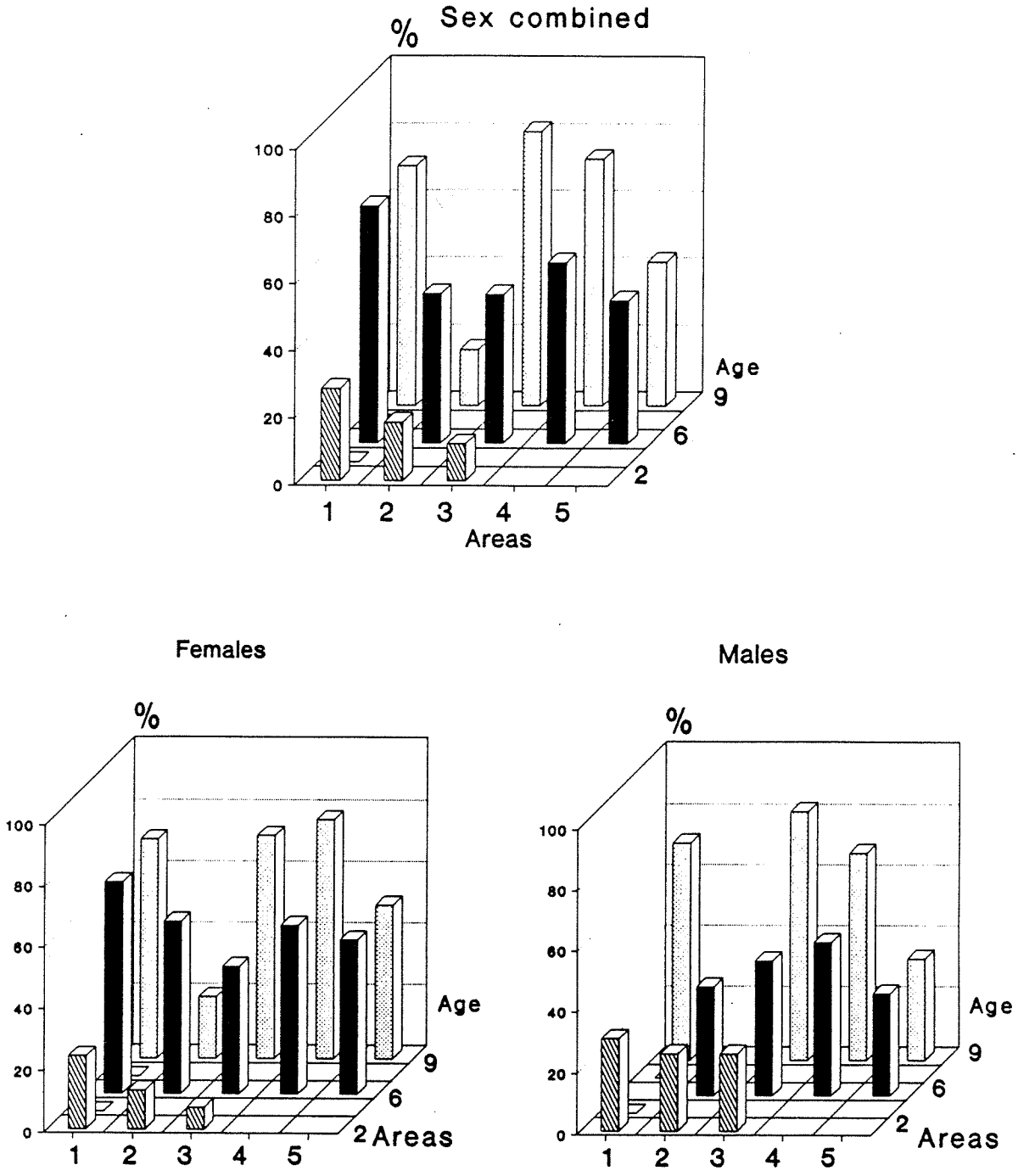


Figure 22. *K. paniformis* prevalence by area and whiting age and sex for 1986.

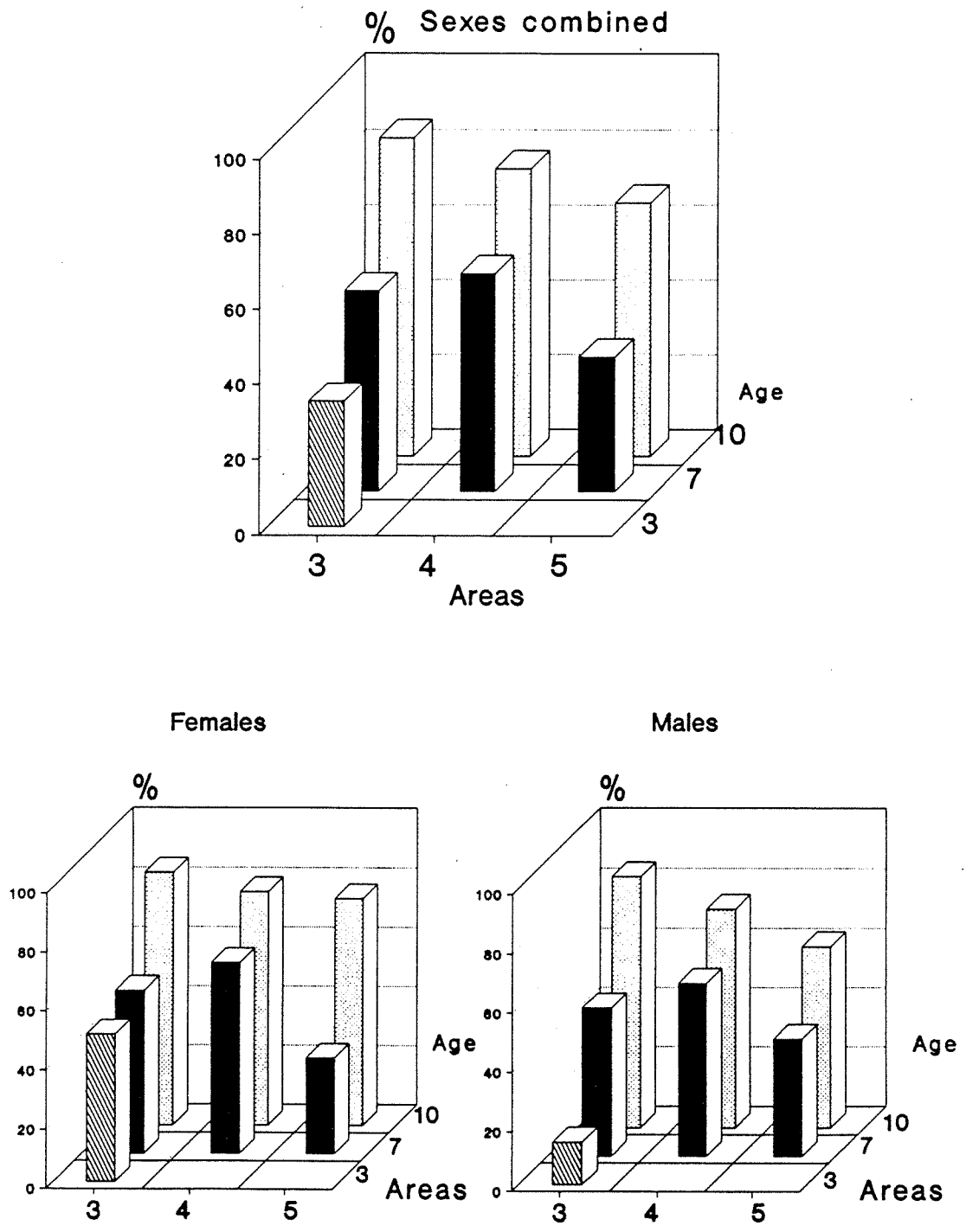


Figure 23. *K. paniformis* prevalence by area and whiting age and sex for 1987.

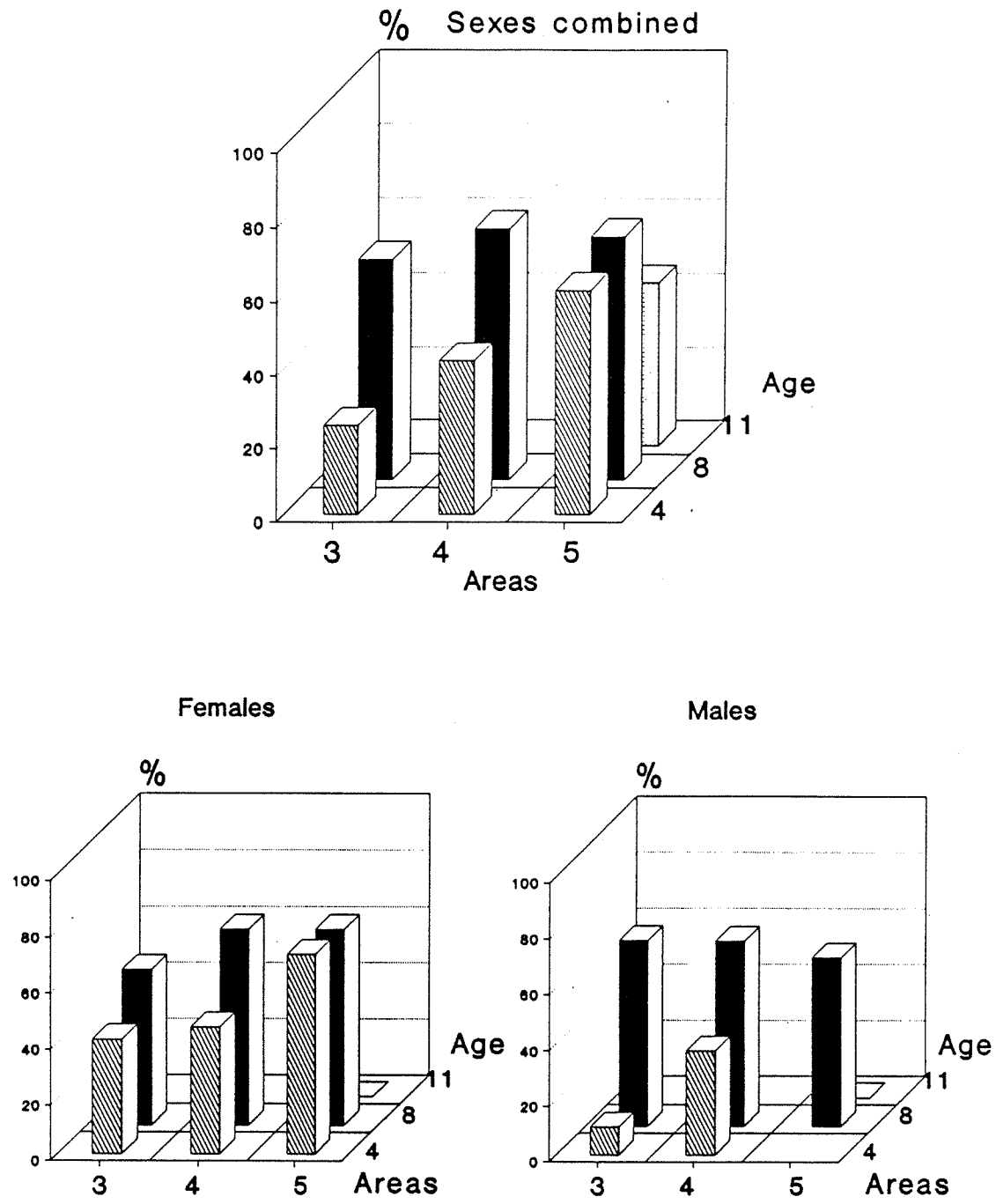


Figure 24. *K. paniformis* prevalence by area and whiting age and sex for 1988.

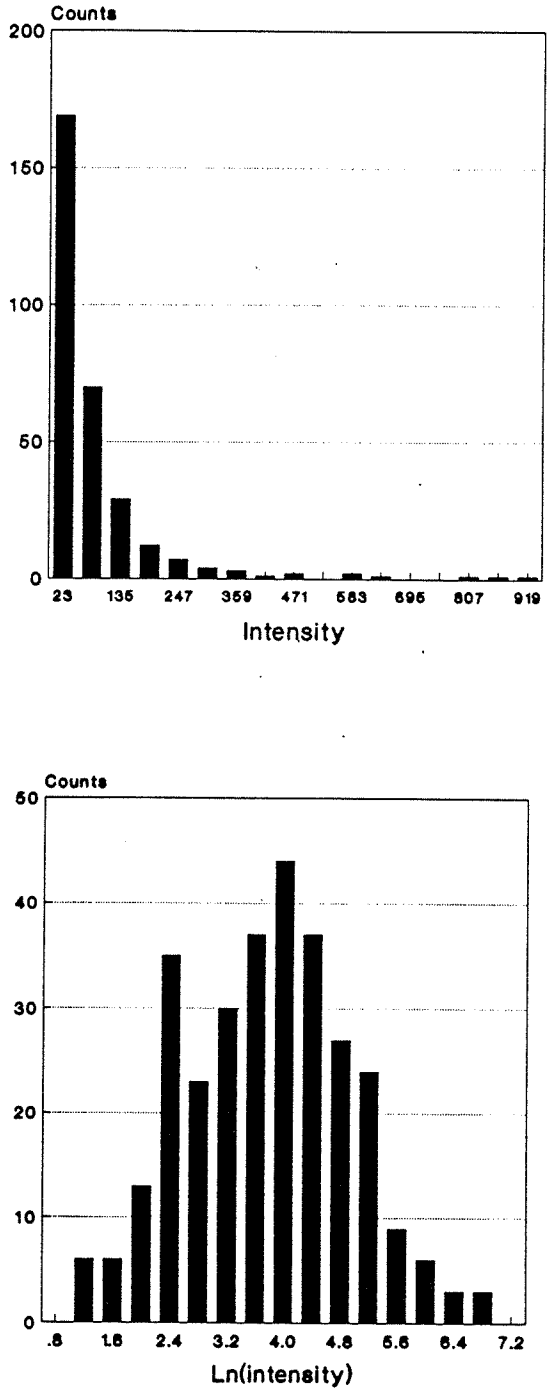


Figure 25. Frequency distribution of (a) *K. paniformis* intensity and (b) logtransformed intensity.

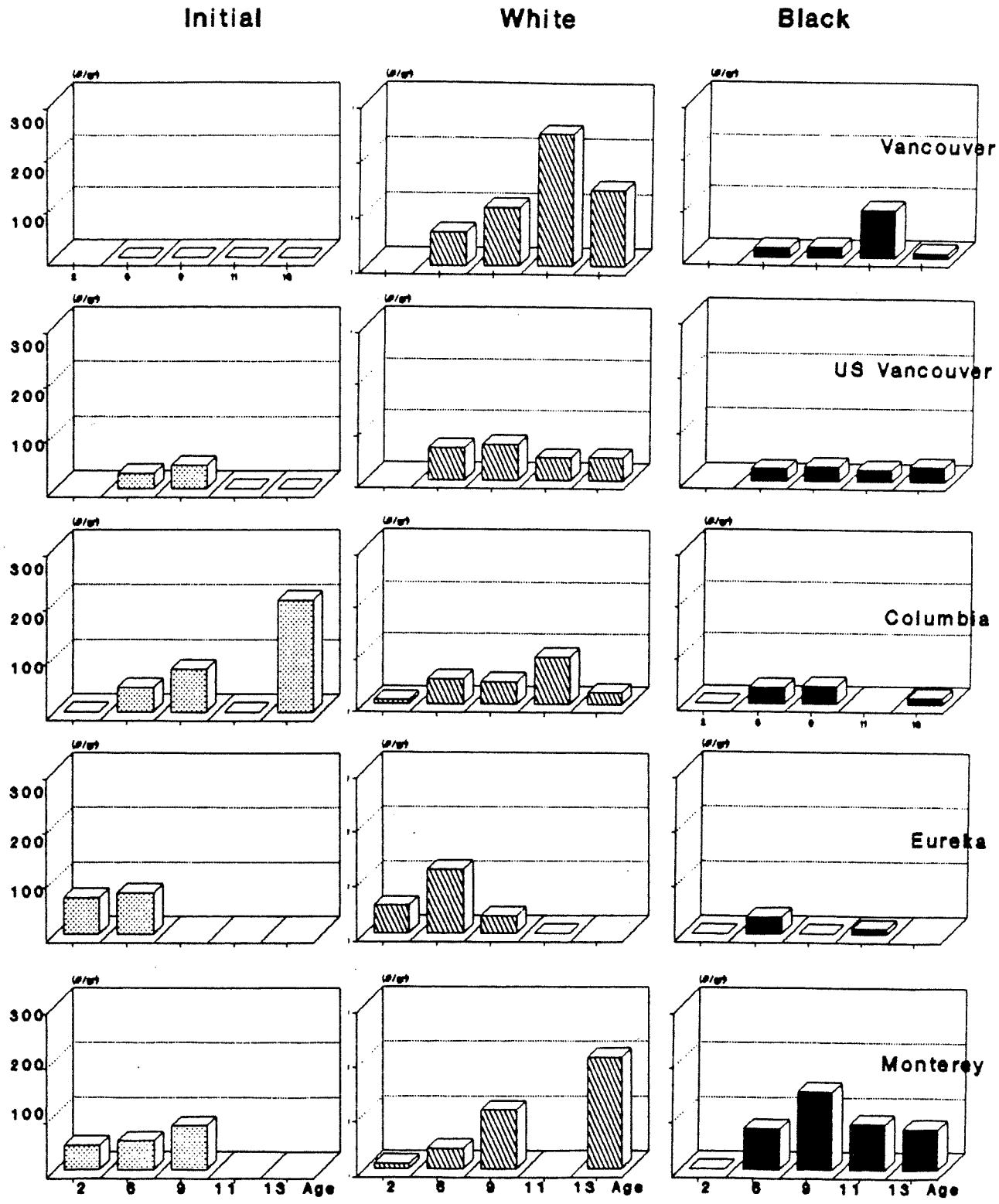


Figure 26. Pseudocyst stages by whiting age and area.

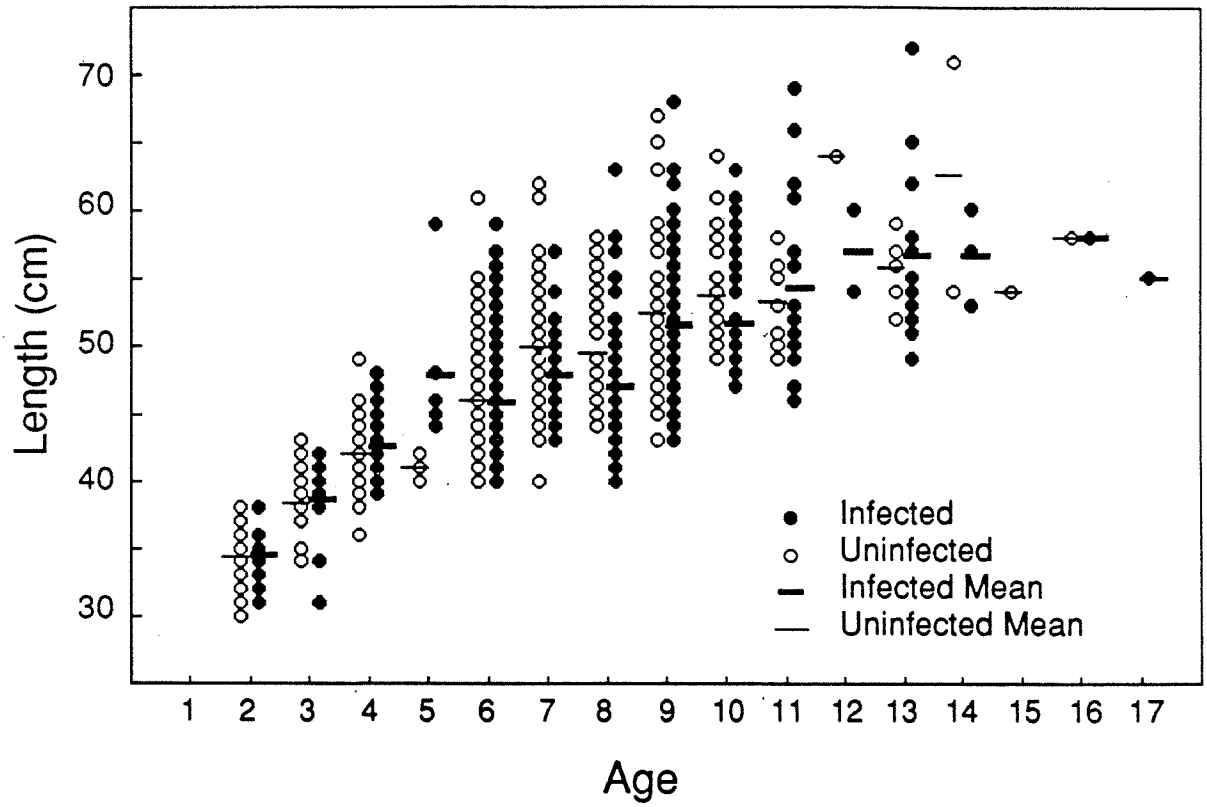


Figure 27. Length at age of infected and uninfected whiting.

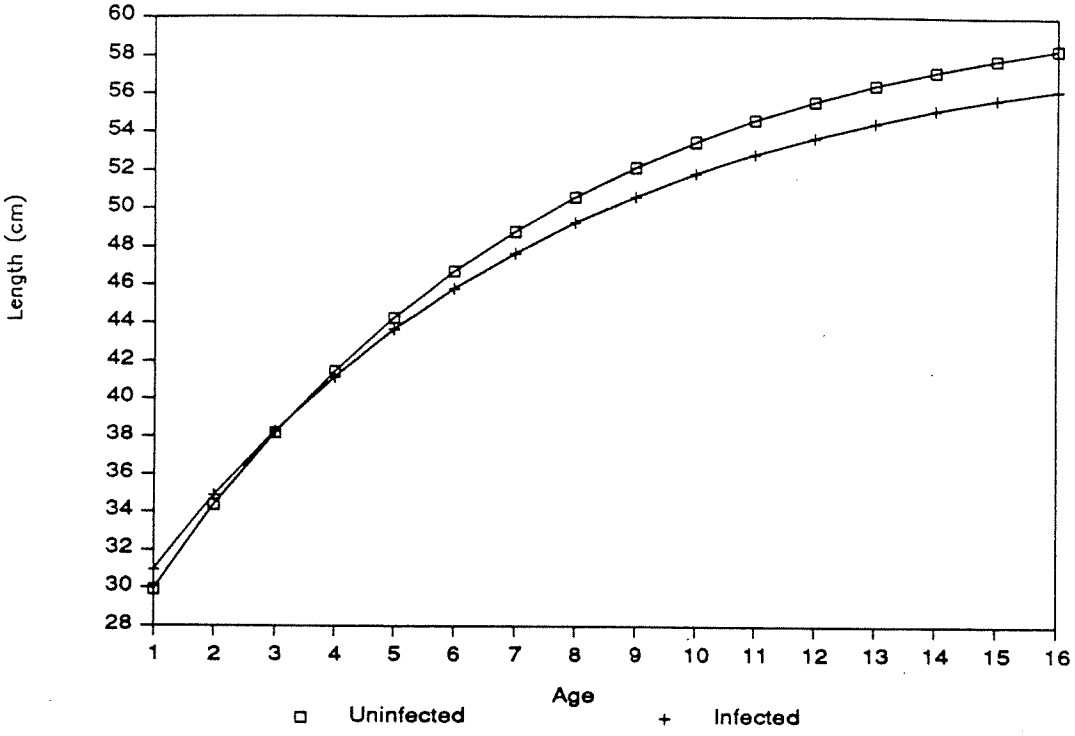


Figure 28. Von Bertalanffy growth curves for infected and uninfected whiting.

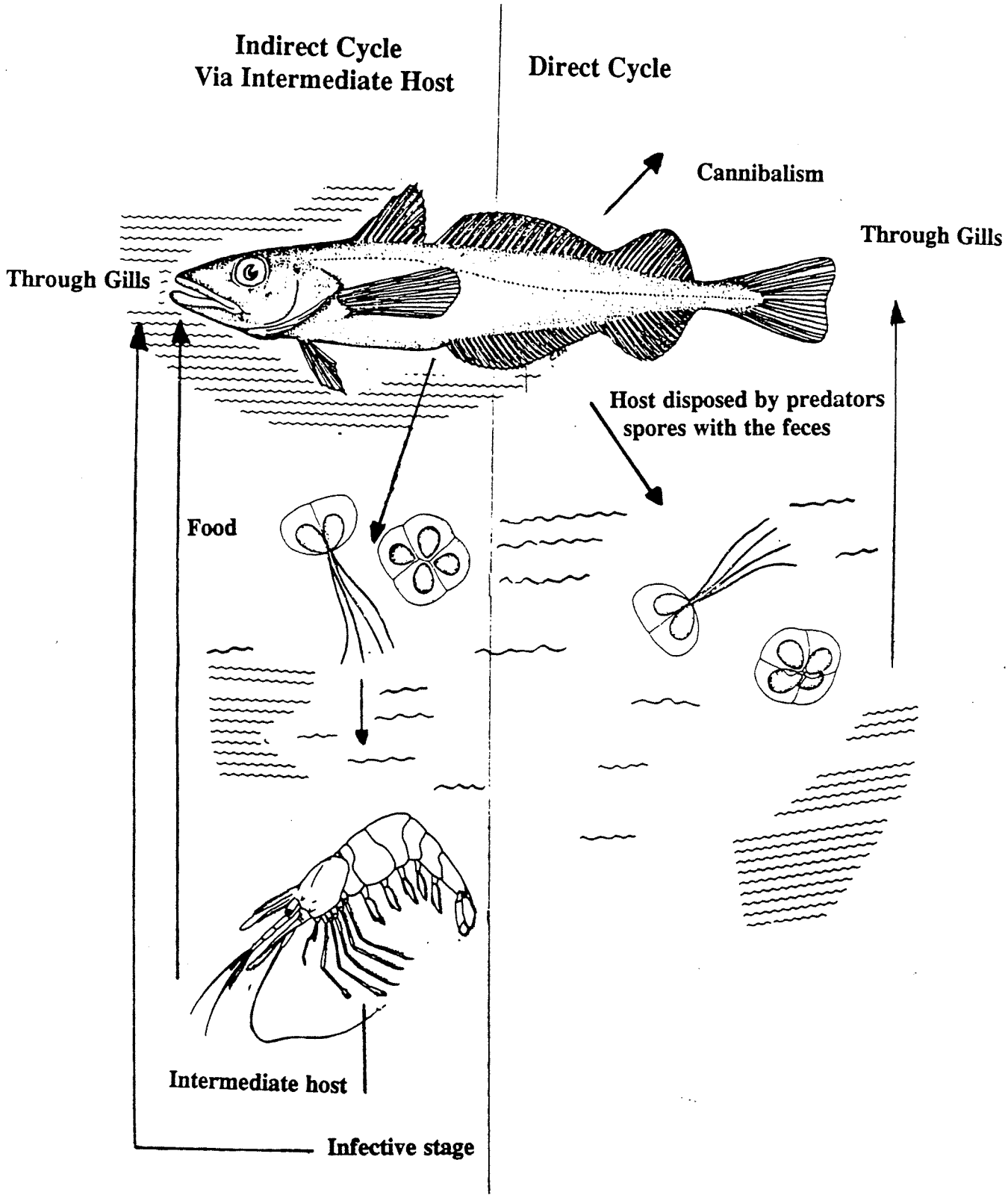


Figure 29. *Kudoa paniformis* life cycle.

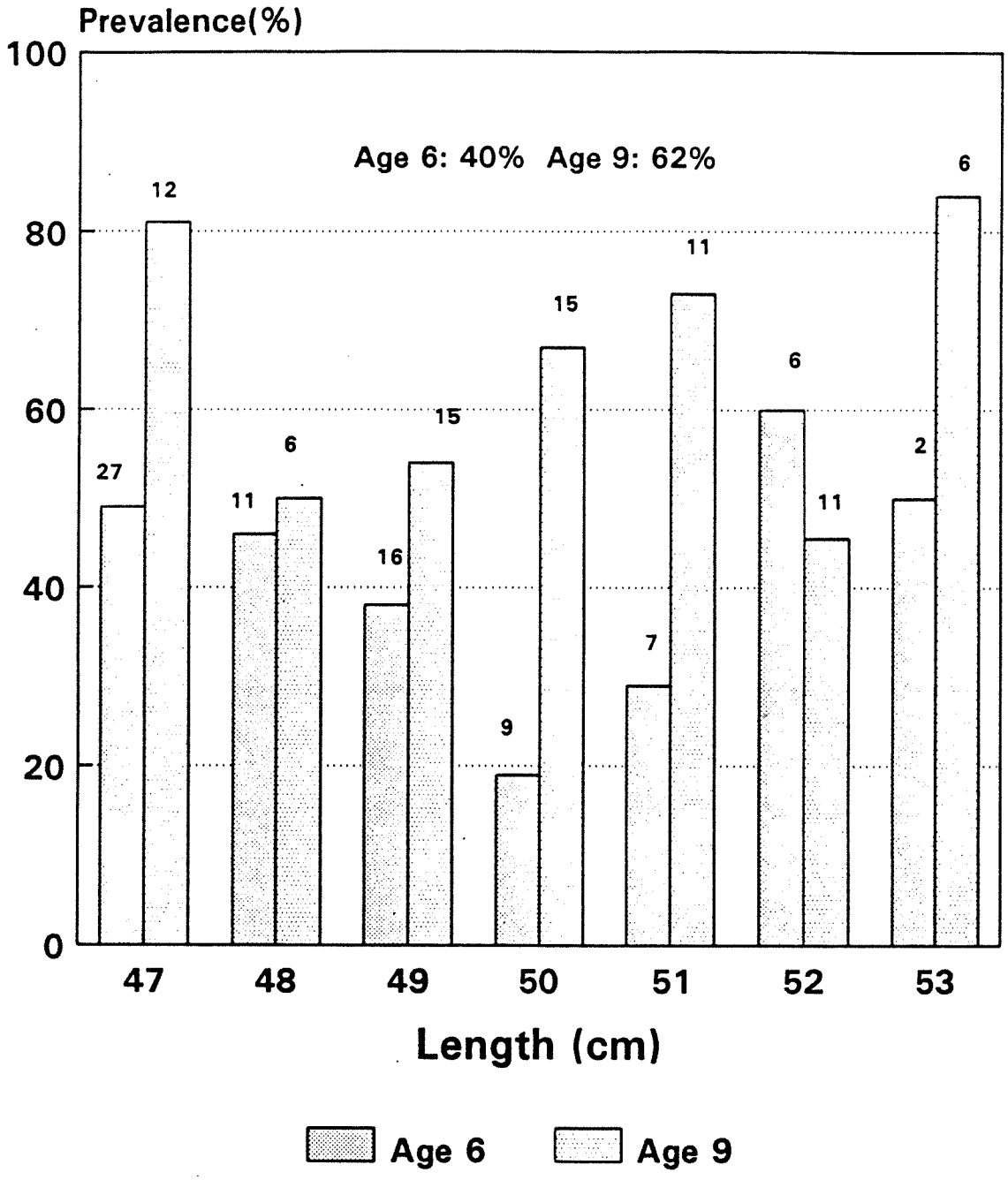


Figure 30. *Kudoa paniformis* prevalence for a range of length of whiting ages 6 and 9.

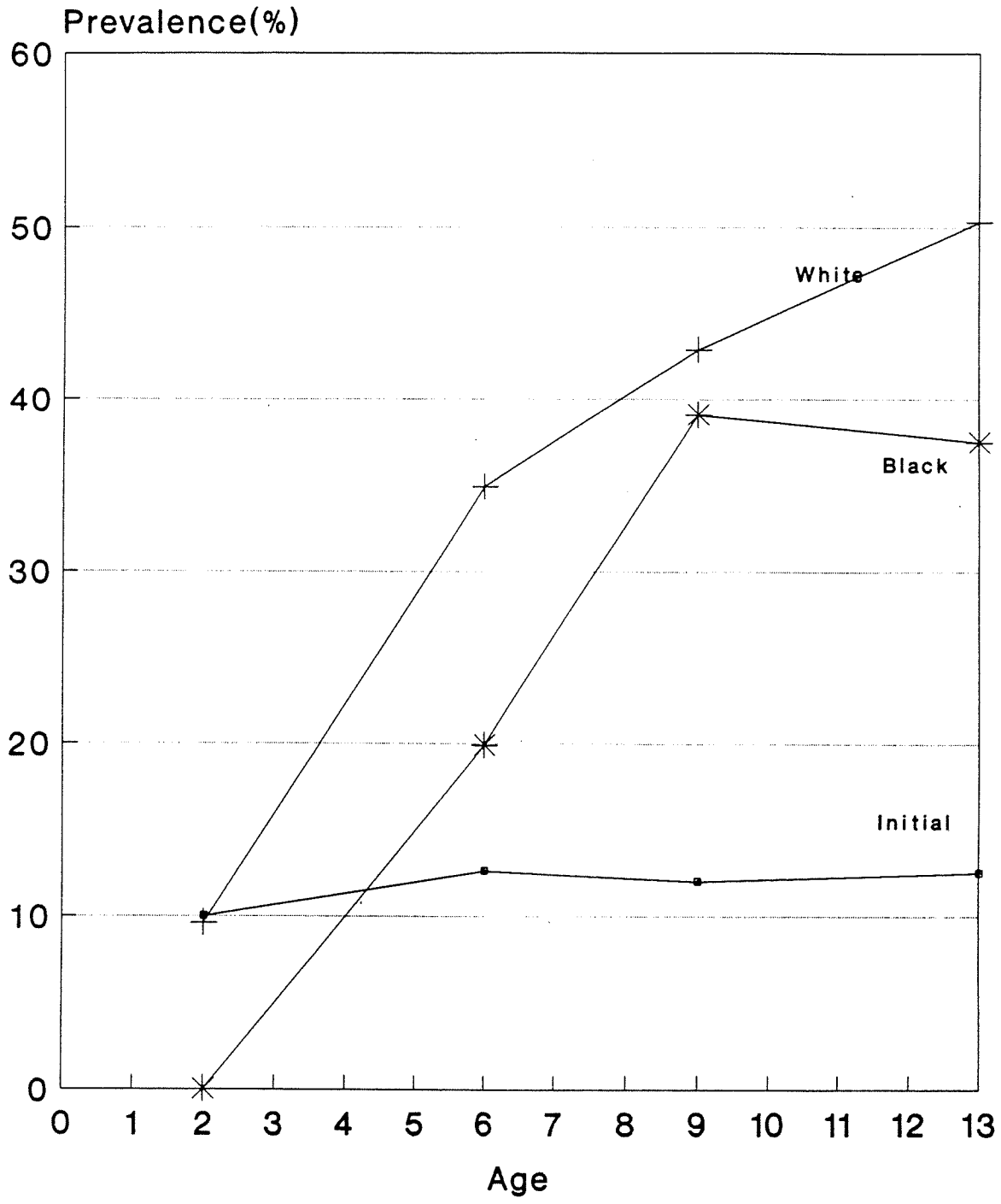


Figure 31. Prevalence of initial, white and black pseudocysts.

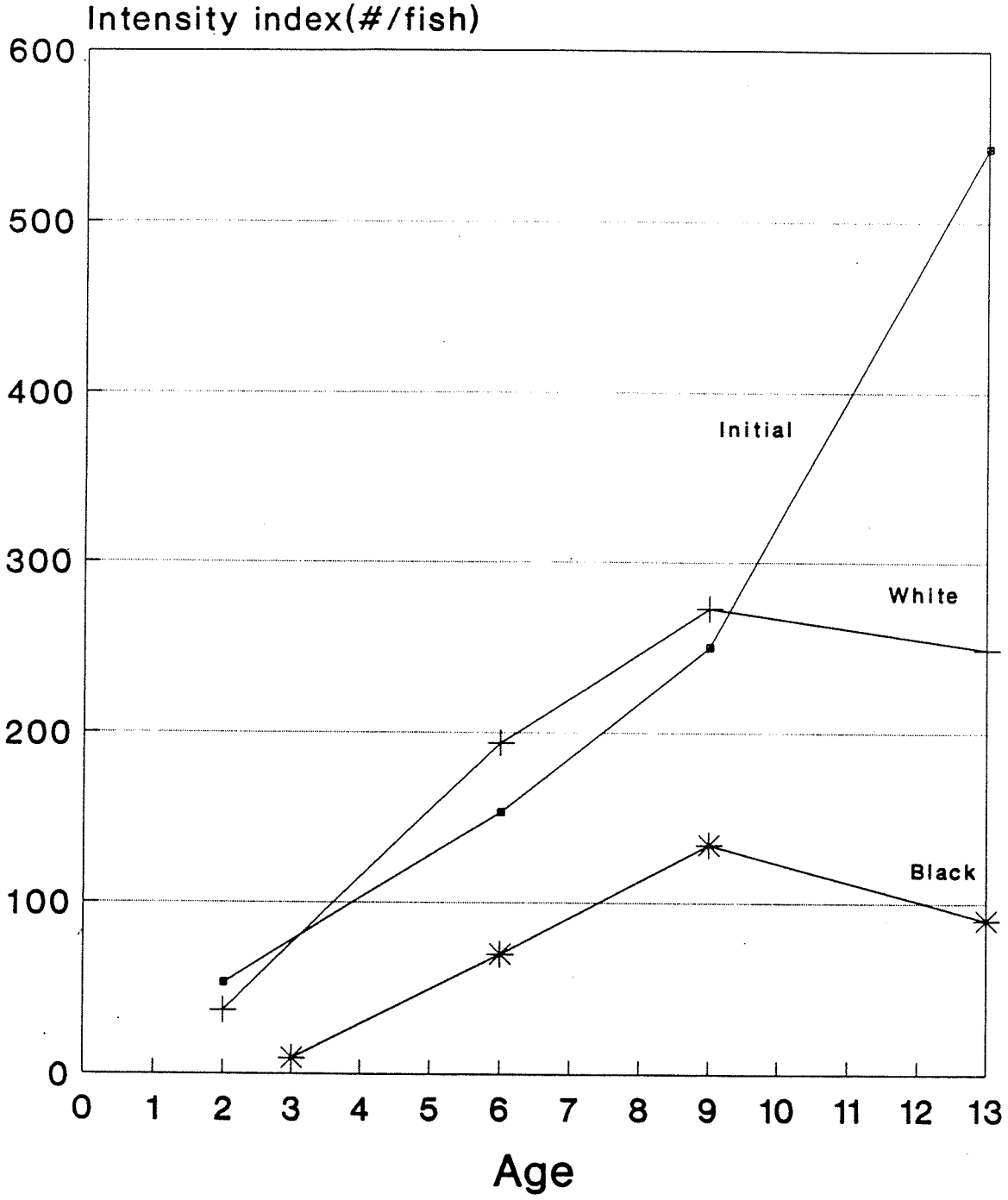


Figure 32. Intensity of initial, white and black pseudocysts.

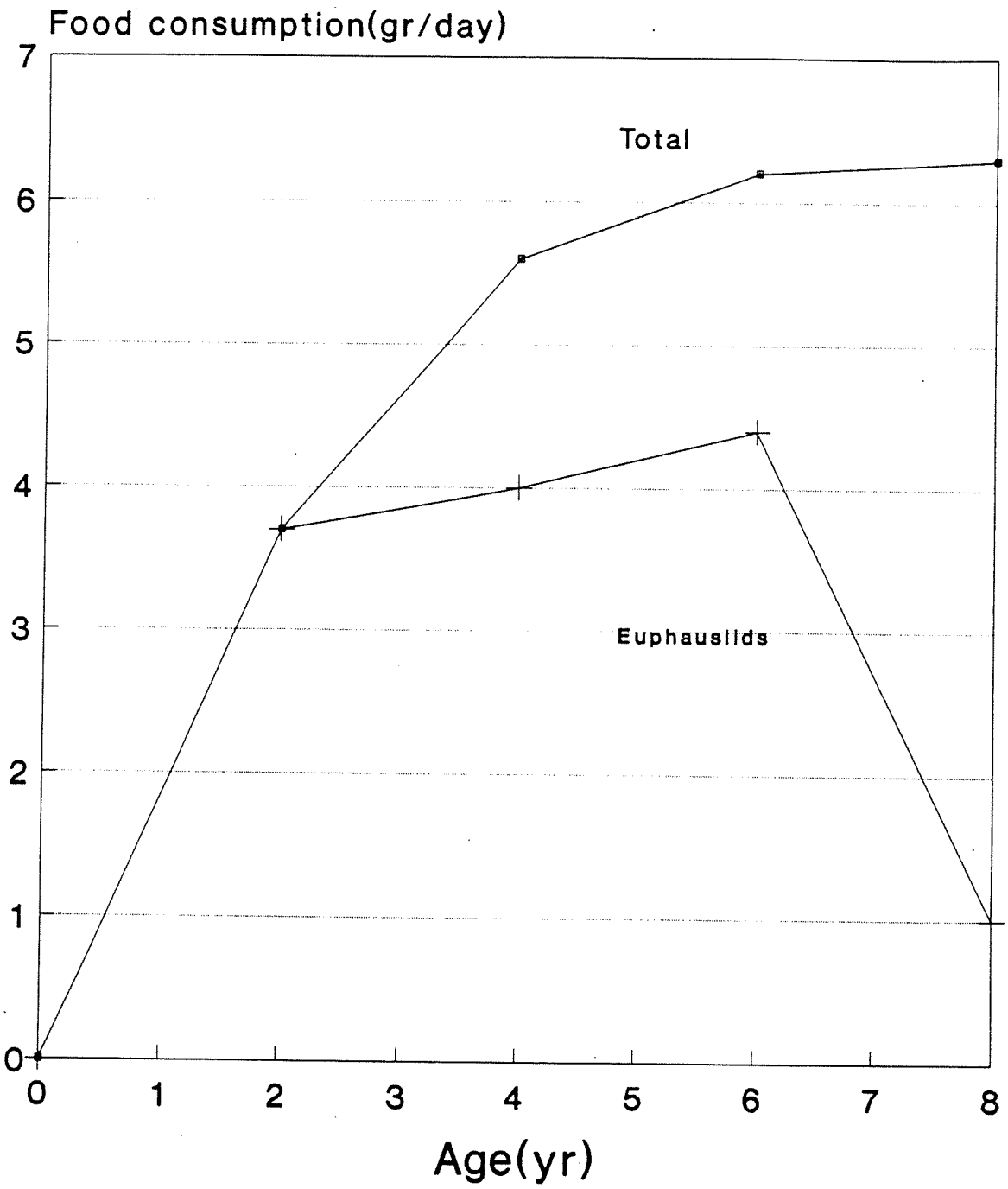


Figure 33. Pacific whiting at age daily consumption and euphausiid consumption in Monterey, 1986.

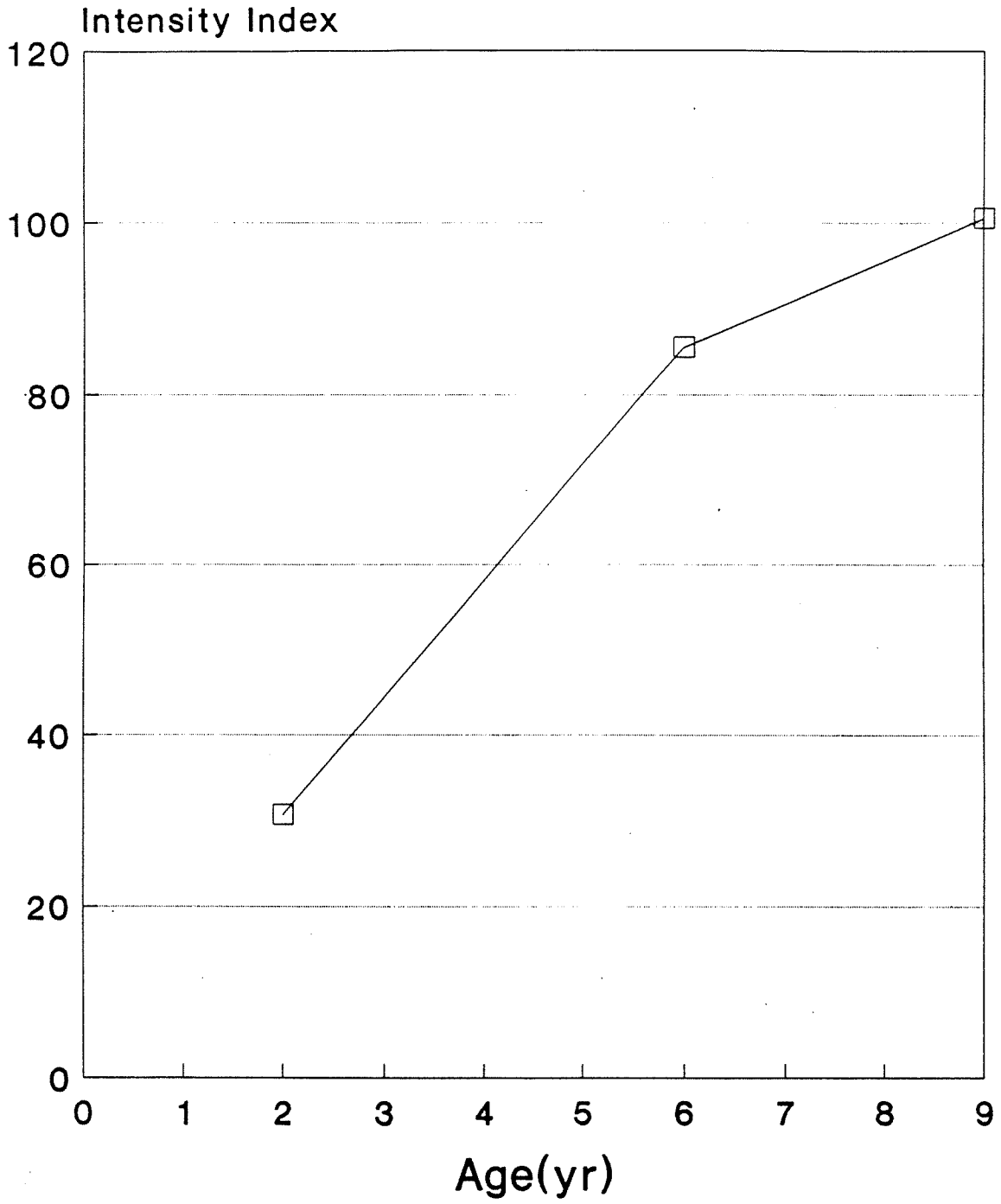


Figure 34. Initial pseudocyst intensity in Monterey 1986 with whiting age.

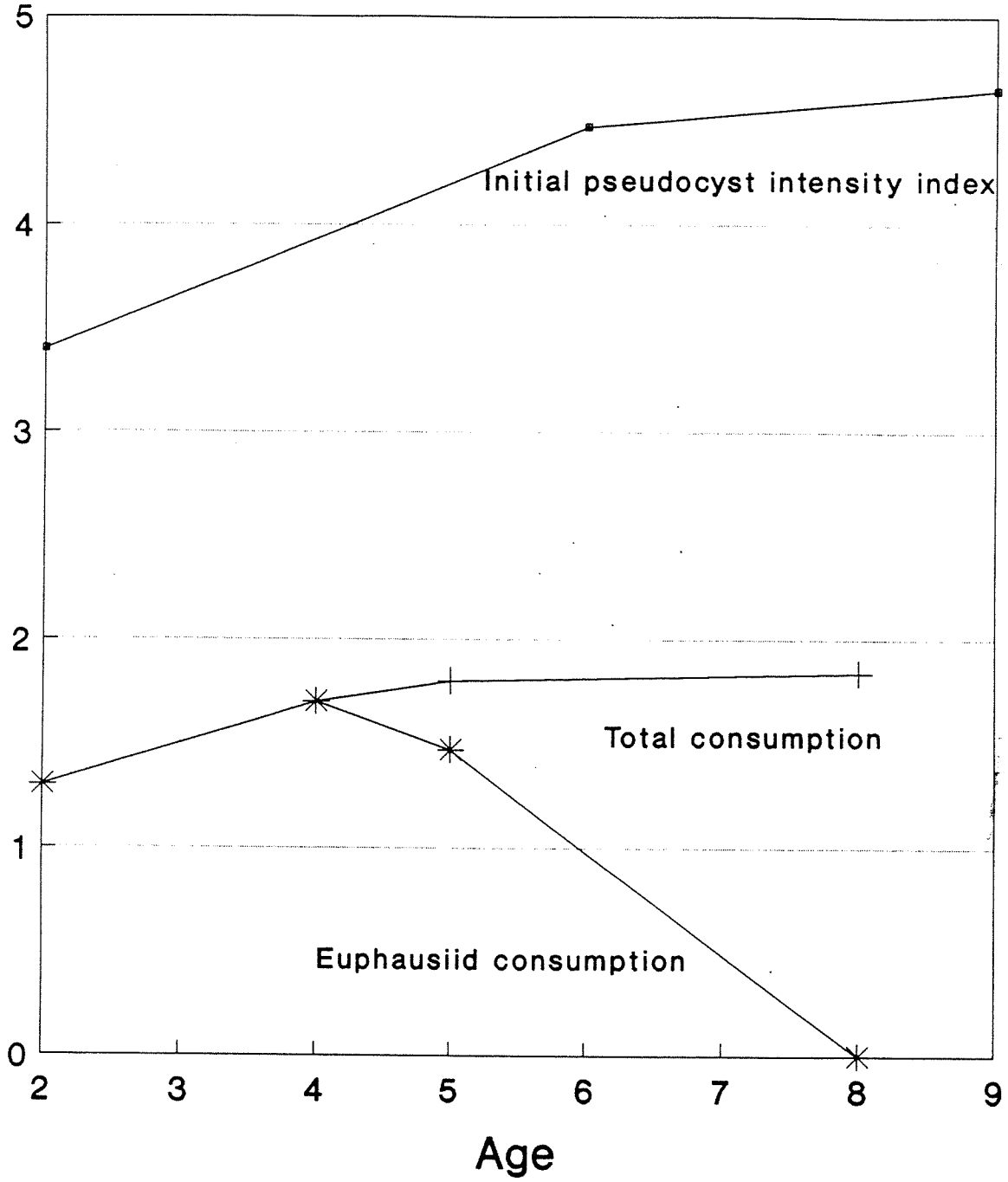


Figure 35. Relationship between parasite log(intensity) and whiting total consumption and euphausiid consumption.

Figure 36. Selectivity curve.

TABLES

Table 1. Number of whiting sampled for parasitological analysis by year and by International North Pacific Fisheries Commission (INPFC) areas.

	Monterey	Eureka	Columbia	U.S. Vancouver	Canada
1986	107	173	119	151	115
1987	0	0	60	90	120
1988	0	0	60	90	120

Table 2. Number of samples for parasitological analysis by INPFC area by year.

	1986				
Age	Monterey	Eureka	Columbia	U.S. Vancouver	Canada
2	58	103	17	-	-
3	2	6	1	-	-
4	-	-	-	-	3
5	-	-	-	-	3
6	17	56	70	78	40
7	-	-	2	2	7
8	-	1	-	3	9
9	28	22	49	28	-
10	-	-	1	4	7
11	1	1	2	3	5
12	-	-	-	-	2
13	1	-	4	11	8
14	-	-	-	-	2

	1987		
Age	Columbia	U.S. Vancouver	Canada
3	18	-	-
6	3	-	3
7	22	56	67
8	1	-	4
9	3	-	7
10	11	34	33
11	1	-	1
12	-	-	1
13	-	-	1
14	-	1	1
16	1	-	1
17	1	-	1

	1988		
Age	Columbia	U.S. Vancouver	Canada
4	37	38	18
5	2	1	3
6	-	-	3
7	-	2	4
8	15	44	80
9	1	-	3
10	-	-	2
11	5	4	9
15	-	1	-

Table 3. Distribution of *K. paniformis* by INPFC area.

	Prevalence (%)	Intensity (#/g)	Relative abundance (#/g)
1986			
Monterey	47.1	102.1±131.9	4.8
Eureka	27.1	116.3±147.1	3.2
Columbia	45.9	47.4±131.8	2.2
U.S.Vancouver	62.3	68.8±105.0	3.8
Canada	42.5	79.8±111.4	3.5
1987			
Columbia	57.4	85.9±110.1	4.9
U.S.Vancouver	59.3	54.4±53.3	3.2
Canada	48.8	9.4±94.2	3.8
1988			
Columbia	36.6	84.9±162.7	3.1
U.S.Vancouver	58.8	96.2±196.7	5.7
Canada	66.4	74.8±154.9	4.9

Table 4. Distribution of the parasite with age of the host.

Age	1986	1987	1988
	Intensity (counts/gram)		
2	45.3 (±39.7)	-	-
3	52.0 (±65.8)	16.3 (±9.9)	-
4	-	-	34.4 (±37.8)
5	28.5 (±30.4)	-	67.2 (±37.2)
6	72.2 (±101.6)	-	54.2 (±40.1)
7	87.8 (±75.4)	40.6 (±30.2)	58.3 (±69.4)
8	50.3 (±53.9)	59.0 (±22.3)	98.6 (±194.3)
9	91.1 (±115.3)	169.6 (±76.8)	-
10	98.5 (±110.1)	85.9 (±74.8)	-
11	115.8 (±148.9)	-	152.3 (±188.0)
13	97.0 (±100.9)	-	-
	Prevalence (%)		
2	19.7	-	-
3	30	33.3	-
4	33.3	-	38.7
5	39.6	-	66.7
6	48.7	66.7	-
7	45.5	41.4	66.7
8	55.5	80.0	66.2
9	65.4	70.0	75.0
10	58.3	75.3	-
11	48.4	-	56.7
13	49.5	-	-

Table 5. Intensity of *K. paniformis* in female and male Pacific whiting.

	Males (counts/gram)	Females (counts/gram)
1986	82.5 (n = 120)	82.3(n = 183)
All years	81.3(n = 255)	79.2(n = 352)

Table 6. Prevalence of *K. paniformis* among female and male Pacific whiting.

	Males (%)	Females (%)
1986	43.8(n=274)	46.9(n=390)
All years	47.9(n=532)	52.0(n=677)

Table 7. Distribution of parasite intensity with whiting age by INPFC area.

	1986				
Age	Eureka	Monterey	Columbia	U.S. Vancouver	Canada
2	33.7(±36.3)	57.6(±40.4)	-	-	-
3	14.0(±4.24)	-	-	-	-
6	61.7(±49.4)	127.4(±191.7)	53.7(±65.1)	59.9(±55.5)	62.1(±51.4)
9	182.1(±170.9)	-	57.4(±44.7)	63.2(±79.3)	79.0(±101.8)
13	-	-	130.3(±139.2)	53.1(±41.9)	87.0(±80.5)

	1987		
Age	Columbia	U.S. Vancouver	Canada
3	16.3 (± 9.9)	-	-
6	54.5 (±48.8)	-	54.0 (+49.7)
7	47.7 (±25.9)	40.1(+24.1)	38.5 (+37.7)
9	142.0(+106.5)	-	190.3 (+53.9)
10	108.0 (±82.3)	71.1(+69.3)	92.5 (+74.8)

	1988		
Age	Columbia	U.S. Vancouver	Canada
4	57.1 (±58.2)	27.8 (±24.4)	25.5 (±28.1)
8	73.9 (±76.2)	108.9 (+233.9)	96.9 (+185.6)
11	172.5(+124.2)	61.0 (+275.3)	23.3 (±31.9)

Table 8. Distribution of parasite prevalence with whiting age by INPFC area

	Year 1986				
Age	Monterey	Eureka	Columbia	U.S. Vancouver	Canada
2	27.6	17.5	5.9	-	-
3	-	-	38.1	-	0
4	-	-	-	-	33.3
5	-	-	-	-	66.7
6	70.6	44.6	44.3	53.6	42.5
7	-	-	100.0	0.0	42.9
8	-	100.0	-	33.3	66.7
9	71.4	16.7	81.8	73.5	42.9
10	100.0	-	100.0	75.0	42.9
11	100.0	100.0	50.0	100.0	40.0
13	100.0	-	100.0	63.6	62.5

	Year 1987		
Age	Columbia	U.S. Vancouver	Canada
3	33.3	-	-
7	54.5	58.2	35.8
10	84.9	68.8	67.7

	Year 1988		
Age	Columbia	U.S. Vancouver	Canada
4	24.3	42.1	61.1
8	60.0	68.2	66.2
11	60.1	100.0	44.4

Table 9. Parasite intensity among male and female whiting in Columbia, U.S.Vancouver and Canada in the three-year study.

Age	Males (counts/g)		Females (counts/g)	
3	71.5	(±79.9)	16.6	(±11.1)
4	36.0	(±4.5)	32.9	(±39.1)
5	81.0	(±3.8)	41.0	(±31.8)
6	45.2	(±9.1)	61.8	(±62.5)
7	43.3	(±35.9)	86.2	(±186.4)
9	80.1	(±101.3)	67.4	(±59.8)
10	103.0	(±156.8)	115.3	(±162.2)
11	143.1	(±205.4)	131.4	(±147.6)
13	48.8	(±44.8)	93.9	(±93.5)

Table 10. Prevalence at age in female and male whiting in Columbia, U.S. Vancouver and Canada in the three-year study.

Age	Male (%)	Female (%)
2	25.0	-
3	22.2	40.0
4	22.5	50.0
5	66.7	66.7
6	44.8	51.6
7	48.1	61.5
8	64.7	67.0
9	64.7	69.4
10	66.7	82.5
11	64.3	68.8
13	71.4	70.6

Table 11. ANOVA of *K. paniformis* intensity. Dependent variable = Ln(intensity); independent variables = 2 factors (area with 5 levels and sex with 2) and 1 covariate (age).

Source of variation	DF	MS	F	Probability of F
Age				
Slope	1	11.98	10.67	0.001
Intercept	1	179.03	159.54	0.000
Area	4	3.61	3.22	0.013
Sex	1	0.34	0.30	0.581
Area by sex	4	0.32	0.28	0.892
Error	246	1.12		

Table 12. ANOVA of *K. paniformis* intensity. Dependent variable = Ln(intensity); independent variables = 2 factors (area with 5 and sex with 2 levels) and 1 covariate (length).

Source of variation	DF	MS	F	Probability of F
Length				
Slope	1	7.05	5.69	0.018
Intercept	1	17.98	14.52	0.000
Area	4	3.58	2.89	0.023
Sex	1	1.58	1.27	0.260
Area by Sex	4	0.44	0.35	0.843
Error	246	1.24		

Table 13. Contrast analysis of intensity of *K. paniformis* among INPFC areas (1986).

Contrasted areas	Coefficient	Std.Err.	t-value	Sig. t
Monterey-Eureka	-0.1860314	0.22455	-8.28460	0.410
Monterey-Columbia	0.5644023	0.21353	2.64324	0.009
Monterey-U.S. Vancouver	0.3342076	0.20247	1.63225	0.100
Monterey-Canada	0.2095756	0.25720	0.81482	0.420
Eureka-Columbia	0.7504338	0.21353	2.64324	0.009
Eureka-U.S. Vancouver	0.5202391	0.22618	2.30016	0.022
Eureka-Canada	0.3956071	0.27354	1.44627	0.150
Columbia-U.S. Vancouver	-2.3019400	0.19787	-1.16340	0.250
Columbia-Canada	-0.3548300	0.25241	-1.40580	0.160
U.S. Vancouver-Canada	-0.1246300	0.24096	-0.51723	0.610

Table 14. ANOVA of *K. paniformis* intensity. Dependent variable = Ln (intensity); independent variables = 3 factors (year with 3 levels, area with 5, and sex with 2) and 1 covariate (age).

Source of variation	DF	MS	F	Probability of F
Age				
Slope	1	24.62	16.09	0.000
Intercept	1	285.59	186.66	0.000
Year	2	1.06	0.69	0.502
Area	2	4.73	3.09	0.046
Sex	1	0.28	0.19	0.667
Year by area	4	2.09	1.36	0.245
Year by sex	2	0.39	0.25	0.777
Area by sex	2	0.66	0.43	0.650
Year by area by sex	4	1.19	0.78	0.541
Error	488	1.53		

Table 15. ANOVA of *K. paniformis* intensity among areas by year. Dependent variable Ln (intensity); independent variables = 2 factors (area with 3 levels and sex with 2) and 1 covariate (age).

Source of variation	DF	MS	F	Probability of F
		1987		
Age				
Slope	1	16.44	17.75	0.000
Intercept	1	67.61	173.03	0.000
Area	2	2.10	1.13	0.325
Sex	1	0.45	0.20	0.994
Area by sex	2	3.55	1.92	0.151
Error	140	129.61		
		1988		
Age				
Slope	1	16.64	6.73	0.010
Intercept	1	60.33	27.71	0.000
Area	2	12.52	2.88	0.060
Sex	1	.54	.25	0.618
Area by sex	2	.16	.04	0.963
Error	149	324.39		

Table 16. Analysis of deviance for factors determining *K. paniformis* prevalence. Scale parameter taken as 1.

Model terms	Model deviance	Model DF	P. incorporated term
Mean	836.9	607	
Mean + Age	753.88	603	<0.001
Mean + Age + Area	738.29	599	<0.005
Mean + Age + Area + Sex	738.11	598	>0.995
Mean + Age + Area+Age.Area	716.57	586	<0.050

Table 17. Parameter estimates for the prevalence model. Prevalence = Mean + Age + Area + Age-Area. Area-age combinations for which no information was available were omitted.

Estimate	Standard error	Parameter
-0.965	0.29	1
1.841	0.61	Age(6)
1.881	0.51	Age(9)
7.189	13.67	Age(11)
7.189	13.67	Age(13)
-0.587	0.39	Eureka
-1.808	1.07	Columbia
-5.664	13.68	U.S. Vancouver
-5.713	13.68	Canada
-0.503	0.71	Age (6) Eureka
0.702	1.22	Age (6) Columbia
4.943	13.64	Age(6) U.S. Vancouver
4.535	13.70	Age(6) Canada
-1.939	1.23	Age(9) Eureka
2.395	1.27	Age(9) Columbia
5.767	13.69	Age(9) U.S. Vancouver
4.509	13.69	Age(9) Canada
0.587	19.33	Age(11) Eureka
-4.416	13.78	Age(11) Columbia
5.664	20.88	Age(11) U.S. Vancouver
-0.916	19.36	Age(11) Canada
1.808	15.31	Age(13) Canada

Table 18. Analysis of deviance for parasite prevalence comparison among years.

Model terms	Model deviance	Model DF	P. subtracted term
Mean +Age+Area+Year	1215.0	923	
-Year	1220.5	925	0.1
-Area	1225.1	927	0.1

Parameter estimates of the model: Mean + age + area + year

Parameter estimate	S.E.	Parameter
-1.6	0.25991	Mean
0.2337	0.03316	Age
0.2041	0.18040	Area(Vancouver)
-0.1748	0.18320	Area (Canada)
-0.03771	0.16620	Year (1987)
0.3591	0.16850	Year (1988)

Table 19. ANOVA of length. Dependent variable length in millimeters, independent variables 2 covariates (age and parasite intensity), and a 2-level factor (sex). Ages in the analysis: 2, 3 and 4. Parameter estimates are for the largest model.

Model 1	DF	MS	F	Probability of F
Sex+ age + parasite intensity	297	112259		
-Parasite intensity	298	112455	0.519	>0.25

Parameter	Estimate	S.E.
Mean	259.2	3.687
Sex (2)	10.90	2.250
Age	39.22	1.230
Parasite intensity	0.03099	0.04298

Model 2	DF	MS	F	Probability of F
Sex/age + sex/parasite intensity	295	110065		
-Sex/parasite intensity	298	110412	0.31	>0.25

Parameter	Estimate	S.E.
Mean	268.0	5.274
Sex(2)	-5.132	7.096
Sex(1) age	35.91	1.843
Sex(2) age	41.89	1.645
Sex(1) parasite intensity	0.03366	0.06645
Sex(2) parasite intensity	0.01220	0.05616

Table 20. ANOVA of length. Ages in the analysis: 6, 7 and 8.

Model 1	DF	MS	F	Probability of F
Sex + age + parasite intensity	585	749001		
-Parasite intensity	586	771462	17.54	<0.005

Parameter	Estimate	S.E.
Mean	372.4	12.48
Sex(2)	23.46	2.999
Age	13.14	1.790
Parasite intensity	-0.063	0.015

Model 2	DF	MS	F	Probability of F
Sex/age+sex/parasite intensity	583	747387		
-Sex/parasite intensity	586	774126	6.95	<0.005

Parameter	Estimate	S.E.
Mean	360.1	19.40
Sex(2)	43.65	26.01
Sex(1) Age	15.01	2.814
Sex(2) Age	11.92	2.322
Sex(1) parasite intensity	-0.076	0.022
Sex(2) parasite intensity	-0.052	0.020

Table 21. ANOVA of length. Ages in the analysis: older than age 8. Parameter estimates are of the larger model.

Model 1	DF	MS	F	Probability of F
Sex + age + parasite intensity	305	557669		
-Parasite intensity	306	567003	5.106	<0.01

Parameter	Estimate	S.E.
Mean	414.3	16.31
Sex(2)	42.75	4.904
Age	9.361	1.602
Parasite intensity	-0.04292	0.0190

Model 2	DF	MS	F	Probability of F
Sex/age +sex/parasite intensity	303	555801		
-Sex/parasite intensity	306	572850	3.09	<0.05

Parameter	Estimate	S.E.
Mean	399.9	29.04
Sex(2)	61.24	35.23
Sex(1) age	10.68	2.892
Sex(2) age	9.008	1.948
Sex(1) parasite intensity	-0.02373	0.02834
Sex(2) parasite intensity	-0.05719	0.02590

Table 22. Mean length-at-age of infected and uninfected whiting, 1986-1988.

	Infected			Uninfected		
Age	Length (cm)	n	STDV	Length (cm)	n	STDV
2	34.5	35	1.2	34.3	143	1.6
3	38.6	9	3.7	38.3	19	2.9
4	42.6	37	2.6	42.1	59	2.2
5	47.8	6	5.6	41.0	3	1.0
6	45.8	134	3.5	46.0	136	3.5
7	47.9	69	2.6	49.9	93	4.1
8	47.0	104	3.7	49.6	53	4.1
9	51.4	97	4.5	52.4	50	5.4
10	51.7	67	4.3	53.7	24	4.2
11	54.4	22	5.9	53.3	10	3.0
12	57.0	2	4.2	-	-	-
13	56.7	7	6.1	55.8	7	2.7

Table 23. Negative log likelihood parameter values derived for the von Bertalanffy growth model in length for infected and uninfected *female* whiting.

	Model(-ln(liklhd))	L_{inf}	k	t_o	Variance
		Variance hypothesis			
All females					
Constant (cte)	3,464	635.6	0.139	-3.73	1,632.0
Cte*age	3,405	617.2	0.157	-3.29	232.9
Cte*age^2	3,412	589.9	0.188	-2.72	40.3
Uninfected females					
Constant(cte)	1,644	646.6	0.144	-3.39	1,457.6
Cte*age	1,601	643.2	0.146	-3.27	229.0
Cte*age^2	1,602	630.4	0.156	-3.08	46.3
Infected females					
Constant(Cte)	1,811	677.2	0.100	-5.66	1,724.7
Cte*age	1,797	641.5	0.124	-4.61	227.9
Cte*age^2	1,803	587.0	0.178	-3.14	33.8

*Length is in millimeters and time in years.

Table 24. Negative log likelihood and parameter values derived for the von Bertalanffy growth model in length for infected and uninfected *male* whiting.

	Model(-ln(liklhd))	L_{inf}	k	t_o	Variance
		Variance hypothesis			
All male data					
Constant(Cte)	2,525	573.8	0.151	-3.99	765.5
Cte*age	2,493	560.8	0.167	-3.52	116.5
Cte*age^2	2,539	550.4	0.183	-3.28	23.7
Uninfected males					
Constant(Cte)	1,301	613.0	0.133	-4.13	682.5
Cte*age	1,283	598.5	0.145	-4.19	119.8
Cte*age^2	1,309	579.9	0.163	-3.41	28.9
Infected males					
Constant(Cte)	1,204	569.9	0.41	-4.50	739.3
Cte*age	1,193	561.9	0.15	-4.19	99.5
Cte*age^2	1,208	558.5	0.16	-4.11	16.3

*Length given in millimeters and time in years.

Table 25. Negative log likelihood and parameter values of the von Bertalanffy growth model in length for infected and uninfected Pacific whiting.

	Model(-ln(liklhd))	L_{inf}	k	t_o	Variance
		Variance hypothesis			
All data					
Constant(Ct)	6,115	607.6	0.144	-3.85	1,436.0
Ct*age	6,009	586.3	0.168	-3.28	205.8
Ct*age^2	6,036	566.6	0.195	-2.78	36.6
Uninfected fish					
Constant(Ct)	2,996	621.8	0.146	-3.52	1,232.0
Ct*age	2,926	615.8	0.151	-3.399	197.4
Ct*age^2	2,937	605.4	0.161	-3.209	41.5
Infected fish					
Constant(Ct)	3,099	639.2	0.109	-5.475	1,569.0
Ct*age	3,073	591.5	0.149	-3.953	206.6
Ct*age^2	3,085	554.8	0.202	-2.833	30.9

*L_{inf} given in millimeters and age in years.

Table 26. Proportion of infected Pacific whiting at age for size range from 47 to 58 cm.

Length	Age 6		Age 9	
	Prevalence	n	Prevalence	n
47 cm	50	27	80	12
48 cm	48	11	52	6
49 cm	38	16	56	15
50 cm	20	9	70	15
51 cm	30	7	75	11
52 cm	68	6	57	11
53 cm	60	2	83	6

Table 27. Prevalence of *Kudoa paniformis* (in % at age) by pseudocyst stage.

Age (years)	Pseudocyst stage		
	Initial	White	Black
2-4 month	0.0	0.0	0.0
2	10.1	9.6	0.0
6	12.6	34.6	19.9
9	12.0	42.9	39.1
13	12.5	58.3	37.5

Table 28. Conversion factors for intensity index.

Age:	2	3	6	9	13
Factor:	1	1.52	2.8	3.4	3.8

Table 29. Intensity of *Kudoa paniformis* by pseudocyst stages, 1986.

Age (Years)	Pseudocyst stage					
	Initial Mean (Range)		White Mean (Range)		Black Mean (Range)	
2-4 month	0		0		0	
2	54	(10-180)	36	(7-100)	0	
3	*		*		9	(1-15)
6	123	(2-504)	194	(3-720)	70	(6-291)
9	250	(68-833)	273	(17-1577)	34	(3-1975)
13	543	(154-828)	249	(21-730)	90	(10-270)

*Insufficient data.

Table 30. Proportion and biomass of euphausiids in Pacific whiting diet in Monterey, 1986.

Age (years)	Length (cm)	% euphausiids (% of total)	Daily ration (grams/day)	Euphausiid biomass (grams/day)
1	<20	100	-	-
2	20-29	100	3.7	3.7
4	30-39	100	5.5	5.5
5	40-49	71	6.19	4.39
8+	>50	16	6.34	1.0

Table 31. Mean intensity and intensity index of initial pseudocysts in Monterey, 1986.

Age (years)	Intensity (counts/g)	Factor	Intensity index (counts/g)
2	30	1	30
6	31	2.8	87
9	31	3.4	105