Ecology on the Feeding of Milkfish Fry and Juveniles, *Chanos chanos* (FORSSKÅL) in the Philippines [*1]

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Abstract

An extensive ecological survey was conducted in the Philippines to study the feeding of milkfish, *Chanos chanos* Forsskål. Types of environments examined included coral reefs, lagoons, mangrove and nipa swamps as well as estuarine systems. It was concluded that organic detritus was the basic nutrient for juvenile milkfish and that depositional environments constitute important nursery and feeding grounds for this species. The main pathway of energy flow in these coastal ecosytems through the detritus rather than the grazing pathway. The feeding of milkfish was described in terms of habitat structures, stomach content, feeding chronology and feeding behaviour. The result suggests that a better understanding of the function of the ecosystem will help to improve present aquaculture practices as well as guidelines for resource management.

INTRODUCTION

In Southeast Asian Countries considerable amount of knowledge exists concerning the culture of fry (pterygiolarvae, BALON (1975)) and juveniles of milkfish, *Chanos chanos* F. Although it is evident that the biomass production in terms of growth rate times stocking density obtained in pond environment is much higher than those occuring in natural habitats, the success of this effort remain a matter of high energy input in form of fertilizer, artificial diet as well as water management. Though the survival rates of fry and juveniles under culture condition are undoubtedly higher than those in the wild, a reduction of mortality during the metamorphic phase from fry to juvenile would still be desirable especially in view of present and future shortage of energy resources as well as shortage of wild seedlings. In spite of progressive culture methods, the need to increase food production has resulted in a massive and rapid widespread modification of the important and once productive coastal nursery and feeding grounds of numerous marine resources.

An attempt to overcome this inevitable diminishing supply of natural seedlings is reflected in the existing knowledge about artificial propagation and techniques of rearing

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fish larvae. However, in spite of the previous and present costly efforts, seedlings production remains hampered by high larval mortalities. Though the survival of these laboratory reared larvae as well as the growth of pond cultured juveniles are undoubtedly influenced by various environmental factors, food seems to be one of the prime responsible factors. Past experiences have shown that adequate improvements cannot be achieved without sufficient fundamental knowledge about morphology, physiology and ecology of the orgamism.

This study deals only with the ecology of feeding of fry and juveniles of milkfish in their natural habitats and is aimed at providing some basic understanding of the functional relationships of the ecosystem needed for ;

a. Ability to develop appropriate aquaculture technology which can maintain ecological balance while still achieving economical production of resources over a long term.

b. Ability to forcast future changes.

and c. Ability to evaluate consequences of human interventions and to suggest optimal solution.

MATERIALS AND METHODS

The procedures and methodologies used in this investigation do not differ from those available and mentioned in various literatures. However, in the course of this study some serious inadequacies in the application of standard approaches were discovered. It was found for example that studies on small lagoon habitats carry with them the inevitable problem of small population size. As pointed out by JENKINS & GREEN (1977) feeding chronology of fish in natural environments cannot be determined over a single 24 hours period with only limited numbers of fish. To remove an appropriate number of fish for this type of analysis may reduce the population level in most study areas to an unacceptable degree, hence the emphasis here will be on the general food and feeding habits of the fish based on average diets and field observations. Nevertheless each stomach content was examined roughly under the disecting or research microscope in order to detect irregularities whenever possible ; after that the contents of several fish of one sample were pooled together and examined. On the other hand in these habitats of limited size a relatively good overview of the entire fish community and their habits could be obtained. Although other more detailed study on the developmental and functional morphology of different organ parts associated with food and feeding are now being conducted to support the observation and conclusion made in this study, it should be noted that some tradeoffs between generality and precision has been made. Here the objective of this ecological study reflects the values of finding a generalization and basic understanding of the functional concept of the system and associating organisms. The author believes that the narrower the focus of an investigation the greater is it's precision but the less applicable the results are to other aspects of the systems. The strategy used here in formulating a hypothesis is to devise linked ecological knowledge obtained from this study with those results from countless laborious field and laboratory works of past investigators.

Monthly collections in a small lagoon with dense mangrove vegetation was made for a period of over one year. Comparative samples were made by day and night and at any tidal level. Stationary gill nets were set in open shore waters, in naturally cleared areas of the lagoon as well as within the entangling prop roots of the mangroves. A bamboo observation bridge was constructed over a naturally cleared portion surrounded by thick mangrove vegetation, thus permitting a relatively clear and undisturbed view of the fish and their behaviour. Night observations were made with the use of a pressurized kerosene lamp of 500 cp. Soil samples were collected in a container by hand for crude qualitative studies. Fresh and dried samples were brought back to the laboratory for feeding experiments. Skin diving in the lagoons as well as adjacent areas allowed direct and clear observation of habitat structure and behavioural pattern of fish community.

Other sampling sites where high probabilities of obtaining specimens regardless of amount were choosen. Through recommendations of past investigators and fishermen and through accidental encounter the locations which have been visited are shown in Fig. 1. These areas consisted of sand / rocky shores, mangrove / coral lagoons, nipa

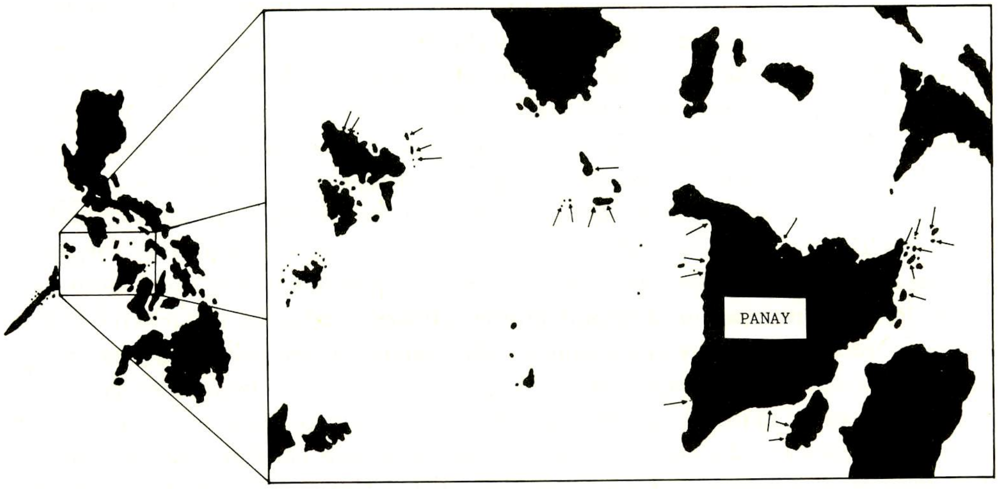

Fig. 1 : Map showing locations covered by this study (indicated by arrows) with insert map of the Philippines Islands.

swamps, sea grass communities and estuarine systems. Temperature, dissolved oxygen and salinity measurements were taken in situ with a calibrated mercury thermometer, a portable oxygen meter and an optical refractometer respectiyely. Over 1200 juvenile milkfish ranging from 16–250 mm in total length have been collected with the use of gill nets of different mesh sizes, cast net, fry seines, dragnet and traps. Considerable number of milkfish fry (pterygiolarvae) were collected for stomach analysis from shore waters, inlets and marginal portion of nipa swamps with the use of commercial fry collecting gears. In order to obtain a better overview of the feeding of the juvenile stage, several adult specimens which were obtained through commercial fishing operations (drift gill nets, fish corrals) have been investigated. A number of morphological observations were made on fresh and preserved specimens which were caught from the wild and have been confined in SEAFDEC tanks or cages for a period of time.

RESULTS AND DISCUSSION

In milkfish, life in shallow coastal habitats begins when the fry appear in shore waters. Whether this mass appearance of fry is voluntary through active migration or accidental through passive drift is the subject of much past and present decision comment and speculation. Although no direct evidence has been presented, several findings suggest that the occurence of milkfish fry is an active feeding migration in the sense of biological necessity. Comparison between stomach contents of fry and juveniles of milkfish in the wild as well as laboratory experiments, showed that the milkfish fry changes its food habit shortly after their arrival to shore waters or with the transition to juvenile stage. By shifting food sources taken from midwater to food sources taken from the bottom sediments the fish abandons the pipette-particulate mode of feeding and assumes filter feeding pattern. Preliminary feeding experiments have shown that in spite of "high quality" diets, milkfish fry cannot grow and develop normally if prevented from "detrital" food resources consisting of faecal matter, leftover of diets or dead planktonic organisms which have settled down on the bottom of the experimental container. This change in food habits is closely related to changes in the digestive system. Therefore, the fry at the transition phase need to obtain a different source of food suitable for the new nutritional requirement. These detritus foods are found in sedimented protected coastal areas, particularly in the extensive intertidal deposits of estuaries, behind barrier beaches, mangrove lagoons and nipa swamps. A question concerning the food of shore caught fry, however, arises. If the movement towards coastal areas is the result of the search for habitat with rich and new food resources, how can the low feeding incidences in fry be explained? Following responsible factors and reasons can be given; Past investigations on food and feeding habits of milkfish fry (as far as the author is aware) were based on materials obtained with commercial fry collecting gear operated along shore waters. Although this gear caused relatively little disturbance or injury to the animal, there is usually a time lapse from collection to preservation for stomach content analyses. In this short period of confinement and handling one can immagine that most or all ingested food have been defecated; a behavioural pattern which can be easily observed in the laboratory. Apart from this possibility the incidence of feeding in fry might be low due to the naturally short gut retention time of ingested food. At the fry stage the digestive system lacks a true stomach, pyloric caeca and the intestinal tract which is the main digestive and an absorptive organ is considerably short and simple. Although the intestine is relatively broad as compared to the fish body, stomach analyses of wild caught fry as well as laboratory fed ones, revealed that ingested food particles are immediately transported to the posterior portion near the anal opening. This especially holds true when zoo-phytoplanktonic organisms are ingested but less when particulate detrital matter are taken. Although this observation is far from being an evidence for short gut retention time in the fry, it strongly suggests that the rapid disposal of ingested food as well as short gut retention time of food represent a kind of behavioural pattern related to predator avoidance strategy. Since disposal of food might significantly increase swimming ability as well as maintain body transparency, this behaviour must be of selective advantage for survival in coastal waters where high predation pressure exists. The factors mentioned above could bring about the appearance of low feeding incidence or even lack of available food in coastal habitats. Through minimum handling and immediate preservation feeding incidence as high as 65% has been obtained. Nevertheless if incidence of feeding is referred not only to the percentage of fry which have food in their guts but also to the amount of food in each gut, then the value of feeding incidence may be interpreted in a very different way. Although knowledge of the food of wild milkfish fry is still fragmentary, in the light of present findings, it can be said that in general feeding incidence in natural waters is extremely low. Observation on numerous fry of other teleost species associating with milkfish fry indicate that factors responsible for empty stomach does not reflect food availability in the environment.

Stomach content analyses of wild caught fry showed that copepodite, benthic diatoms, faecal pellets among other undefinable particulate matters were ingested. The types of food ingested indicate that milkfish fry are particulate feeders. The feeding behaviour of milkfish fry and juvenile has been studied by KAWAMURA and HARA (1980). Food selectivity is not apparent but moreover ingested food is a function of adequate size and ability to sight and attack the particles. Benthonic source of food is ingested when resuspended in the water column by wave action. Direct benthonic feeding probably does not occur until the fry enter the calm waters of the lagoon and estuary systems. Moderately turbulent sea conditions positively affect feeding incidence of fry due to probably higher food abundance as a result of resuspension.

Laboratory experiments have shown that most monocellular algae are not digested and in many instances they are even defecated alive. This suggests that the fry cannot discriminate between digestible and undigestible food but that feeding is activated upon visual stimulation. Feeding experiment with very small food particles less than 100 μ diameter indicate that fry cannot detect these small objects inspite of the high density of 20-30 particles per ml. Deprived of "planktonic" food in the water column the fry will turn to feed on the bottom sediments. If, however, these sediments are often siphoned out and accumulation prevented, mortality will occur or development will be much retarded.

Inspite of the low feeding incidence there has been no evidence for starvation or weakening of the wild caught fry. Stocking techniques of commercial fry concessionaires as well as laboratory experiments clearly show that fry are not sensitive to food deprivation or starvation up to several days after their capture. Judging from the swimming activity of the fry and the efficiency of the fishing gear, it seems reasonable to believe that gear avoidance by more healthy fry is not applicable for milkfish. The active but not feeding fry is therefore representative for milkfish fry appearing at shore waters. Since there is a multiplicity of ecological and species specific adaptation used for survival strategy, a hypothetical explanation for this low feeding level in fry is suggested. It is long accepted that predation is considered to be one of the greatest causes of larval fish mortality, although this is somehow restricted to mostly laboratory experiments and little field evidence. The ecology of the oceanic larval stages of milkfish is a matter of speculation. As in other teleost larvae, possibility exists that predation might have been the secondary cause of mortality, primarily caused by weakening of the larvae due to lack of food which render them more vulnerable to predation. As stated above milkfish fry are not weak and it is very evident that they are caught together with large numbers of larvae and juveniles of numerous predatory fish species. Since tha adult and juvenile stage of these predators are known to prey on fishes it has been postulated and implied without direct evidence that they prey on milkfish fry in shore waters. This kind of extrapolation has resulted in some misunderstanding and confusion between potential predators and actual predators. The Ten pounder *Elops hawaiensis* R. and the Tarpon *Megalops cyprinoides* B., for example, have been regarded as the most important predators of milkfish fry. Although this holds true in their juvenile and adult stages and in pond conditions no published literature is known to the author concerning their predation on milkfish in natural environment and especially during their larval stage or the stage when they are caught in large numbers with milkfish fry. Mouth morphology and dimension of these two species supported by considerable numbers of stomach analysis clearly show that predation on milkfish at this stage is practically impossible. Even though quantitative estimates of the magnitude of mortality caused by predation in natural habitat is still far from possible, direct evidences of predation have been collected in the course of this study. Observation on the act of attack as well as stomach content analyses show that following juvenile fish species are actual predator of milkfish fry and that predation takes place in shore waters.

Species	Average size	Total No. of stomach investigated	Total No. of milkfish fry ingested
Therapon jarbua	46-66 mmTL	45	13
Therapon theraps		6	2
Therapon sp.	9-13 mmTL	579	5
Ambassis sp.	14-23 mmTL	890	10
Epinehelus sp.	23 mmTL	1	1
Lutianus sp.	45 mmTL	1	4
Sphyraena sp.	52-55 mmTL	2	1
Meracanthus grammistes		1	6
Chaetodon sp.		3	15
Oxyurichthys microlepis		5	3
Scatophagus sp.	7-8 mmTL	6	1

It should be reminded that the results shown here do not allow any other further conclusion except that it provides an evidence of fry mortality through predation. Considering the numbers of larvae and juveniles of potential and actual predatory fish which amount to a daily recruitment into estuarine system of estimated several thousands, the magnitude of mortality through successful predation or fatal injury cannot be underestimated during the fry stage in shore waters and shortly thereafter in the nursery grounds.

In the light of this finding it is proposed that the low feeding incidence in milkfish fry might be an adaptive behaviour caused by high predation pressure in shore waters. The activity of fry suggests that high feeding activity and accumulation of energy might take place in off shore waters prior to the movement towards shallow waters. Upon arriving in coastal waters all activity is concentrated on the movement into the nursery ground where shelter from predators is available. If feeding activity is minimized the risk of predation is lowered. Similiar feeding behaviour of juvenile sockeye salmon has been described by EGGERS (1978).

Usually the term "critical period" or the period when high mortality occurs is considered as the period when the larval fish are most sensitive to environmental factors owing to their own endogenous changes in metabolism coinciding with the transition of development from one phase to another. The cause of this high mortality is believed to be lack of food and the inability of the larvae to cope with periodic starvation. If the high mortality occurs during the fry and/or metamorphic phase of milkfish the term "critical period" should be understood differently. Here food supply or other endogenous factors do not seem to be the responsible factors but more over intense predation pressure. This critical period can be but need not coincide with the metamorphic phase since obviously predation is not a function of developmental phases. The fact that large numbers of fry can be collected along shore waters whereas practically not a single juvenile milkfish has been caught in the same environment, indicate that coastal waters represent a kind of transitional environment in the sense that milkfish fry found in coastal waters are in fact on their way to the nursery grounds (back waters). Field observations also show that metamorphosis from fry to juvenile does not take place in shore waters (transitional environments) but takes place in back waters or nursery grounds several days thereafter. Since predation is the most probable cause of high mortalities in this transitional environments (shore waters and adjacent areas of the back water system) the term "critical environment" is suggested. In other words the cause of high mortality during the critical period is different from that of the critical environment. It also implies that the transitional phase can occur separately from the critical period and that transitional phase can be passed through uncritically especially since detrital food sources are available in superabundance. In spite of the high fecundity of the species the mass occurence of fry also suggest high survival rate up to the fry stage when high mortality occurs. Although the seasonal and daily recruitement pattern of milkfish fry will be published elsewhere, it is of interest in this connection to note that the peak occurence of milkfish fry is somewhat negatively corellated with the peak abundance of fry and juveniles of predatory fishes. An anti-predation adaptive measure therefore exists.

As mentioned above the fry migrate towards shore waters from the open sea and enter intertidal estuarine or lagoon systems. Here metamorphosis is completed, feeding behaviour completely changes and schooling habits becomes more pronounced. If one concludes that those locations where juvenile milkfish of different sizes can be caught or has been reported are the nursery and feeding grounds, the next step is to identify the general unifying characteristics of the habitat. Fig. 2 illustrates the schematic crosssectional view of some types of environments covered by this study and showing characteristic habitats which are utilized as nursery and feeding grounds for fry and juveniles of milkfish. The ecological factors shared by all these environments (mangrove lagoon, nipa swamps, sea grass communities etc.) are habitats with rich bottom deposits, relatively still waters of shallow depth. The fish finds here abundant food and a certain amount of shelter from predators. These habitats are either relatively isolated permanent bodies of water, carrying a very specialized fish fauna adapted for life in this type of environment or they are a temporary part of the intertidal zone carrying a much more varied fish fauna. Most habitats are shallow relatively clear calm waters often over leaf carpeted bottom debris or organic mud. Primary production in most cases is extremely low especially in location with dense mangrove and/or nipa vegetation cover. The substrate is rich in hydrogen sulfide and dissolved oxygen content in the water column over the sediment may drop to zero at certain time of the day. Except in seagrass community, primary producers are represented only by benthonic diatoms along exposed river banks or on the higher reach of nipa groups. Patches of macrobenthic filamentous algae may be found attached to the proproots or submerged twigs of the mangroves. In two coral lagoons where juvenile milkfish have been collected *Caulerpa* sp. among other marine benthic algae constitute the overwhelming majority of primary producers. Depending

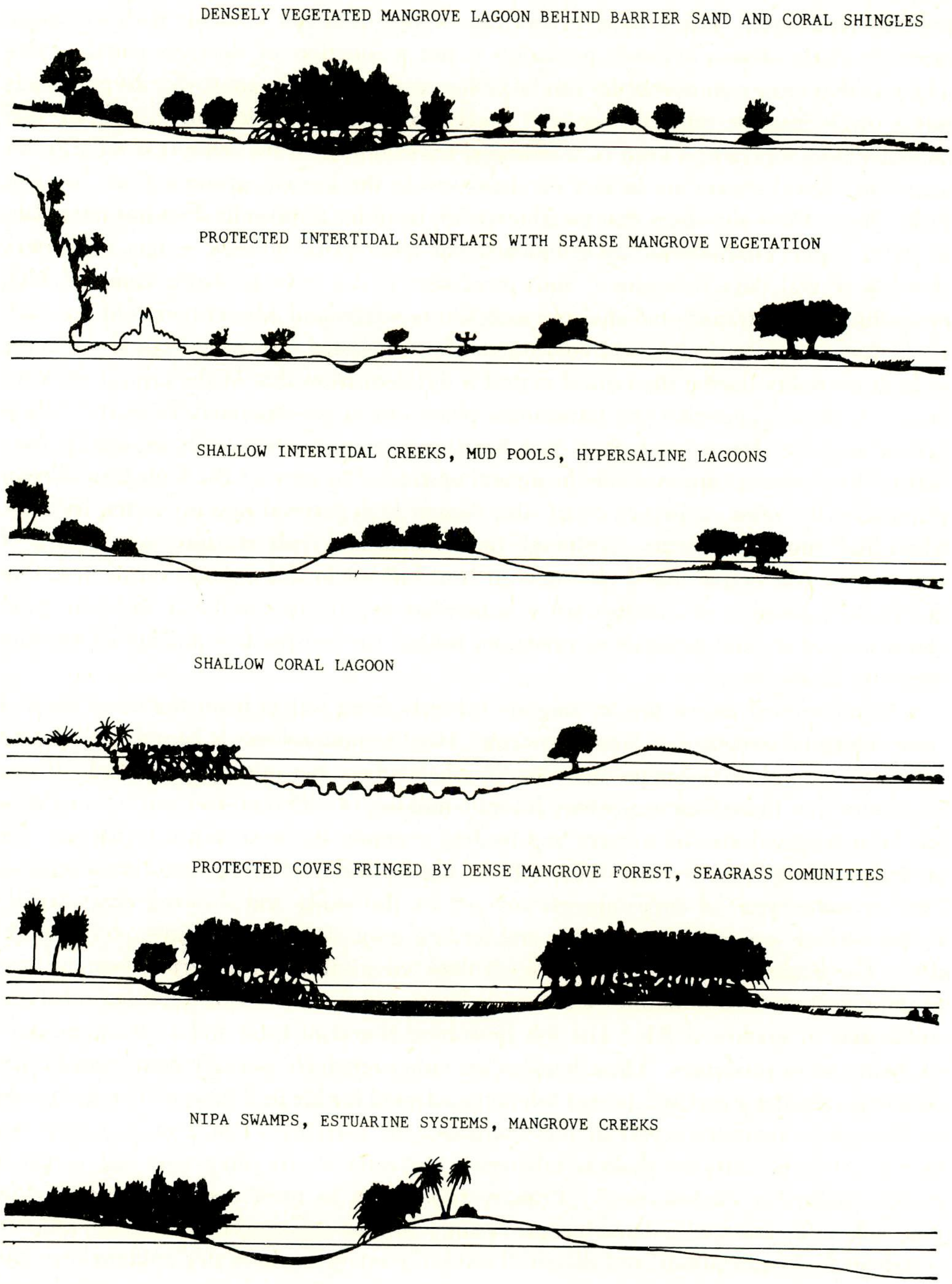

Fig. 2 : Schematic crossectional view of environmental types used by fry and juvenile of milkfish, *Chanos chanos* F. as nursery and feeding grounds. (for detail see Text).

therefore on the geomorphological character of the system, location as well as surrounding vegetation cover, the bottom sediment or detritus of each habitat may vary from decomposing mangrove leaves (leaf fall), terrestrial plant materials and mountainous sediments (flushed in through land run off), sea grass blades and marine algae (through daily tidal transport or seasonal storms) etc. Mechanical and microbiological breakdown of these trapped materials have led to the formation and accumulation of rich organic detritus. In calm areas between the dense root structures and far from the action of waves and tidal flow, the bottom sediments may be flocculant in nature, consisting of finest organic detritus which can be resuspended upon slightest disturbance. Other areas along the intertidal line and where wind and tidal current is noticeable, the bottom organic mud is more compact and contains a considerable amount of sand or coral fragments. Areas which are constantly affected by waves action or are submerged only at spring tides are mostly covered with pure sand or coral shingles. The extent and accessibility of these apparantly bare biotops are governed mainly by the state and level of tides. In some "closed" lagoon systems where connection to the open sea only occurs during extreme springtides or seasonally during storms, the water is relatively clear but lackes sufficient dissolved oxygen and salinity may drop to near zero or increase over that of seawater depending on the location. In most cases, the absence of true filter (planktonic) feeders reflect the absence of midwater organisms and plcnktonic primary producers. Fish communities usually compose of bottom feeders (mullet, milkfish), surface dwellers (halfbeak) and predators. If studied in detail, however, there is a continuous change of diversity in the course of time especially with the change in water levels affecting ecological niches, food availability, immigration and emigration of species from the adjacent areas. On the other hand when the habitat becomes limited and environmental conditions becomes extreme, only species with closely indentical ecology can exist. It can be recognized thct generalist feeders such as milkfish which utilizes food resources that are superabundant and homogeneous may have a greater adaptive advantage over other more specialized trophic forms. In some relatively less disturbed habitats fish predators such as birds and reptiles are still numerous.

As indicated above, the milkfish fry metamorphose to juvenile in all depositional environments with marine, brackish or freshwater condition. The most evident change is the appearance of pelvic fins and the loss of body transparency due to the development of irridophores (silver pigments) over the peritoneal membrane with a general darkening of the dorsal surface. Most important internal changes include the elongation, convolution and differentiation of the intestinal tract, development of the gill rakers and the epibranchial organs; the detail studies of these will be published elsewhere. Schooling habits becomes more pronounced (see also KAWAMURA and HARA, 1980) whereby the size of school is negatively corellated with size of schooling individuals.

Regardless of body size or age, detritus constitutes the bulk of the diet of juvenile milkfish. When feeding the fish make a quick dive to the bottom and take in a quantity of sediment. After working it for several seconds, some of the roughest and most undigestible portions of the ingested food are rejected. These are sand particles, molluscs, and coral fragments. The characteristic spitting out can be observed as materials sinking down through the water column from individuals in the school which had just fed on the bottom. The clouding of water "mullet water" characteristic for feeding mullets (BURI, unpublished Thesis), however, has not been observed in milkfish. In mullet this phenomenon has been observed to result from finest materials which are jetted out through the gill-opercular chamber openings or it is due to the feeding disturbance and resuspension of the substrate. In the first case part of the ingested materials which are too fine to be retained by the gill rakers are jetted out with the respiratory waters. In some instances this clouding of water is caused by a kind of cleaning activity of the gill rakers and filaments from "disturbing" particles. Here the flow of water is abruptly reversed and sediment loaded water is jetted out through the mouth. When feeding the milkfish sucks in the upper most surface layer of the sediment such that disturbance of the surrounding substrate is rarely niticeable. Comparative morphology of gill rakers of mullet and milkfish suggest higher filter efficiency in milkfish. Fig. 3 shows the

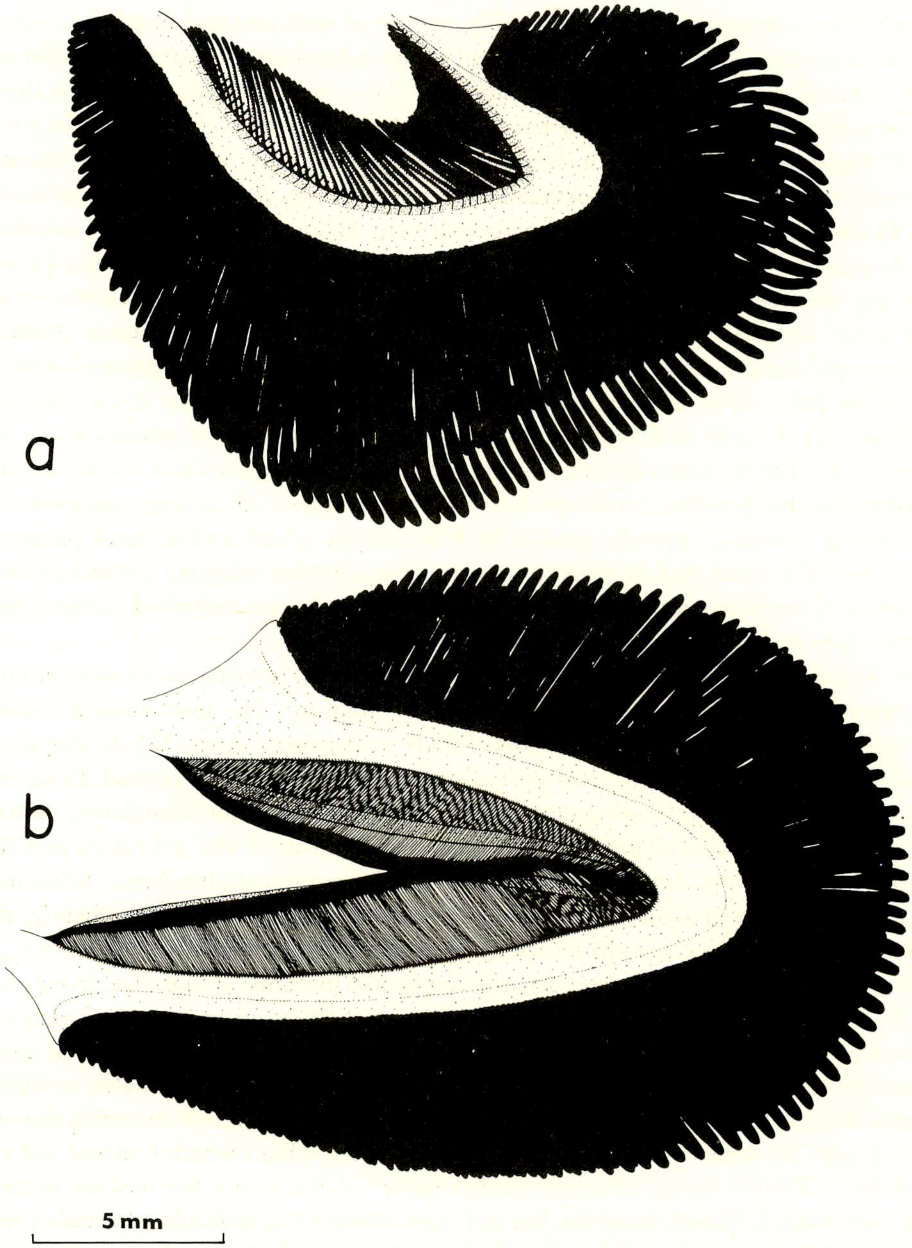

Fig. 3 : Illustrations of the left first gill arch of a. mullet, *Mugil* sp. and b. milkfish, *Chanos chanos* F. showing the difference in strucure and numbers of gillrakers. (see Text).

illustration of gill rakers of mullet, *Mugil* sp. and Milkfish, *Chanos chanos* taken from the first gill arch of individuals of similiar forklength. Although the feeding techniques of mullet and milkfish differ in detail only in the sense of substrate depth, i.e. mullet feeds deeper into the substrate than milkfish, it seems clear that both species are aiming at the finest material of the surface sediment layer. The ecological significance of this fine particle selection has been demonstrated by ODUM (1968).

In the daytime milkfish feed in school; after having circled an area one individual will make the first dive to the bottom to be followed immediately in quick succeeding sequence by other members of the school. In many instances repeated visits to the same spot are made indicating a kind of renewed investigation of what had been found previously to be a good area. It is suggested that depressions found in the substrate might be the consequence of this feeding technique.

JENKINS and GREEN (1977) have pointed out that it is not possible to conclude about the feeding of fishes without the support of long term experimental analysis. As stated above, it is, however, not possible in the course of this study to sample large numbers of fish (even within a single 24 hour period) without severely disturbing and exploiting the whole population. Therefore all that can be described from the present data and observation is that at different times of the 24 hour period there appears to exist different feeding intensities. In milkfish the absence of a visually significant variation in stomach content (fullness) between different sampling times seems at first sight to suggest that feeding is continuous throughout the day. However, direct observation in natural environment shows that major differences in feeding intensity do exist, but are not well reflected by stomach fullness. Without identifying clearly the responsible factor which causes the temporal discontinuity or activity of feeding this kind of observation has led to some contradicting conclusions. In the grey mullet, *Mugil cephalus,* ODUM (1970) for example suggested that the rate of ingestion is corellated to the state of tide whereas DE SILVA and WIJEYARATNE (1977) suggested that feeding activity in the same species is a function of light intensity or time of the day. Judging from the present study the author believed that both observations were correct but the conclusions incorrect. The reason here lies probably in the difference of the habitat geomorphology.

Although feeding activity could be caused by a wide variety of exogenous and endogenous factors, it is suggested that state of tide, time or light intensity *per se* should not affect the feeding activity of these two detritus feeders. Measurements of water parameters indicate that dissolved oxygen content in these depositional environments is the most important abiotic factor affecting and motivating feeding activity. Since it was found on one dand that in habitats with poor primary production oxygen level is mainly a function of rate of tidal exchange or on the other hand in habitats with rich benthic primary producers it is a function of light intensity. When one of these factors improves oxygen level feeding activity commence or intensify. The use of time, light intensity or state of tide as one of the variables seems therefore incorrect but tolerable, providing one is aware of the true responsible factor which affect this biological process.

In many depositional environments investigated, the size of the aquatic habitat fluctuates greatly and periodically with tide. The fish can be confined in shallow pools at low tide and are subjected to extreme environmental conditions such as high temperature (up to 42 ℃), high salinity (up to 38 ‰) and extremely low oxygen content (approaching 1.5 ppm in surface layers). Special adaptation for promoting greater ability to obtain sufficient oxygen for respiratory needs is shown in the development of larger gill surface area resulting in relatively longer head length. Feeding activity is much reduced at low tide due to lack of oxygen and the bahaviour of drawing water from the better oxygenated surface waters in intervals between dives to feed on the bottom can be observed. Although not directly ralated to food and feeding, it is worth mentioning that other organs have undergone developmental adaptations in relation to the specific abiotic condition of the habitats. Among these are the development of larger eye balls and lens in habitat with prevailing low light intensity due to the presence of thick vegetation cover and turbidity of water, development of rounded caudal fin tips as adaptation to shallow water depth and changes of body coloration as adapted to underlying sediment types. More data is needed to confirm the preliminary findings that shape of lower jaw, relative size and thickness of gizzard and length of intestinal tract are governed by the texture and probably nutritive value of the average diet found in the habitat. Depending on habitat to habitat the intestinal ratio in milkfish can therefore vary from 4 to 7 (length of intestine/fork length).

At high tide juvenile milkfish smaller than 100 mm in total length forms large monospecific school of relatively uniform size. The number of individuals in a school probably depends on the existing population size. These schools move with the rising tide to feed in the shallowest farthest reaching portion of the habitat. Since these areas are usually bare of any protection from aquatic or terrestrial plants the fish are exposed to predation by birds and piscivorous fish, the formation of a dense school and its ecological advantage can therefore be recognized. Further studies will be needed to explain the nutritive value of these apparantly bare and upproductive areas. Shortly before the beginning of low tide the schools are observed to move out of these shallow feeding areas and return to deeper waters. Although these tidal pools occur daily and are numerous in many locations, there is no single evidence where milkfish are trapped and exposed to lethal conditions. This behavioural pattern of retreating before the water level drops might therefore indicate the existence of an endogenous rhythm which is of selective advantage for survival.

At low tide small loose schools may be formed by individuals of different size groups. In general, however, the number of individuals per school decreases with the increasing size of the schooling fish. Schools of milkfish are often joined by individual mullets of comparable size. As said above, feeding intensity is much reduced at this time with long intervals between feeding dives.

Although at low tide less protective areas may be available, prey and predators may be confined together in a small body of water, no evasive activity of prey or attack by predators has been observed. Most predators were solitary stalking (Baracudas) or stationary sit and wait (Goby) species. Both types have been caught in cpnsiderable numbers by gill nets and traps during day and night period, but none have been found to contain milkfish in their stomachs. This again might be due to the generally reduced feeding (predation) levels when physico-chemical conditions are unfavourable. In contrary to this observation, crowding in habitats of more constant and stable environmental conditions such as shore waters, lagoon and estuarine inlets, will result in higher mortality due to predation. Direct observation on the act of attack and stomach content analysis in the field suggest that milkfish fry are more susceptible to predation when they are concentrated together with predators in the collecting gears or during their transport and movement through the narrow inlets. Here chances of encounter and being encountered are high and feeding levels (appetite) are not hampered by unfavorable conditions.

Despite the high number of predators of different categories, the population of larger fishes in the nursery grounds seems to remain relatively constant. This is probably a characteristic of selective predation on small fishes. The higher vulnerability of small fishes may reflect also in the formation of larger schools.

During the night, schooling habit is more or less abandoned. Night observation as well as night collection confirm that school breaks up without negatively affecting feeding activity. At nocturnal low tide, however, schooling is completely abandoned and individual fish are found scattered and resting motionless over the substrate. These fish do not react to light or shadow movements and tolerate slight disturbance such as leaf fall or small twigs droped into the water directly over them. It is believed that with experience and patience these "sleeping" fish can be captured by hand. At night juveniles of other species which have been attracted or blinded by the light can be touched without affecting the sluggish movement of the fish. More intense disturbance will cause the "sleeping" fish to dash away a few feet and to rest on the bottom again. When caught these fish show distinctively empty stomach.

Schooling milkfish in the daytime split into segregates when disturbed but reform again after a short time. Frequent disturbance will drive the school into protected densely vegetated areas.

Standard methods commonly used in qualitative and quantitative stomach analyses posed some severe inadequacies. Although the exact feeding areas are known, and stomach contents as well as corresponding sediment samples can be obtained, the difficulties remain of how to quantify the nutritive value of the diet. The question is how to detect what is digestible and how much of it is digested, and how to obtain comparable sediments. Since this problem has not yet been solved satisfactorily, only a general picture of the diet of juvenile milkfish is presented. It can be said that all types of detrital matter which are abundant in the particular habitat are more or less represented in the stomach content of milkfish. A great portion of the ingested food are in their advanced stage of decomposition and therefore nondistinguishable. Those portions of particulate matter mostly of plant origin can be observed in all portions of the intestinal tract, indicating that these plant materials are practically indigestible. It is suggested, based on previous workers (ODUM & de la CRUZ, 1963; DARNELL, 1967; ODUM, 1968; WELCH, 1968; and MELCHIORRI-SANTOLINI & HOPTON, (Eds., 1972)) that bactcrial films and dissolved organic matter associated with decomposition process form the basic energy resources for the detritus feeding fish; here the milkfish. Primary producers such as multi-and unicellular algae as well as terrestrial plant materials if ever ingested show no sign of mechanical or chemical breakdown and probably passed through the intestinal system undigested. Nematods, small crustaceans and bivalves are extremely underrepresented in most cases. Sponge spicules, diatom shells, marine benthic algae and fragments of seagrass blades are found occasionally in higher percentage especially during and after storms, when these materials are flushed into the lagoon in large amount. Although the overall picture of the stomach content of juvenile milkfish seems to suggest a nondiscriminating type of feeding, the question concerning selective or nonselective feeding in milkfish can be answered only through more detailed studies on the functional property of organsystem acssoiated with feeding. The amount of undigestible sand particles and coral fragments in the stomach differs from one fish to another so that the question is raised of whether ingested food is a function of availability, its nutritive value or palability.

In very few cases monospecific diet composing of monospecific phytoflagellates has been observed. The fullness of the intestinal tract indicate a highly selective feeding. The fish after having discovered the dense patch of the planktonic organisms, must have remained there and show a high level of food intake. This type of feeding has been found also in adult milkfish. Local fishermen observed and concluded that milkfish also feed on epiphytic filamentous green algae growing on the submerged portion of mangrove roots or branches. This observation was not supported by stomach contents. Underwater observation revealed that these algae trapped large amount of finest sediments. It is therefore possible that milkfish may be observed to visit these areas. Judging from the mouth morphology of the fish, it can be postulate that only loose or decaying portion of the algae might be detached and ingested together with the sediments.

Comparative monthly collections of juvenile milkfish population from two different habitats (one with max. water depth of 5 cm and the other with max. water depth over 80 cm) revealed that in nature stunting effects do occur and can be achieved through limitation of living space Raumfaktor or condition factor) in spite of sufficient food resources. In one location where average water depth rarely exceeds the body depth of the fish, large numbers of juvenile milkfish belonging to a stunted population were caught in successive monthly collections. In this extreme habitat low diversity of species were found consisting mainly of milkfish and mullet species. Although the growth rate of these small bodied fish appeared to be very low, there was no evidence of lack of food or starvation. On the contrary, the condition index of these stunted fish were significantly higher than those caught in habitats with apparantly more balanced and favourable environmental conditions. The higher condition index value is also evident from the presence of fat ribbons around the intestinal tract. It appeared also that very rapid growth could be readily achieved without any sign of ill effect when environmental conditions become favourable (connection to the sea etc.). Further studies could provide interesting and useful insights into the question of stunted fish and stunting techniques. From the nutritional point of view this phenomenon indicates that it is not only the absolute amount of food available which establishes the limit of growth or population but also the rate at which this food can be processed by the animal. In other words the selection of food might not be based primarily on the nutritive value of the food but rather on its availability and palability.

Although in all habitats studied it was found that more than one species are tapping essentially the same type of food, it appears that inter-and intraspecific competition among the low level feeders such as milkfish and mullet plays a minor role. Apart from that detritus food seems to be in superabundance, species taking the same food resources are in many ways halping to increase the nutritive value of the substrate by the breakdown of large particulate organic matter into smaller bacteria riched particles. KEAST (1970, 1977) and HOBSON & CHEES (1976) have shown that two species might collect and utilize the same food in different ways, by concentrating on larger or smaller particle size which are obtained at different feeding levels in terms of mouth morphology and feeding habits. Coinhabiting species differ also widely in their numerical abundance and biomass. Territoreal behaviour has never been observed in these two deposit feeders. Although the numerical abundance of wild seedlings of mullet species in general is far from comparable to that of the milkfish it should be stressed that in all habitats where milkfish were caught at least one mullet species was presented, however, milkfish are not necessarily found in locations where mullet are abundant.

CONCLUSIONS

Coastal sedimentary areas which develop highly productive intertidal estuaries, nipa and mangrove swamps are important if not the only feeding and nursery grounds for fry and juveniles of milkfish, *Chanos chanos* F. The accumulation of particulate organic matter (mostly terrestrial and marine primary producers) which is acted upon by micro-organisms constitute the dominant part of the diet of the fish after the fry enter these depositional environments and remain there throughout the juvenile stage. In these habitats the role of macroorganisms (grazer and browser) is the reduction of particle size through physical breakdown, whereas the role of microorganisms is to chemically break down the organic matter and make them available to the macroorganisms. When detrital matter is ingested, dissolved organic matter and associating microorganisms are utilized whereby most plant materials are passed out undigested. The faeces are recolonized and ingested again. The cumulative result of this process is a steady reduction of particle size with the consequence increase of surface-area-volume ratio, leading to an increase in microbial population and nutritive value. The functional concept and evidence of this trophic pathway is well documented in MELCHIORRI-SANTOLINI & HOPTON (Eds.) (1972) and cited literatures therein. The ecology of the best known marine fish which utilizes detritus as its major source of food is the striped mullet, *Mugil cephalus*. Another successful species of similiar ecology and of high aquaculture potential is the milkfish, *Chanos chanos* F. Result of this ecological study presents evidence that in nature the grazing pathway in which fresh plant materials are ingested and utilized is practically insignificant. The majority of the primary production, moreover, enters the detritus food chain in which plant materials are attacked by micro-organisms before they could be utilized by the macroorganisms. This pathway of energy flow as shown schematically in Fig. 4. is not restricted to natural ecosytems but most

Fig. 4 : Schematic diagram showing the trophic and energy pathways utilized by fry and juvenile of milkfish, *Chanos chanos* F. with photograph of a typical densely vegetated nursery and feeding ground of the species.

probably also prevails in pond environments.

In almost all locations that have been studied it was found that the abundance of milkfish fry are closely related to the extent and natural condition of the depositional environments. This relationship among others gives strong hints that the mass appearance of fry along shore waters is a kind of collective feeding movement towards the nursery grounds. In nature the food of milkfish fry derives from four main sources; 1) diatoms, 2) zooplankton, 3) zooplankton excretion and 4) resuspended materials from the bottom, whereas the food of the juveniles derives from decomposing organic matter produced in the habitat or brought in from adjacent areas. This change of food habits reflects the different metabolic needs at different stages as well as availability of resources. The successful colonization of these coastal habitats by this detritus feeder is due to the short food chains which are bioenergetically cheaper and more advantageous. The high number of predators as well as the evidence of predation during the fry stage suggest that the search for food exerts a stronger selective pressure over predation avoidance. Although preventive measures through adaptive morphological and behavioural pattern exist, high mortality due to predation occurs in the transitional habitat and during the metamorphic phase.

The absence of a significant feeding periodicity as determined from stomach content might be due to generally low digestibility and assimilation efficiencies of the sediments thus accounting to high ingestion rate. Feeding intensity as observed in nature, however, is not a function of time, accessibility of diets (KEAST & WELSH, 1968), light intensity or state of tide but reflects a kind of optimal foraging strategy by minimizing feeding activity wden metabolism is constrained by suboptimal oxygen level and vice versa by increase foraging activity and maximize energy assimilated when oxygen level improves.

In the technique of rearing larval fish considerable amount of single cell phytoplankton (green water) is added together with other food organisms. Although the phytoplankton are not directly intended to serve as food for the larvae, experiences have shown that these plant cells are found in the gut lumina of the fish. Whether they are ingested directly from the water column or indirectly through the guts of the zooplankton diets is not of concern here. The problem is, if these phytoplankton cannot be digested in the more developed intestinal tract of fishes of more advanced stages, how much more impossible it seems for the larvae to utilize this food source. Since larval fish are particulate feeders and feeding activity is motivated by visual contact of the suspended particles regardless of their nutritive value, possibility of encounter and chances of ingesting this abundant but "useless" food source is high. The high energy expenditure wasted in foraging activity and low energy reserves in larvae suggest that the use of green water (in spite of its other advantages) is one of the responsible factors of past and presence unsuccessful attempt to increase markedly the survival rate of reared fish larvae. It should be reminded that the conclusions presented here are postulated from indirect evidences in nature, further studies therefore will be needed to confirm this generalization.

Apart from the complexity of the nature of this ecological investigation, one dominating difficulty at the present lies in the scarity of undisturbed natural habitats which can serve as indications for baseline conditions. None of the locations that have been covered by this study can be considered as absolutely "virgin". The few relatively untouched habitats are of such small size that it is not possible to remove the animals without disturbing and significantly destroing that which was to be measured. Nevertheless the knowledge obtained from this study indicates that, whether milkfish population as well as milkfish fry industry in the Philippines can manage to persist or not will depend on the availability of these diminishing depositional habitats as a connecting link between the oceanic stages (larvae, fry, subadult and adult) of the species. Although the practical implications of this ecological study for environmental management as well as for the development of appropriate aquaculture technology are still meagre, it is hoped that the promising value of ecological knowledge can be recognized.

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