BIOLOGY OF MILKFISH
(*Chanos chanos* Forsskal)

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AQUACULTURE DEPARTMENT
SOUTHEAST ASIAN FISHERIES DEVELOPMENT CENTER
Tigbauan, Iloilo, Philippines

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PREFACE

Milkfish is a fascinating creature. It is a primitive species, dating back about 40 million years, but it is also highly differentiated. It has a rather complex life history and a high degree of ecological and physiological flexibility. Once called the mysterious milkfish, it is slowly yielding its secrets. In the next hundred pages, I composed a biography of milkfish based on studies I have been personally involved with, as well as data in the literature.

The present monograph is a comprehensive up-to-date account of milkfish biology, excluding the technical details of artificial propagation, culture, nutrition, and pathology. Its origins lie in my involvement in the Milkfish Ecology Project of the SEAFDEC Aquaculture Department that in 1975-1985 conducted studies on the occurrence, distribution, natural life history, feeding, growth, and reproduction of milkfish, particularly around Panay Island in west central Philippines. Details of these ecological studies have been summarized and discussed by Dr. Shigeru Kumagai in his Ph.D. dissertation, and have come out in several separate publications by Senta, Kumagai, Bagarinao, and other colleagues. This monograph includes the results of these ecological studies, together with a review of the scattered literature on milkfish, including the old and nearly forgotten (from the 1920s), the obscure and almost unknown (local/national journals), the virtually inaccessible (institutional progress reports), and the current and very recent (international journals). Data on milkfish in culture are used to complement data on milkfish in nature. I have incorporated as much information as I found relevant and reasonable.

Due to this conscious effort to be comprehensive, the monograph may have less focus and depth. Rather than being "mean and lean," it brings together a large body of mostly disparate information, perhaps at the cost of losing interpretative strength and at the risk of perpetuating uncritical conclusions (e.g., from journals lacking peer review). However, the monograph does fulfill an important function. Between these pages, one can find out what has gone on before in many areas of milkfish biology. Interested biologistscan then act accordingly: reject the information, check it out, or test it by doing further work. Now it is no longer accurate to say "little is known of milkfish biology..." nor to assume that "nobody knows." Although replication is the hallmark of science, reinventing the wheel by sheer ignorance is unnecessary and costly. The monograph provides a good measure of how much milkfish biology is known, all in an accessible package. The knowledge is incomplete to be sure, but therein lies the challenge. Let the monograph be a springboard for more concerted and better directed efforts in the future. For indeed much more research needs to be done.

The importance of milkfish to the livelihood and nutrition of the Asian-Pacific peoples is evidenced by the enormous amounts of land, water, and human resources involved in milkfish culture. Close to three-quarters of a million hectares of ponds and inland waters are currently utilized to culture milkfish. The culture industry (fry fishery and marketing, grow-out culture, and related enterprises) employs more than a million people. People have been trying to understand and control milkfish since about four centuries ago (in primitive ponds), but only recently has it been studied enough to be controlled (as in artificial propagation). Perhaps biological knowledge will enable us to exploit milkfish to the fullest. Better yet, maybe it will enable us to reap the benefits within sustainable limits.

This monograph is written for biologists, students, and laymen. Use of technical terms is minimized. There are nine major chapters that vary in amount of detail and interpretation. They are more or less independent of each other, and may be consulted separately. For expanded treatments of specific topics, readers should consult the cited primary literature.

I composed most of the tables and figures in this monograph using numerical data from published sources (all properly acknowledged), or my own calculations based on unpublished material. Some figures and tables were modified from Dr. Kumagai's dissertation. Very few of the tables and figures in this monograph appear elsewhere.

The Milkfish Ecology Project at the SEAFDEC/AQD generated some of the materials included in this report and the members are hereby acknowledged: Dr. T. Senta, Dr. S. Kumagai, V. Baftada, P. Buri, N. Castillo, R. Salde, A. Trifto, A. Unggui, L. Ver, A. Villaluz, and W. Villaver. I thank Drs. R. Ferraris, J. Juario, C. Marte, and members of the AQD Publications Review Committee for criticism of the manuscript. Dr. F.J. Lacanilao of the SEAFDEC Aquaculture Department and Dr. F.B. Davy of the International Development Research Centre (Canada) supported publication of the monograph. M. Castanos, J. Lagoc, and R. Rivera guided the manuscript through revision spasms and finally into print. Maraming salamat po. Lastly, I pay homage to *Chanos chanos* for providing me years of intellectual stimulation.

Teodora Bagarinao
Tigbauan and La Jolla
September 1991

BIOLOGY OF MILKFISH (CHANOS CHANOS FORSSKAL)
September 1991

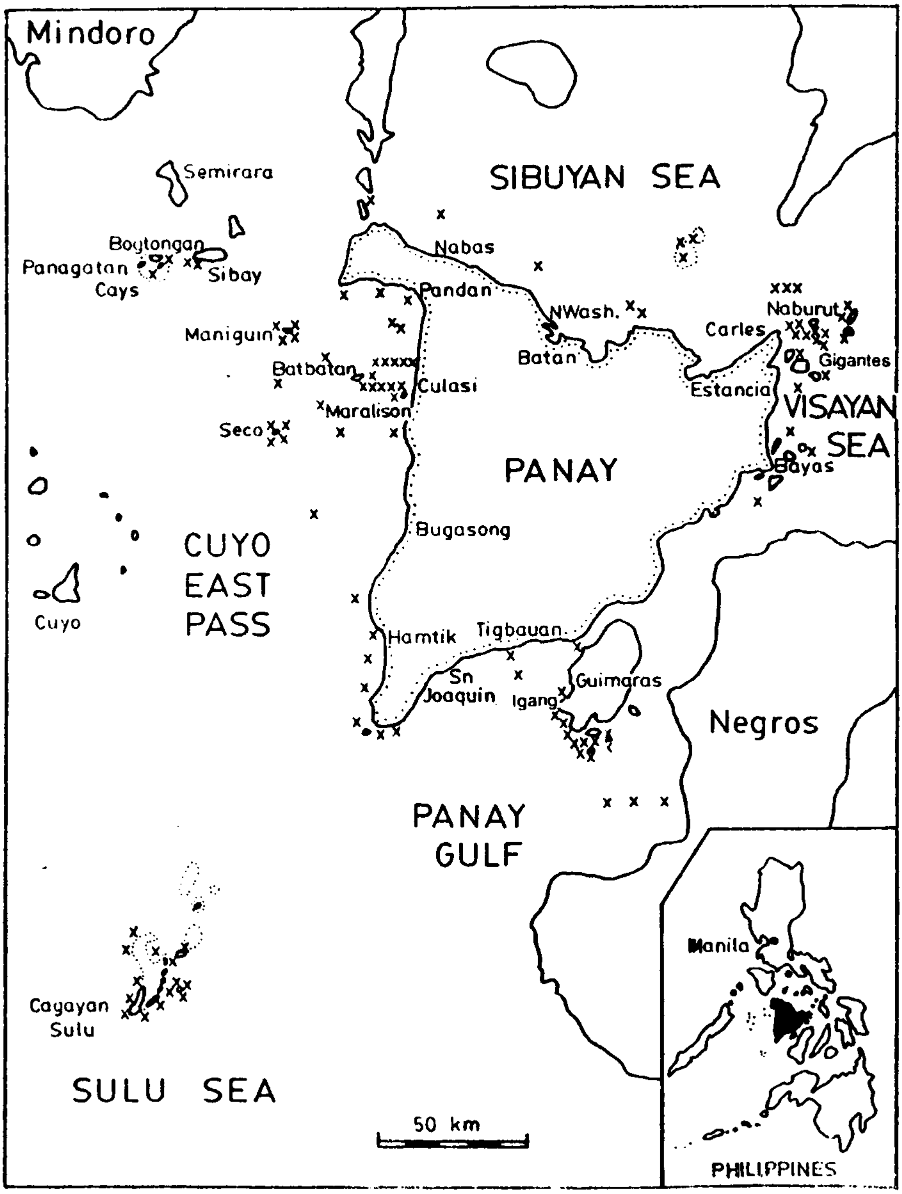
CONTENTS

INTRODUCTION

Milkfish (*Chanos chanos* Forsskal 1775) is one of the few well-studied tropical marine fishes to date. It has been the subject of numerous studies of varied extent and depth by investigators from Madagascar to Mexico and from Japan to south Africa. Most of the advances in biological knowledge on milkfish came about within the past 15 years as a result of research conducted in support of efforts to artificially propagate the species in several countries in the Indo-Pacific, particularly the Philippines, Taiwan, Indonesia, and the USA (Hawaii). Recent conferences have reviewed advances in artificial propagation, culture, economics, nutrition, and pathology (Juario et al. 1984a; Lee & Liao 1985). Earlier, Schuster (1960) and Crosby et al. (1982) wrote synopses of milkfish biology. Accounts of milkfish in aquaculture books (e.g., Bardach et al. 1972; Iversen 1976) have mostly been lifted from Schuster (1960) and are now outdated or erroneous.

The monograph begins by considering the morphology, phylogenetic relationships, geographic distribution, and genetic variation of milkfish, mainly from the work of American taxonomists and evolutionary biologists. Then it lays out what is known of the natural life history, this based mostly on the ecological studies conducted by the SEAFDEC Aquaculture Department. Feeding and growth at different stages in the life cycle both in the wild and in the pond or laboratory are described in general terms. Information on feeding and growth has immediate relevance to aquaculture, and the readers are urged to consult the primary authors for technical details and discussions of applicability. Age, growth, and mortality data on cultured milkfish abound, but little is known of milkfish population biology in nature. No stock assessment has been conducted. A chapter deals with milkfish reproduction, combining data from nature and the results of artificial propagation at SEAFDEC/AQD and elsewhere. The behavior of milkfish, particularly its migration habits at sea, is definitely a gray area, with few specific studies. Data from various unrelated studies in environmental physiology of milkfish are combined into one chapter. Critical studies in this field are few and fairly recent; there is certainly need for more. The monograph ends with a short discussion of community relationships of milkfish, studies of which are little more than species listings. Certainly, a great deal has been learned about milkfish, but much more still remains a mystery.

Ecological studies conducted by SEAFDEC/AQD form the backbone of this monograph. These studies were concentrated in the waters around Panay Island in west central Philippines (see map). In this report, repeated references will be made to places in Panay where particular studies or collections were conducted, so a brief orientation is warranted. Iloilo, the major city in southern Panay, is an hour's flight from Manila. Tigbauan, 25 km from the city, is where the main station of SEAFDEC/AQD is located and where laboratory studies are conducted. Pandan and Pandan Bay on the northwest coast is where SEAFDEC/AQD used to have a station for breeding and ecological studies. Hamtik on the southwestern coast is a highly productive milkfish fry collection



Map of Panay Island, central Philippines, where much of milkfish research has been conducted. Places mentioned in this report are indicated. The stations occupied for plankton sampling are indicated by x.

ground. Around Panay Island, particularly in Tigbauan, Hamtik, and Pandan, are situated seasonal fish corrals and *otoshi-ami* set nets that catch adult milkfish migrating along the coast. Maralison, Batbatan, Seco, and Maniguin islands in Cuyo East Pass, and Cagayan Sulu in the Sulu Sea have been identified as milkfish spawning grounds based on the collection of milkfish eggs and larvae. Naburut, Gigantes, and Bayas islands off northeastern Panay, and Bogtongan, Sibay, and Semirara islands off the northwestern coast have mangrove lagoons where wild juvenile milkfish have been collected. The southern and western coasts of Panay are mostly sandy beaches where milkfish fry are commercially collected. The northern and eastern coasts are mostly mangrove areas with large portions converted to culture ponds. SEAFDEC/AQD's floating cages of milkfish broodstock are located in sheltered coral coves in Igang on Guimaras Island. On Mindoro Island is Naujan Lake, the freshwater lake inhabited by milkfish of pre-spawning age.

Repeated references are also made in this monograph to investigations conducted by other institutions. Before SEAFDEC/AQD came into existence, the University of the Philippines and the Philippine Bureau of Fisheries and Aquatic Resources took the lead in milkfish studies. In Hawaii, research on milkfish is conducted by the Oceanic Institute; and in Taiwan, by the Taiwan Fisheries Research Institute and recently by private fish farmers. The Research Station for Coastal Aquaculture is developing artificial propagation techniques for milkfish in Bali, Indonesia. The Central Marine Fisheries Research Institute of India has been conducting studies on milkfish since the 1950s. A number of Japanese researchers have been involved in milkfish investigations mostly as a result of the association of the Japan International Cooperation Agency (JICA) with SEAFDEC/AQD. Elsewhere in the Indo-Pacific, studies on milkfish are incidental to other investigations. The following account attempts to put all the information together into a picture of this fascinating species.

SPECIES IDENTITY AND HISTORY

Taxonomy

Chanos chanos is the sole species in the family Chanidae in the Order Gonorynchiformes. It was first described as *Mugil chanos* by Petrus Forsskal in 1775; the type specimen (dried skin) from the Red Sea is now housed at the Zoological Museum of the University of Copenhagen in Denmark (Klausewitz & Nielsen 1965). Lacepede used the name *Chanos arabicus* in 1803, elevating the specific name to generic level. Cuvier & Valenciennes described milkfish under 10 different names, while 15 other authors described it under 18 other synonyms (Herre & Mendoza 1929; Schuster 1960; Crosby et al. 1982). In part these different synonyms may have been due to apparent geographic variation.

The Order Gonorynchiformes is characterized as follows (Nelson 1984): Epibranchial organ present, consisting of lateral pouches on the posterior part of the branchial chamber; mouth small; jaws toothless (except in phractolaemids); first 3 vertebrae specialized and associated with 1 or more cephalic ribs; 5-7 hypural plates; intermuscular bones present. There are 4 families, 7 genera and 27 species in the Gonorynchiformes: Chanidae (1 species, marine to freshwater, Indo-Pacific), Gonorynchidae (1 species, marine, Indo-Pacific), Phractolaemidae (1 species, freshwater, tropical Africa), and Kneriidae (24 species, freshwater, tropical Africa and Nile).

The Gonorynchiformes is placed in the Series Anotophysi of the Superorder Ostariophysi, Infradivision Euteleostei, Division Teleostei, SubClass Actinopterygii, Class Osteichthyes, Phylum Chordata (Nelson 1984).

Morphology

Detailed morphological description of milkfish can be found elsewhere (Herre & Mendoza 1929; Jordan & Evermann 1973). The FAO Species Identification Sheets (Fischer & Whitehead 1974) gives this description:

> Body elongate, moderately compressed, without scutes along belly. Eye covered by a fatty outer corneal layer (adipose eyelid). Four branchiostegal rays. Maxilla short, not reaching back beyond eye center; lower jaw with symphysial tubercle. Supramaxilla absent. No gular plate (small bony plate between arms of the lower jaw common in clupeids). Dorsal and anal fins with basal sheath of scales. Large axillary scales at base of pectoral and pelvic fins. Caudal fin deeply forked. Scales small, cycloid (smooth). Lateral line present. Color: back olive-green, sides silvery. Dorsal and caudal fins with black margin. Inside of pectoral and pelvic fins dark.

None of previous descriptions mentions a rather obvious character: the line of small, thin, scale flaps on the dorsal aspect of the caudal peduncle (Fig. 1). Morphometric and meristic data on adult milkfish in Pandan Bay are shown

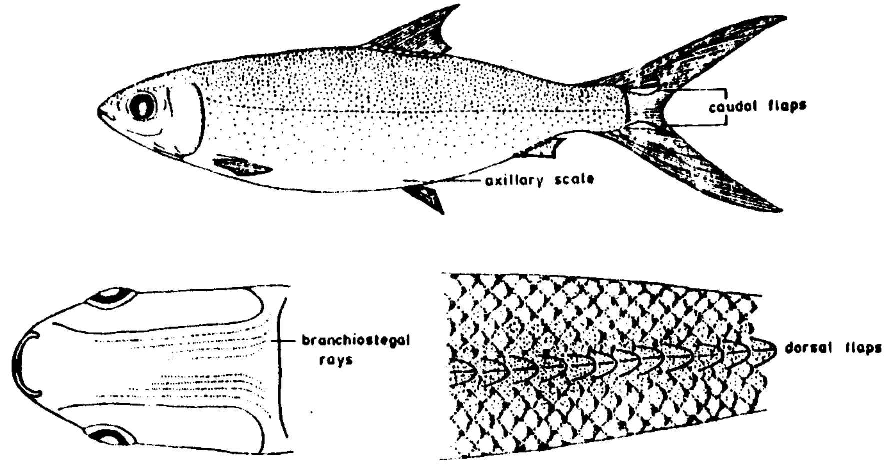


Fig. 1. Milkfish, *Chanos chanos* (Forsskal): the countershaded coloration, deeply forked caudal fin, and the fusiform, streamlined, and muscular body indicate a pelagic and migratory habit (*Modified* from Kumagai 1981).

in Table 1 together with data of other authors for milkfish from other localities. Variation in counts and body proportions is apparent, due to methods used and to some real differences. Table 2 gives regression equations among different length measurements of milkfish in different life stages and localities.

Table 1. Meristicsand morphometry of adult milkfish from various localities

Character	Philippines		Indonesia	India	Hawaii	Papua-N Guinea
	(Kumagai 1981)	(Herre & Mendoza 1929)	(Sunier 1922)	(Day 1958)	(Jordan & Evermann 1973)	(Munro 1967)
Dorsal fin	ii-iv,10-14	II,12-14	14-16	13-16	II,12	13-17
Anal fin	i-ii,7-9	II,8-9	10-11	9-10	II,9	9-11
Pectoral fin	i,13-16	I,15-16	16-17	16		16-17
Pelvic fin	ii,9-12	I,10-11	11-12	11		11-12
Ll scales	79-88	80-90	83-90	80-90	86	75-91
Above Ll	11-15	12-13		12	12	
Below Ll	10-16	10-11		15	14	
Vertebrae		44	44-45	44	45	
SL/HL	4.26	3.5-3.8		5.2-55*	4.4	3.2-45
SL/BD	4.21	3.5-3.8		4.6-5.3*	4	3.5-4.8
HL/snout	4.40	4.1-4.6			3.5	
HL/eye	4.42	3.2-3.5		3.5-3.8	3.5	3-3.6
HL/maxilla	4.01				4.3	

*Relative to TL not SL. Ll, lateral line; SL, standard length; HL, head length; BD, body depth. For fin counts, roman numerals refer to spines; arabic numbers, rays. Measurements and counts are ranges or means.

Table 2. Regression equations for length measurements of milkfish

Locality	Stage/ FL (cm)	n	Regression equations*
Philippines[1]			
Pandan Bay	adults 60-110	41	$\mathrm{TL} = 14.2163 + 1.0463\ \mathrm{FL}$ $\mathrm{TL} = 20.2469 + 1.0324\ \mathrm{SL}$ $\mathrm{FL} = 6.3454 + 0.9793\ \mathrm{SL}$
Naburut Is.	juveniles 2-17	225	$\mathrm{TL} = -3.9908 + 1.2310\ \mathrm{FL}$ $\mathrm{TL} = -2.1594 + 1.3388\ \mathrm{SL}$
Hamtik	fry 1-1.5	20	$\mathrm{TL} = 0.0059 + 1.0303\ \mathrm{FL}$ $\mathrm{TL} = 0.1050 + 1.1248\ \mathrm{SL}$ $\mathrm{FL} = 0.2510 + 1.0792\ \mathrm{SL}$
Taiwan[2]			
Tungkang	fry (early season)		$\mathrm{TL} = -0.4331 + 1.0608\ \mathrm{FL}$
	fry (late season)		$\mathrm{TL} = -0.5121 + 1.0640\ \mathrm{FL}$
India[3]			
south	juveniles-adults 30-100	29	$\mathrm{TL} = 2.7279 + 1.2215\ \mathrm{FL}$
Sri Lanka[4]			
Negombo	juveniles 8-17	31	$\mathrm{TL} = -2.1881 + 1.2934\ \mathrm{FL}$ $\mathrm{TL} = -6.1488 + 1.3923\ \mathrm{SL}$
Hawaii[5]			
Kona ponds	adults 50-70	50	$\mathrm{TL} = 3.8563 + 1.0203\ \mathrm{FL}$
Christmas Is.[6]			
Pelican Lagoon	juveniles-adults 30-40	29	$\mathrm{TL} = -3.1784 + 1.2287\ \mathrm{FL}$
Te Bati Lagoon	juveniles-adults 30-75	17	$\mathrm{TL} = 18.3567 + 1.1959\ \mathrm{FL}$
Pond 14	juveniles-adults 40-50	15	$\mathrm{TL} = 25.0278 + 1.1773\ \mathrm{FL}$

*Units are cm for adults and mm for juveniles and fry. Equations were derived from data at SEAFDEC/AQD and from data of various authors: [1]Kumagai 1981; [2]Liao et al. 1977; [3]Tampi 1958; [4]Bagarinao & Thayaparan 1986; [5]Nash & Kuo 1976; [6]Oceanic Institute 1980. FL, fork length; SL, standard length; TL, total length.

Body proportions change with growth. In addition, there may be geographic differences. For example, using multivariate analysis, Winans (1985) found Philippine milkfish to have smaller head features and larger tails than equatorial Pacific and Hawaiian specimens.

Varieties

A specimen of milkfish with distinctly elongated dorsal, pelvic, and anal fins, and a caudal fin as long as the body (Fig. 2) was made available to the author by a fish farmer (D. Jamandre) in Iloilo in 1983. This goldfish-type

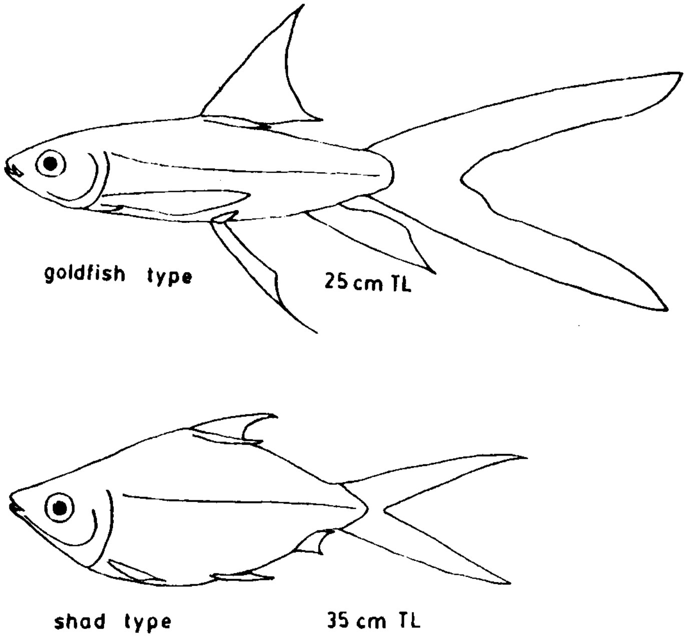


Fig. 2. Varieties of milkfish: the gold fish-type recorded from Iloilo, Philippines; and the shad-type recorded from Indonesia (traced from photograph in Sunier 1922).

milkfish is probably similar to one from Indonesia mentioned by Schuster (1960). Dwarf or hunchback (shad-type, Fig. 2) specimens of milkfish, with length-to-depth ratio of 2.0-25 instead of the usual 3.5, have been recorded in Indonesia and Australia (Sunier 1922; Jordan & Evermann 1973). Although these shad-type juveniles have shorter bodies, they have the normal number of scales and vertebrae. Table 3 compares the morphometry of normal and variant types of juvenile milkfish. Recently, milkfish of unusual coloration - red head, red fins, and brillant-blue dorsal surface - was reported from Darwin Harbor in northern Australia (G. White, pers. comm.). Nothing is known about these varieties of milkfish since they rarely occur. Dwarf specimens, however, may be produced through stunting under conditions of limited space or very high salinity (Schuster 1960; Crear 1980).

Karyotype

Milkfish has a diploid chromosome number of 2n = 32, consisting of 7 pairs of metacentric, 2 pairs of submetacentric, and 7 pairs of acrocentric chromosomes (Arai et al. 1976). This diploid number is low compared to other primitive (i.e., early) teleosts. The original chromosome number may have been 50 because all the 2-arm chromosomes are approximately 2x larger than any 1-arm chromosome and appear to have been formed by centric fusion. Milkfish may be considered a much differentiated species, notwithstanding its primitive phylogenetic status.

Table 3. Morphometry of normal and variant juvenile milkfish

Character	Normal	Goldfish type	Shad type A	Shad type B
Standard length(SL)/ head length (HL)	3.7	3.5	3.2	3.4
SL/body depth	3.6	3.5	2.0	2.5
SL/predorsal length	1.9	1.9	1.8	
SL/preanal length	1.2	1.2	1.2	
SL/prepelvic length	1.7	1.7	1.6	
HL/snout length	4.3	5.8	3.4	3.5
HL/eye diameter	4.0	3.7	3.9	3.0
HL/maxilla length	4.0	5.8	6.3	
SL/dorsal fin length	4.7	2.3	3.8	
SL/anal fin length	6.1	2.6	10.0	
SL/pelvic fin length	7.6	2.4	5.6	5.0
SL/pectoral fin length	10.5	2.5	4.0	4.0
SL/caudal fin length	2.8	1.1	1.7	1.8
Total length (cm)	30.5	25.2	35.6	
Fork length (cm)	24.5	19.5	25.8	
Standard length (cm)	22.3	18.2	22.2	

Normal and goldfish type (Bagarinao, unpubl.). Shad type A measured from the photograph in Sunier (1922:201); B from Jordan & Evermann (1973).

Phylogenetic Relationships

Chanos was placed in the Order Clupeiformes by earlier authors, but Greenwood et al. (1966) on the basis of morphological studies concluded that:

1) *Chanos* is not a clupeiform because it lacks the intracranial diverticulae characteristic of the group;

2) *Chanos* shares many derived characters with *Kneria, Cromeria, Phractolaemus,* and *Gonorynchus* and thus constitute a close-knit and natural assemblage, the Order Gonorynchiformes;

3) *Chanos* and the gonorynchiforms are closely related to the traditional Ostariophysi, probably derived together from a common ancestral salmoniform.

The traditional Ostariophysi (defined by the presence of the Weberian apparatus) consists of the cypriniforms, characiforms, and siluriforms that together make up 72% of the world's freshwater fishes and somewhat over 25% of all teleost species. The Weberian apparatus consists of distinctive modifications of the anteriormost 4 or 5 vertebrae associated with movable ossicles that connect the swimbladder to the inner ear for sound transmission. Many vertebral characteristics of *Chanos* and other gonorynchiforms collectively define a trend toward the ostariophysan condition (Rosen & Greenwood 1970). Other similarities include: (1) presence of alarm reaction cells and alarm substance (Pfeiffer 1977), (2) details of the caudal skeleton, and (3) chambered swimbladder. Following an extensive comparative osteological study, Rosen & Greenwood (1970) and Fink & Fink (1981) concluded that gonorynchiforms and the traditional Ostariophysi are sister-groups, and in a phylogenetic classification, placed the former in the Series Anotophysi within an expanded Ostariophysi, the fishes with a Weberian apparatus being in the Series Otophysi. Fink & Fink (1981) suggested that *Chanos* is the sister-group of all other recent gonorynchiforms, and *Conorynchus* the sister-group of the African freshwater forms.

Biochemical studies corroborate the phylogenetic status of milkfish suggested by its morphological relationships. Investigation of the lactate dehydrogenase enzymes in 12 euteleostean species showed that milkfish expresses the C4 isozyme in the liver, a finding that: (1) supports the hypothesis that the Gonorynchiformes and the Otophysi are sister-groups and (2) falsify the monophyly of gonorynchiforms and clupeiforms (Mok et al. 1988). The primitive status of milkfish is confirmed by 2 studies. Like the chondrostean species *Polypterus senegalus,* and unlike species of more advanced teleosts ranging from catfish to butterflyfish, milkfish lacks the enzyme catalase (Rabie et al. 1972; Smith 1976). Oncofetal proteins, particularly carcinoembryonic antigen (CEA), have been found in adult milkfish (Smith 1978a). Oncofetal proteins are interesting because: (1) they are found as normal components of developing mammalian and avian fetuses; (2) they occur in increasingly larger amounts in animals earlier in the evolutionary tree, e.g., sea cucumber has more CEA than milkfish; and (3) they are produced during certain types of malignancy (cancers), as if by embryonic or evolutionary regression.

Evolutionary History

The origin of the species *Chanos chanos* has not been precisely dated. The fossil chanid *Tharrhias* occurs in the upper Cretaceous Santana formation of Brazil (Patterson 1975), and *Parachanos* in the lower Cretaceous of Gabon and equatorial Guinea (Taverne 1974). Fossil species of *Prochanos* and *Chanos* occur in the Cretaceous, Eocene, and Miocene (Jordan 1905). Fossils of *Chanos* and *Gonorynchus,* or at least their close allies, are known from Eocene (about 40 million years ago, mya) freshwater deposits in north America (Greenwood et al. 1966) and in Italy and Lebanon (Ekman 1953; Patterson 1967).

The Ostariophysi is a very old group with a long and complex biogeographic history. All sister taxa among the major lineages are thought to have been broadly sympatric over Gondwanaland (Novacek & Marshall 1976). The divergence of the Gonorynchiformes from the Otophysi must have been an early event. The earliest known gonorynchiform (Upper Cretaceous, about 100 mya) is a gonorynchid that differs little from living forms; unmistakably otophysan fossils extend only to the Lower Paleocene (about 65 mya) (Patterson 1967). Novacek & Marshall (1976) suggested the following scenario. A population of pre-Ostariophysi occurred on both Africa and south America when these were still united. The Otophysi differentiated from a gonorynchiform-like ancestor in south America probably during the early Cretaceous after the initial opening of the south Atlantic. African gonorynchiforms underwent little change and are represented today by 2 relict families. By about 100 mya, a pronounced phase of marine transgression commenced that led to the union of the south Atlantic and the Tethys Sea by an epicontinental sea.

It could have been during this marine transgression that *Chanos* and *Gonorynchus* or their immediate ancestors invaded the sea and became members of the circumtropical Tethys Sea fauna. The Tethys Sea existed between Gondwana and Eurasia from the Jurassic to the Paleocene; its fauna became fragmented when the isthmus of Panama formed and Asia and Africa became connected during the Miocene and Pliocene (Ekman 1953; Novacek & Marshall 1976). Great climatic changes occurred at this time, resulting in drastic cooling of the Atlantic and the extinction there of many tropical invertebrates and fishes, including milkfish. Conditions remained largely favorable in the Indo-West Pacific and most of the fauna, including milkfish, persisted. Milkfish has since then colonized the east Pacific, probably by dispersal via the Equatorial Countercurrent (Briggs 1961), although debate still rages regarding such mechanism (Leis 1984; Rosenblatt & Waples 1986).

It is very interesting that milkfish has not speciated, given its old age and wide geographic distribution. Genetic divergence of milkfish populations is strictly quantitative (i.e., no fixation of alternative alleles) and low (Winans 1980). Milkfish has somehow remained in stasis for at least 40 million years. No evolutionary biologist has yet examined the developmental constraints or the stabilizing selection that may be operating on milkfish.

GEOGRAPHIC DISTRIBUTION AND VARIATION

Distribution

Southeast Asia appears to be the center of present-day distribution of milkfish. Aside from the Philippines, Indonesia, and Taiwan, milkfish occurs along the coasts of Thailand (Thiemmedh 1955), Vietnam (Kuronuma & Yamashita 1962), and Burma (Htin 1969). Milkfish is abundant in Sri Lanka, India, and around the Andaman, Nicobar, Laccadive, Maldive, and Chagos Islands in the Indian Ocean (Ramanathan 1969; Rao 1970; Tampi & Bensam 1976; Dorairaj et al. 1984). It occurs in the Red Sea (Ben-Yami 1968), the type locality being Jeddah. Milkfish ascends freshwater lakes in Madagascar and also occurs around the Comoros, Mauritius, and Reunion Islands (Therezien 1976). Along the south African coast, Whitfield & Blaber (1978) recorded 50-cm milkfish in Lake St. Lucia. Milkfish is said to be rare south of Durban (Smith 1961), but Marais & Baird (1980) obtained 4-kg adults in the Swartkops estuary in Port Elizabeth, latitude near 34°S, the southernmost record of milkfish. Milkfish occurs in New Guinea (Munro 1967), the Solomon Islands (Blaber & Milton 1990) and around Australia except the southern coast and rarely south of Queensland (Roughley 1951; Blaber 1980; Blaber et al. 1985, 1989). Milkfish larvae have been collected near Lizard Island, Carter Reef, and Yonge Reef in the Great Barrier Reef lagoon (around 15°S) (Leis & Goldman 1987). There is an old record of *Leuciscus* (*Ptycholepis*) *salmoneus*, a synonym of milkfish, in New Zealand (Richardson 1843 as cited by Herre & Mendoza 1929). In the northern hemisphere, adult milkfish has been recorded as far as 34°N in Wakayama, Japan and milkfish fry have been collected in Tosa Bay and the islands to the south (Senta & Hirai 1980; Senta et al. 1980b; Kinoshita 1984).

Milkfish is common throughout the Pacific Islands, from Guam to Tuamoto and from Hawaii to Tonga (Fowler 1938; Van Pel 1955; Kami et al. 1968; Jordan & Evermann 1973; Bagnis et al. 1974; Muench 1978; Crear 1980; Johannes 1981; Wainwright 1982). Milkfish is abundant in Kiribati, Fiji, Tonga, and New Caledonia, where culture from natural seed has been attempted (J. Juario and S. Kumagai, pers. comm.) and in Hawaii, Tahiti, and the Christmas Islands where breeding programs have been initiated. In the December 1921 issue of *National Geographic,* there is a picture of a quaint native Nauru dancer with milkfish as ceremonial ornament (Rhone 1921).

Milkfish is one of the few Indo-West Pacific species that occur on the other side of the East Pacific Barrier (Briggs 1961; Rosenblatt et al. 1972). Along the American coast, milkfish is common in bays and lagoons in Mexico (Castro-Aguirre 1978; Warburton 1979). It also occurs in Guatemala and Nicaragua (Miller 1966, 1976), El Salvador (Ramirez-Hidalgo 1975), and Panama (Rosenblatt et al. 1972). Chirichigno (1978) recorded a very rare occurrence of milkfish in Peru. Fowler (1938) collected 4 specimens of milkfish 30-cm long from Tower Island in the Galapagos, but there has been no report from there since then. On the other hand, milkfish was reported from Magdalena Bay in Baja California in 1929, and from San Pedro and San Diego Bays (latitude near 33°N) in 1979 and 1982-1983 (Duffy & Bernard 1985). These milkfish are probably strays from the Mexican population. There is no indication that the introduction from Hawaii in 1877 (100 milkfish stocked in a small stream at Bridgeport, Solano County, California) persisted (Duffy & Bernard 1985).

Figure 3 shows a plot of the various records of milkfish in the Indo-Pacific. The distribution appears to be more restricted than Schuster's (1960) illustration indicated. Milkfish has not been collected through offshore fishing fleets (e.g., for tunas). It apparently stays relatively close to islands and the coasts of continents. Distribution seems to be limited to waters with temperatures greater than 20°C, as defined by the winter surface isotherms. Milkfish is not found in tropical waters affected by cold ocean currents, as in Ecuador and Peru, but occur in temperate waters affected by warm oceanic currents, as in southeastern Africa and southern Japan. The latitudinal range of milkfish seems to coincide with those of reef corals which are also restricted to clear, shallow, saline, and warm waters > 20°C (Carcasson 1977).

Variation Across the Indo-Pacific

The relatively old age and wide Indo-Pacific distribution of milkfish raise the question of geographic variation and the existence of different populations in widely separated locations. Indeed, 2 types of evidence (protein electrophoretic data and morphological data) show that there are about 9 major

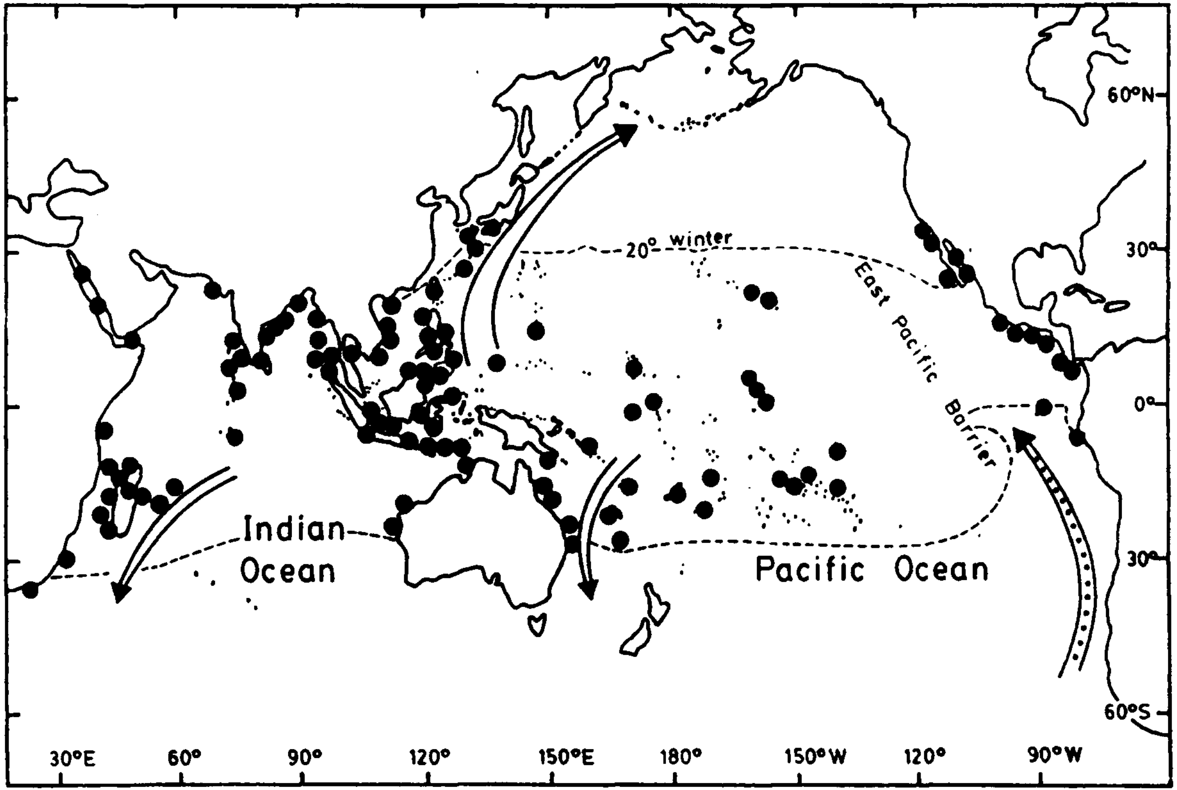


Fig. 3. Records of milkfish occurrence in the Indo-Pacific. Plain arrow, warm current; dotted arrow, cold current; dotted lines, 20°C surface isotherms in winter (Sverdrup et al. 1942). The East Pacific Barrier is an area of deep water without islands that prevents most fishes in the Indo-Pacific from crossing over to the American coast; milkfish is one of the exceptions (*Modified* from Kumagai 1981,1990).

populations of milkfish across the Indo-Pacific (Fig. 4). Through a statistical study of the variation in vertebral number of milkfish fry, Senta & Kumagai (1977) identified 4 populations: Indian, Thai, Philippine-Taiwan-Indonesian, and Tahitian. Fry samples from Kiribati, Tonga, and Hawaii, and of juveniles from Panama indicate 4 other populations (Senta 1982; Kumagai 1990). No sample has been obtained from the African coast, but it is most likely that there is at least one other population there. Winans (1980, 1985) analyzed electrophoretic variation at 38 loci and morphological variation in 6 meristic and 19 morphometric characters in milkfish from 15 locations in the Pacific. He found both similarities and differences between the patterns of morphological and electrophoretic variation, a not unusual finding that shows the two may be independent. He concluded, based mostly on electrophoretic data, that the genetic population structure of milkfish in the Pacific consists of 3 distinct groups: Philippine, equatorial Pacific (Palau, Kiribati, Fanning, Christmas Is.) including Tahiti, and Hawaiian. Tahiti may be provisionally considered a different population, following Senta & Kumagai (1977), whose results Winans (1980, 1985) did not know about. Winans' morphometric data separated Tahiti from the equatorial Pacific group, although his electrophoretic data did not. Winans did not include vertebrae among his meristic characters (samples were juveniles 9-37 cm FL, which were difficult to process for vertebral counts), and he found no differences among samples in the meristic characters he did study.

Winans' (1980) findings from protein electrophoresis are very interesting. One, milkfish populations in the Pacific Ocean have high genetic similarity, i.e., high level of gene flow, a phenomenon known among oceanic populations of other marine animals. For milkfish, the average generic distance (D, a measure of the variation at each locus summed over all loci) is 0.0001 between samples from the same island groups, and 0.0033 among island groups (D is ≤ 0.1 for conspecific populations). These values are low, considering the great distances (1700-10 000 km) separating these locations, and in comparison with other species. Two, milkfish has relatively high genetic variation; average heterozygosity per locus (for 38 loci) is 0.075, and about 16-23% of the loci are polymorphic. In comparison, the mean heterozygosity per locus is 0.063 for 6 marine species, and 0.043 for 9 freshwater species (Gyllensten 1985). Three, genetic variation in milkfish does not change with latitude, but decreases with increasing distance from the Philippines. The highest genetic variability in a species is usually found in the region of greatest effective population size, southeast Asia in the case of milkfish.

Both Smith (1978b) and Winans (1980) concluded that the milkfish around Oahu Island is a different population from that around Hawaii Island, only 320 miles away. This is a reflection of the high level of endemism that has occurred in the Hawaiian fish fauna.

Variation Within the Philippines

Winans (1980, 1985) found that 8 samples of milkfish from the Philippines were indistinguishable from each other on the basis of protein electrophoretic variation, and except for one location, on the basis of multivariate

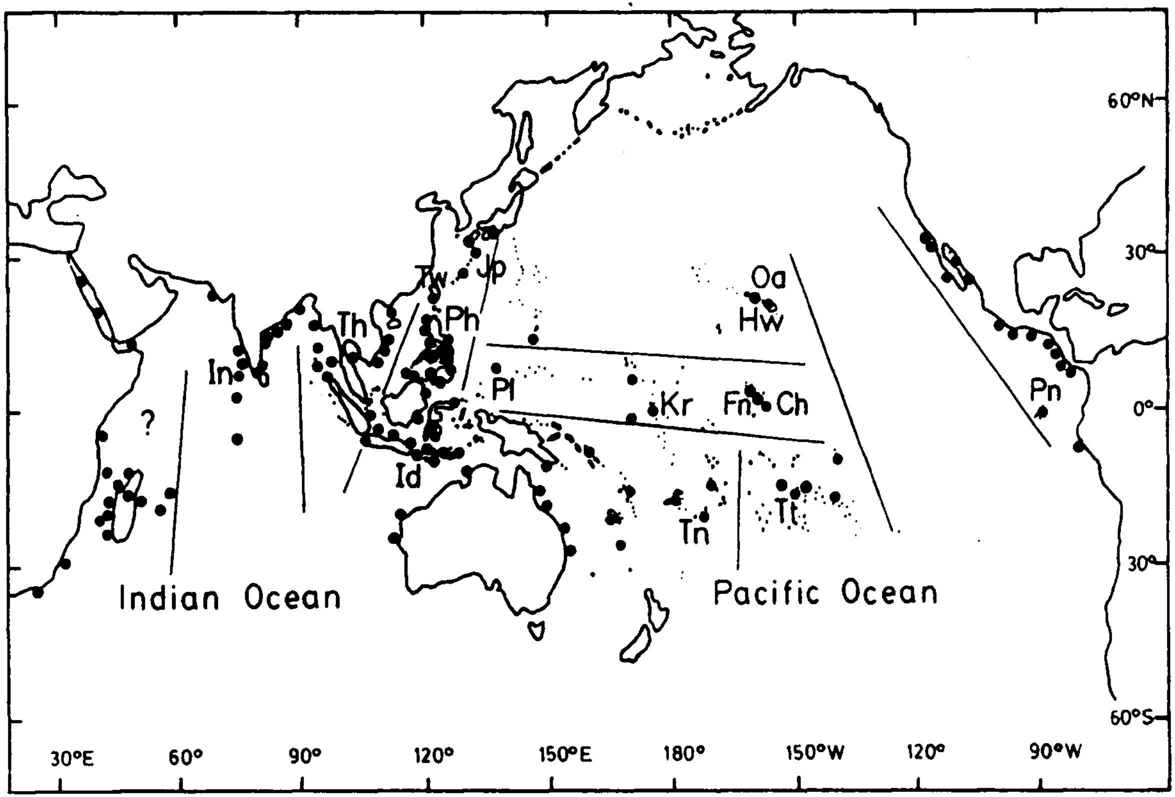


Fig. 4. Populations of milkfish in the Indo-Pacific as inferred from variation in vertebral number (Senta & Kumagai 1977; Senta 1982; Kumagai 1990), protein electrophoretic variation (Winans 1980),and multivariate body shape differences (Winans 1985). Two-letter abbreviations, localities sampled (In, India;Th,Thailand;Tw,Taiwan; Ph, Philippines; Jp, Japan; Id, Indonesia; PI, Palau; Kr, Kiribati; Fn, Fanning; Ch, Christmas Island; Tn, Tonga; Tt, Tahiti; Hw, Hawaii; Oa, Oahu; Pn, Panama; no sample obtained from African coast); lines, approximate boundaries of populations (*Modified* from Kumagai 1981,1990).

body shape differences as well. However, J. Macaranas and L. Benitez (pers. comm.) found genetic differences among milkfish from 3 localities in the Philippines and between those from the Philippines and Taiwan. Moreover, Villaluz & McCrimmon (1988) showed that the number of ventral fin rays in milkfish fry from 5 localities in the Philippines differed consistently to suggest 3 distinct populations: south China Sea, Pacific Ocean, and Celebes Sea.

Kumagai (1981, 1990) analyzed the vertebral numbers of milkfish fry around Panay (all samples collected during the same season to minimize the effect of temperature) and suggested that there may be 5 different spawning groups. It is not likely that a pelagic, strong swimmer like milkfish would establish isolated populations around such a small island. However, it is possible that milkfish forms small schools or local groups that migrate from time to time and spawn in different localities. In a study of LDH isozymes, Requintina et al. (1981) observed that the patterns in milkfish fry from Hamtik and Tigbauan in Panay Island are essentially the same, but that the dominant bands differ between fry caught in 2 seasons, April-June and October-November.

LIFE HISTORY AND HABITAT

Figure 5 diagrams the natural life history of milkfish.

Adults

Adult milkfish (50-150 cm total length, TL) are fish of the open sea, swift and powerful swimmers. During the breeding season, they frequent coasts where reefs and sandy-rocky shores are well-developed. Fishermen report that milkfish often form large schools and move slowly along the coast or around islands, oftentimes with dorsal fins sticking out of the water like sharks. During the March-June milkfish season in Panay, adults get caught in the *otoshi-amis* in Pandan Bay and in the fish corrals in Tigbauan, San Joaquin, and Hamtik (see map on p. 2), presumably during their coastal spawning migrations. Catches along the western coast are higher and tend to peak later in Pandan than in Hamtik (Fig. 6). Catches along the southern coast are lower than along the west, and those in San Joaquin come later than in Tigbauan. These differences may be related to the migration pattern of the adults. Some 3418 adult milkfish were caught by fish corrals in Morong, Bataan near Manila in 1952 (Ronquillo 1971). There is no fishery for adult milkfish in the Philippines (it is illegal to catch them), but they are occasionally caught by hook and line, longlines, gill nets, and other gear used in coastal waters for fishes like tuna and carangids (Manacop 1975). Only sometimes are milkfish seen in the vicinity of fish aggregating rafts (locally known as *payaw*) set 20-50 km offshore.

Adult milkfish are abundant in freshwater lake in Naujan, Mindoro, Philippines but annual catches have declined from 23-63 tons (t) (about 12 500

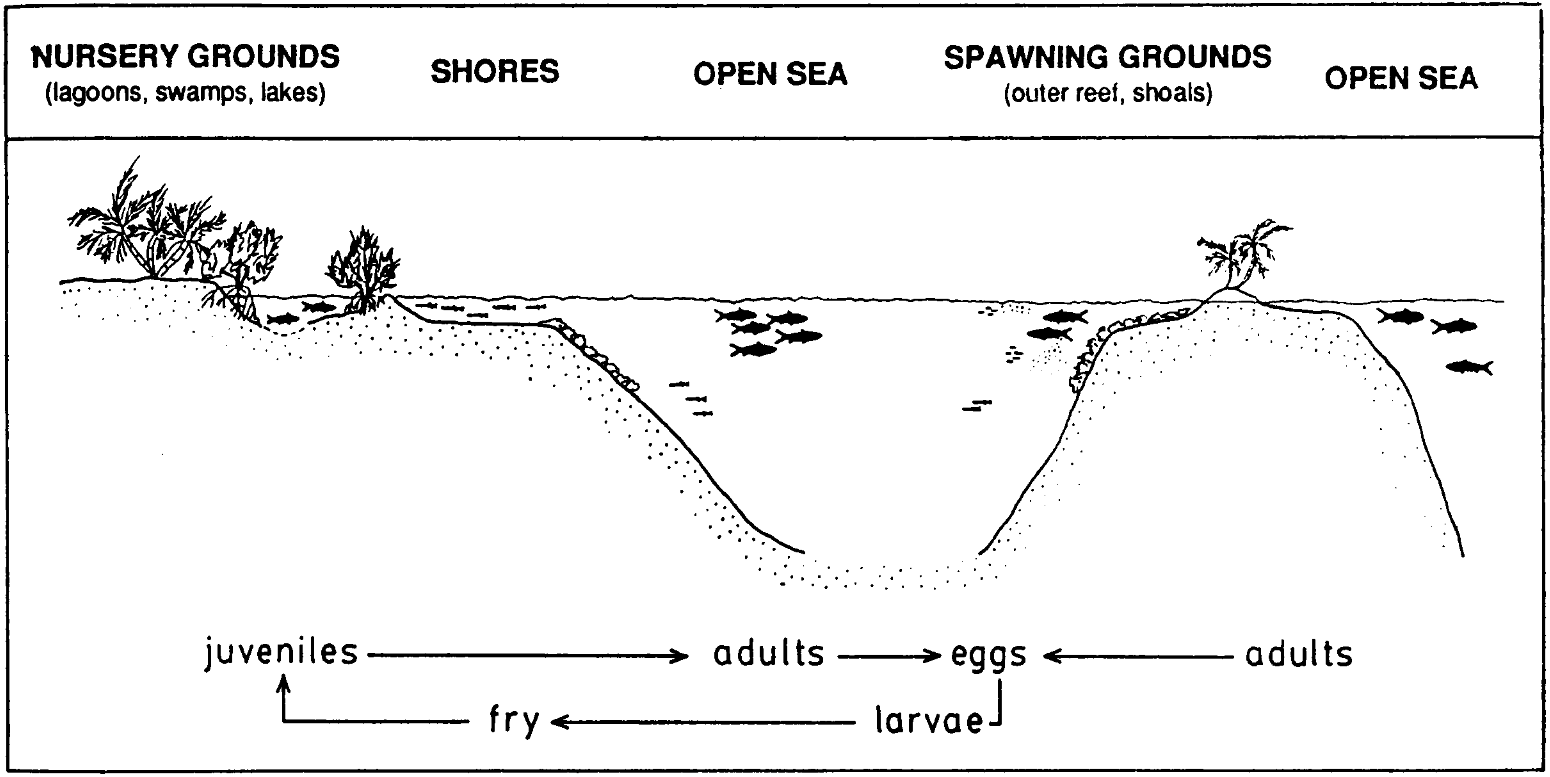


Fig. 5. Schema of the natural life history of milkfish. Land mass could be a large island/continental coast (left) or small island/shoal reef (right) Nursery grounds vary considerably (*Modified* from Buri et al. 1981).

individuals) a year in 1958-1967 (Delmendo & Angeles 1971) to 1.6-2.61 (335-537 individuals) a year in 1977-1978 (Reyes 1978). Milkfish leave the lake throughout the year, but peak migration occurs in November and December (Reyes 1978). All milkfish leaving the lake measure about 3-4 kg BW, 60-70cm TL, and are sexually immature (Delmendo & Angeles 1971). They apparently undergo sexual maturation within a relatively short period at sea. Milkfish (4-8 kg, 65-80 cm TL) caught in adjacent Naujan Bay from March to June are mostly sexually mature (Angeles 1971).

Taal Lake and Pansipit River, another freshwater system in southern Luzon, used to be populated by large numbers of adult milkfish. Catch records from fish corrals set across the river indicate that 7000-14 000 milkfish were caught per year in 1888-1890, 1000-2000 in 1926-1927, and 3000-6000 in 1933-1934, with seaward migration highest in March and October and lowest in January and May-June (Villadolid 1936).

Large schools of adult milkfish are reported near the coasts of Indonesia in shallow waters but annual catches are also low (Schuster 1952; Tjiptoaminoto 1956). They are caught by gill nets between midnight and early morning in waters 2-10-m deep (Martosudarmo et al. 1976). Adult milkfish inhabit the reefs and atolls of the Pacific and Indian Oceans and are considered excellent game. Along the American coast, the large coastal lagoons in southern Mexico have large populations of adult milkfish contributing about 1000 t a year to the fishery (J. Castro-Aguirre 1978, pers. comm.). In Madagascar, juvenile and adult milkfish are abundant in freshwater lakes and support a substantial traditional fishery (Therezien 1976). In the Red Sea, schools of milkfish (400-800 kg at one time; individuals 6-kg body weight) could be caught by purse seines; they apparently form local inshore populations along certain sections of the coast (Ben-Yami 1968).

Eggs and Embryonic Stages

Spawning takes place in the open sea and the eggs are pelagic. Delsman (1926, 1929) was probably the first person to have taken note of milkfish eggs when he examined the oocytes and later collected 15 eggs from the Java Sea. His identification of milkfish eggs was verified in 1977 when milkfish was first induced to spawn in captivity at SEAFDEC/AQD (Vanstone et al. 1977). Fertilized milkfish eggs are spherical (1.1 -1.25 mm in diameter) with finely granulated yolk, no oil globule, narrow perivitelline space, and no structures on the chorion (Fig. 7).

Embryonic development follows the usual course of teleost eggs (Vanstone et al. 1977; Chaudhuri et al. 1977, 1978; Liao et al. 1979). For purposes of ecological studies (e.g., determining when and where spawning took place), the following staging system may be employed (Fig. 7; Senta et al. 1980a). The shortest approximate time from fertilization to the end of each stage (water temperature, 26.4-29.2°C) is indicated.

Aa: Fertilization until blastoderm covers one-third of yolk and germinal ring becomes distinct. 6 h.

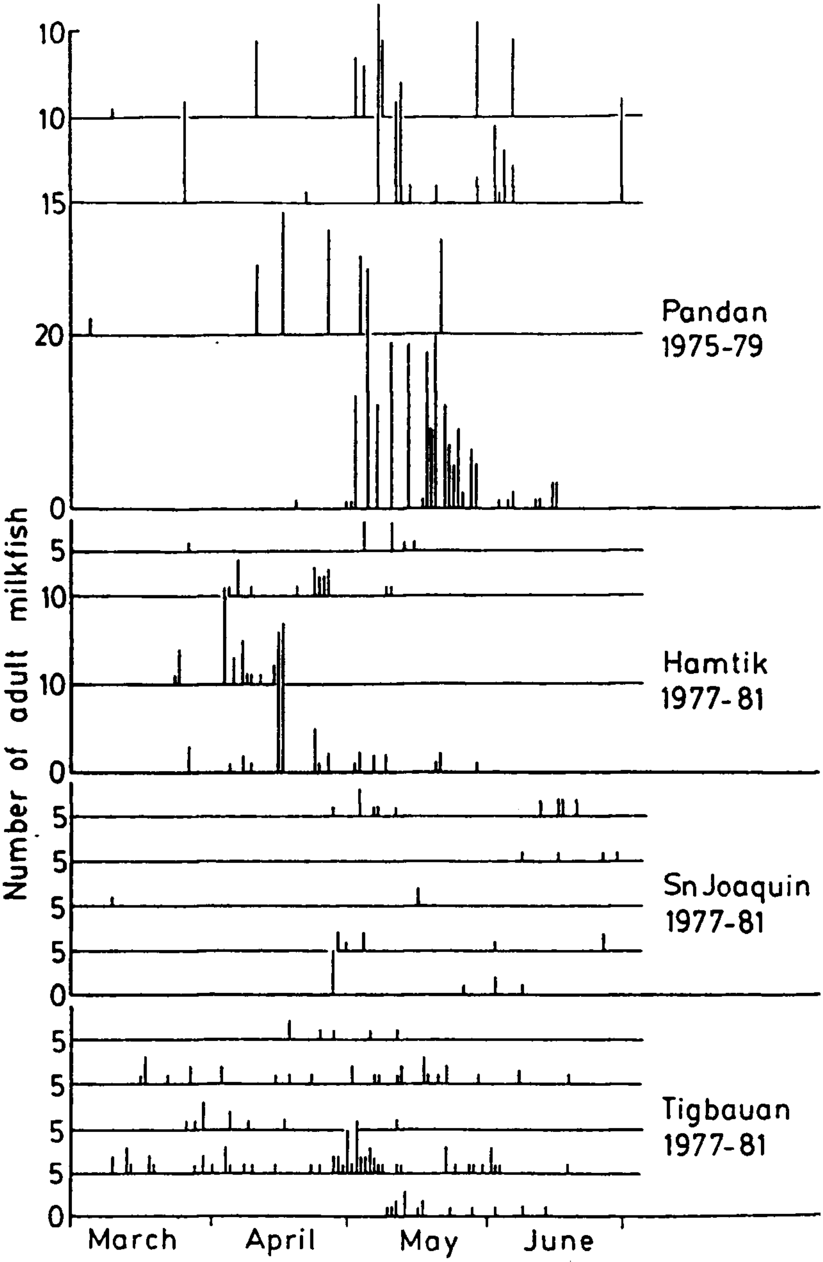


Fig. 6. Catches of adult milkfish in southern (San Joaquin and Tigbauan) and western (Hamtik and Pandan) Panay coasts by fish corrals and *otoshi-ami* in March-June 1975-1981. Earlier years at bottom of panel; Pandan data (1976-1977) combined, likewise Hamtik (1977-1978). Both gears were operated October-June; however, adult milkfish can hardly be caught outside March-June (Bagarinao, unpubl.).

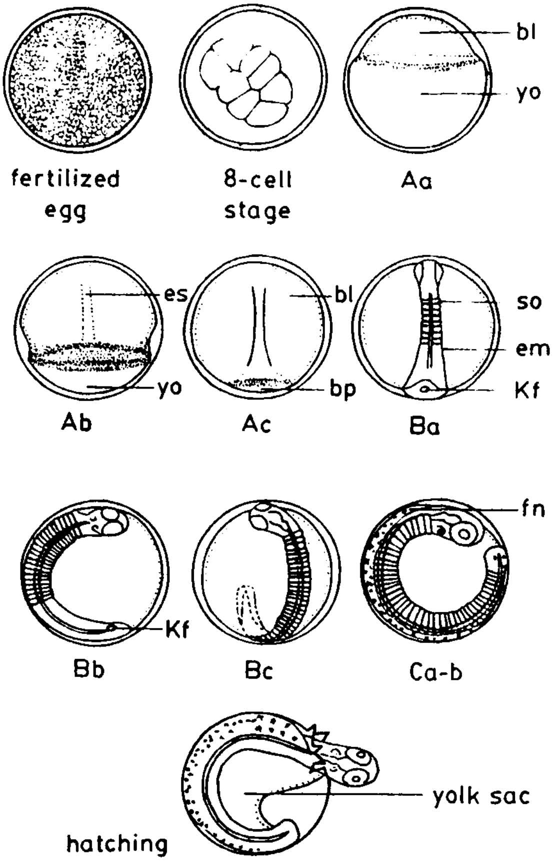


Fig. 7. Fertilized egg of milkfish, with finely granulated yolk and narrow perivitelline space. The stage of embryonic development, Aa to Cb, are shown minus details of the yolk (bl, blastoderm; yo, yolk; es, embryonic streak; bp, blastopore; so, somite; em, embryo; kf, Kupffer's vesicle; fn, finfold) (*Modified* from Kumagai 1981).

Ab: Blastoderm covers two-thirds of yolk; embryonic streak appears. 8-10 h.

Ac: Blastoderm completely covers yolk: blastopore visible; embryo without differentiated somites. 10-13 h.

Ba: Embryo with 9-10 somites: Kupffer's vesicle visible; optic vesicles start to develop. 11.5-15.5 h.

Bb: Embryo curled in a C-position with its posterior end still flat; head and optic and otic vesicles differentiated; 19-20 somites visible. 14-19 h.

Bc: Embryo forms girdle over yolk, its posterior end swelling to a profile vertical to yolk surface; brain differentiation in progress. 17-23 h.

Ca: Tail of embryo starts to separate from yolk but not yet elongated; unpaired finfold appears; optic lenses form; heart starts to pulsate. 20-29 h.

Cb: Embryo fully developed, its tail elongated and almost reaching the head; just before hatching. 25-35 h.

Incubation periods varied among investigations, but ranged 20-35 h at temperatures of 26-32°C and salinities 29.5-34 ppt (Vanstone et al. 1977; Chaudhuri et al. 1977, 1978; Liao et al. 1979; Juario et al. 1984b; Liao & Chen 1984).

Milkfish eggs have been collected from western Panay by plankton net tows (Senta et al. 1980a; Kumagai 1981,1990). Table4 may be used to identify and distinguish milkfish eggs from other species in plankton collections from Panay and possibly southeast Asia. Due to the granulation of the yolk, live milkfish eggs appear slightly yellowish when held against the light and can easily be sorted on-site. After formalin preservation, the granulation is difficult to discern and milkfish eggs may be mistaken for other species with similar characteristics particularly the clupeid *Etrumeus.* One way to resolve the confusion is to puncture the chorion and cut the yolk with pins. Milkfish yolk appears rough while the others appear smooth.

Table 5 shows the vertical distribution of milkfish eggs in western Panay In 1980, when the plankton survey was intensive, the densities of milkfish eggs per successful tow were 19,8, and 5 at depths of 0,20, and 30 m, respectively in the Culasi, Batbatan, and Maralison areas (see map on p. 2). Although no tows were made at 10 m, it seemed likely that the density would

Table 4. Characteristics of milkfish eggs and other species from plankton samples in Panay (Philippines) and southeast Asia (Senta & Kumagai, unpubl.)

Milkfish	Other species (examples)
pelagic	pelagic (many marine species) demersal, adhesive (*Siganus*)
discrete	discrete (many marine species) massed (*Antennarius*)
spherical	spherical (majority of species) ellipsoid (*Stolephorus*)
diameter 1.1 -1.25 mm	1.1 -1.3 mm (*Etrumeus*) <1.1 mm (majority marine species) >1.2 mm (eels)
oil globule absent	absent (*Etrumeus, Fistularia*) single (*Mugil, Scomberomorus*) multiple (*Siganus, Cynoglossus*)
perivitelline space narrow	narrow (majority of species) wide (eels)
chorion smooth*	smooth (many species) sculptured (*Synodus, Mugil*) with filaments (*Hemiramphus*)
yolk finely granulated, yellowish	finely granulated (*Etrumeus*) homogenous (*Fistularia*)
embryo with <45 myotomes at hatching, finfold pigmented	embryo with >50 myotomes at hatching (*Etrumeus*)

*Chaudhuri et al. (1978) and C Marte (pers. comm.) observed patterns on the chorion, which may be resolved under a scanning electron microscope.

Table 5 Vertical distribution of milkfish eggs in Batbatan, Culasi, and Maralison (Philippines)

Depth of tow (m)	Total tows	Positive tows	Total eggs	% positive tows	Eggs/ positive tow
1976-1979*					
0	77	15	80	19	5.3
10	67	18	71	27	3.9
20	66	12	47	18	3.9
1980**					
0	245	40	773	16	19.3
20	136	24	205	18	8.5
30	157	28	140	18	5.0

*Surveys exploratory, extensive over a wide area, and collected few eggs; **survey more defined, sampled particular spawning areas, and obtained more eggs *(Modified* from Senta et al. 1980a; Kumagai 1981, 1990). Catch differences by depth in 1980 were statistically significant (x^2=10.16, $p<0.05$).

have been between 20 and 10. There was no difference in distribution by developmental stage. Milkfish eggs float in still water of salinity >34 ppt, but the turbulence at sea would carry eggs from the surface to deeper layers.

Aside from Delsman (1926, 1929), other reports of milkfish egg collections from the open sea are those of Jacob & Krishnamurthi (1948) from Ennore, Madras, and Chacko (1950) from the Krusadai islands in the Gulf of Mannar. It is not certain that milkfish eggs were correctly identified by these authors.

Larval Stages

Milkfish larvae are constituents of open sea plankton. They have been described in detail by Liao et al. (1979) based on artificially spawned and hatchery-reared specimen, and further by Miller et al. (1979) based on plankton collections.

Newly hatched larvae measure 3.5 mm TL at hatching, have a large yolk sac (volume, 0.5 μl), unpigmented eyes, and no mouth. They grow to about 5 mm in 36 h, consuming about 90% of the yolk, and grow very little until day 5 when the yolk is completely exhausted (Fig. 8). Egg size, larval size, amount of yolk, and mouth size are greater in milkfish than in many other tropical marine fishes (such as the sea bass, *Lates calcarifer* and the rabbitfish, *Siganus guttatus).* This size advantage is probably one reason for the relative ease in rearing milkfish larvae in the hatchery and for the abundance of milkfish fry in the wild (Bagarinao 1986).

For purposes of ecological study, the larval period may be broken down into 5 stages based on morphological and behavioral characteristics (Fig. 9) following the system of Kendall et al. (1984). Total lengths are given for larvae from the plankton measured in the preserved condition and for larvae reared in the laboratory and measured in the fresh state (in parentheses).

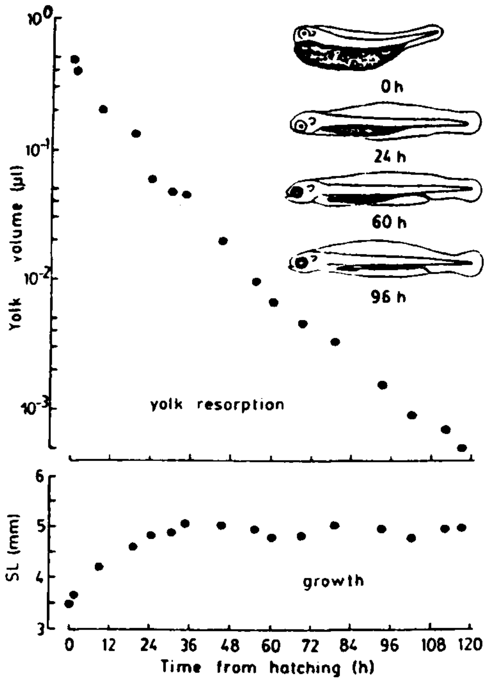


Fig. 8. Yolk resorption and early growth of milkfish larvae in the laboratory at 26-30°C (*After* Bagarinao 1986).

Stage I. Yolk-sac larvae: TL 3.3-4.4 mm (3.2-5.4 mm). Yolk present. Finfold pigmented particularly at the dorsal and ventral margins. Larvae suspend head down in the water column, sink slowly, and execute intermittent 360° turns. Stage lasts 3 d.

Stage II. Pre-flexion larvae: TL 3.4-5.6 mm (5.0-6.2 mm). Yolk absent. Eyes fully pigmented. Two lines of pigments dorsal and ventral of trunk from behind head to caudal peduncle. Notochord tip straight. Pectoral fins present. Larvae keep horizontal position in the water column and react to light and currents. Mouth functional and larvae shift from yolk to external food. Stage lasts 5 d.

Stage III. Flexion larvae: TL 4.4-9.9 mm (5.4-10.0 mm). Notochord tip flexed. Dorsal, anal, and caudal fins start to differentiate from the finfold. The swimbladder develops and is inflated at night. Line of pigments dorsal to the trunk becomes indistinct. Another line of pigments develops ventral to the abdomen starting from the throat. Pigments develop on the caudal fin rays. Larvae are transparent except for the eyes. Larvae begin to school; phototaxis and rheotaxis become stronger. Stage lasts 6 d.

Stage IV. Post-flexion larvae or fry: TL 9.5-16.5 mm (6.4-14.9 mm). Dorsal finfold disappears. Caudal fin forked. Vertebral column completely ossified. Adult complement of fin rays present (Taki et al. 1986). Dorsal

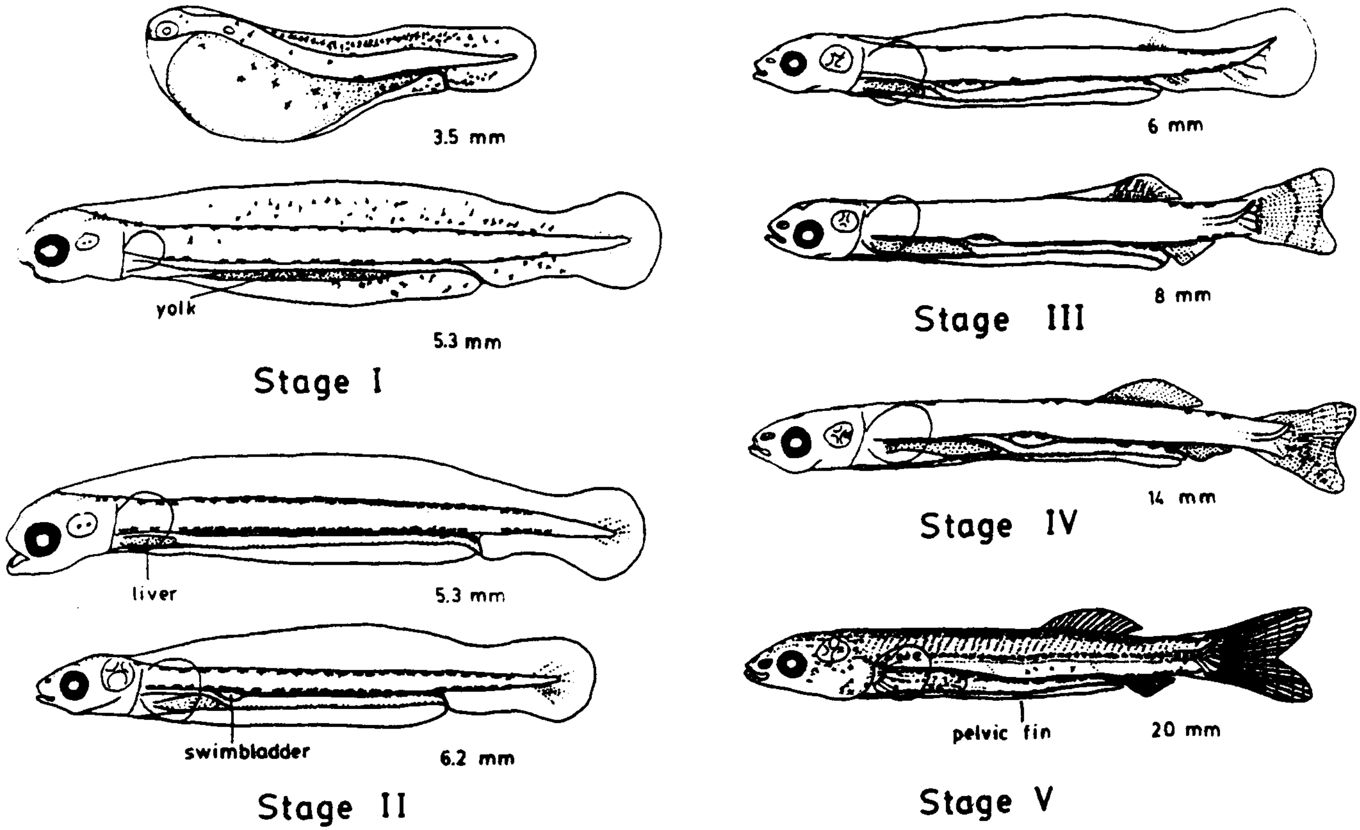


Fig. 9. Stages of larval development in milkfish: I, yolk-sac; II, preflexion; III, flexion; IV, post-flexion or fry; V, transformation. Details of myotomes and skeleton are omitted. Note changes in pigmentation pattern and the development of the fins (*Modified* from Kumagai 1981,1990).

contour lined by widely spaced pigments interrupted at the fin. Ventro-abdominal line of pigments extend more than half-way along intestine length. Larvae very transparent. React instantly to external stimulation; highly resistant to sunlight exposure, salinity changes, crowding, and even injury. Stage lasts 7 d.

Stage V. Transformation larvae: TL 9.5-16.5 mm (6.4-14.9 mm). Pelvic fins develop and the ventral finfold recedes. Peritoneal pigmentation silvery. Body surface covered with pigments, densest dorsally. A medio-lateral line of pigments develops anteriorly from the caudal peduncle. Scales develop about a month after fry stage or capture from shore waters (Kawamura & Hara 1980a). Larvae begin to feed on the bottom and form more cohesive schools. Stage lasts 2-4 wk.

Larvae in the Plankton

Larvae of stages I-IV have been collected from the open sea by plankton net tows. Figure 10 shows the vertical distribution of different stages of milkfish larvae in Culasi, Maralison, Batbatan, and Lipata off western Panay (Bagarinao & Kumagai 1987). Of 594 tows made, 42 tows yielded 44 larvae. About 45% of larvae of all stages occur in surface tows; younger larvae also occur in 20- and 30-m tows. About 70% of the larvae occur within 1-2 km of land in waters <100-m deep; the others in stations as far as 6 km from land in waters 325-m deep (Table 6). Younger larvae occur both far and near shore, but older larvae only near shore.

Younger larvae occur with the fry (specimens 5.8-14.6 mm TL; n = 1500) in the bag net of the *otoshi-ami* set 500 m offshore in 30-m deep water in Pandan

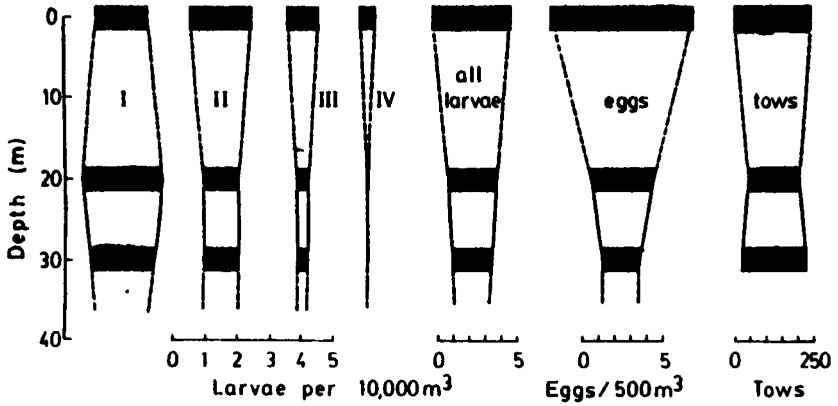


Fig. 10. Vertical distribution of milkfish larvae by developmental stages in Maralison, Batbatan, and Culasi off western Panay, Philippines in April-May 1980 (Bagarinao & Kumagai 1987). The vertical distribution of milkfish eggs collected during the same period is shown, especially with stage I larvae. Note that the density of eggs is on a scale 20x greater than that of the larvae.

Bay (Kumagai et al. 1976). Greater numbers of these younger larvae occur at the *otoshi-ami* during periods preceding the new moon and full moon, while greater numbers of fry occur on the shore during periods following the same (Fig. 11), suggesting movement shoreward with accompanying growth. The seasonal occurrence pattern at the *otoshi-ami* parallels that on the shore, except that the *otoshi-ami* is not operated during the stormy months (July-September).

Ronquillo (1971) reported collection of 23 specimens of 4.5-9.5 mm milkfish larvae together with 10-14-mm fry and 22-25-mm juveniles from fry grounds in Zamboanga, western Mindanao (Philippines). Those 23 smaller larvae were probably not milkfish. Even Delsman (1929) seemed to have misidentified 3 of his 5 milkfish larvae (Senta 1982; Kumagai 1984).

Miller et al. (1979) collected milkfish larvae with standard lengths (SL) of 4.8, 8.5, 10.2, and 13.5 mm by plankton tows in nearshore surface waters in Hawaii. More recently, Leis & Goldman (1987) collected milkfish larvae by plankton net from shallow waters in the Great Barrier Reef near Lizard Island, Carter Reef, and Yonge Reef.

Fry and the Transformation Stage

Milkfish fry are most abundant in shore waters and constitute a valuable fishery that supports the centuries-old pond culture industry in southeast Asia. Fry caught in shore waters are all within a narrow range of 10-17 mm TL

Table 6. Distribution of milkfish larvae in various stations off Culasi in western Panay (Philippines) in April-May 1980 (*After* Bagarinao & Kumagai 1987)

No.	Stations Depth (m)	DFNL* (km)	Number of tows	Number of larvae by stages (density/10 000 m^3)				
				I	II	III	IV	Total
1	40	1	44	1 (1.3)	2(2.5)			3 (3.8)
2	60	0.8	45	3(3.7)	2 (2.5)	1 (1.2)		6(7.4)
3	95	1.2	46	6 (7.3)	2(2.4)	1(1.2)		9 (10.9)
3A	60	0.7	26	2 (4.3)	1 (2.1)	1 (2.1)		4 (8.6)
3B	90	2.2	26					
4	250	3	46		1 (1.2)	1 (1.2)		2(2.4)
5	215	6	45	3(3.7)	1 (1.2)			4(4.9)
6	315	4	44	1 (1.3)	1 (1.3)			2(2.5)
7	95	2	41	1 (1.4)	1 (1.4)			2(2.7)
8	30	0.4	41	2(2.7)				2(2.7)
9	325	3	40	1 (1.4)	1 (1.4)			2 (2.8)
10	240	6	40		1 (1.4)			1 (14)
11	190	4	40	1 (1.4)		1 (1.4)		2 (2.8)
12	80	1	40		2(2.8)	1(1.4)		3 (4.2)
13	5	0.1	30				2(3.7)	2(3.7)
Total			594	21 (2.0)	15(1.4)	6(0.6)	2(0.2)	44(4.1)

*Distance from nearest land.

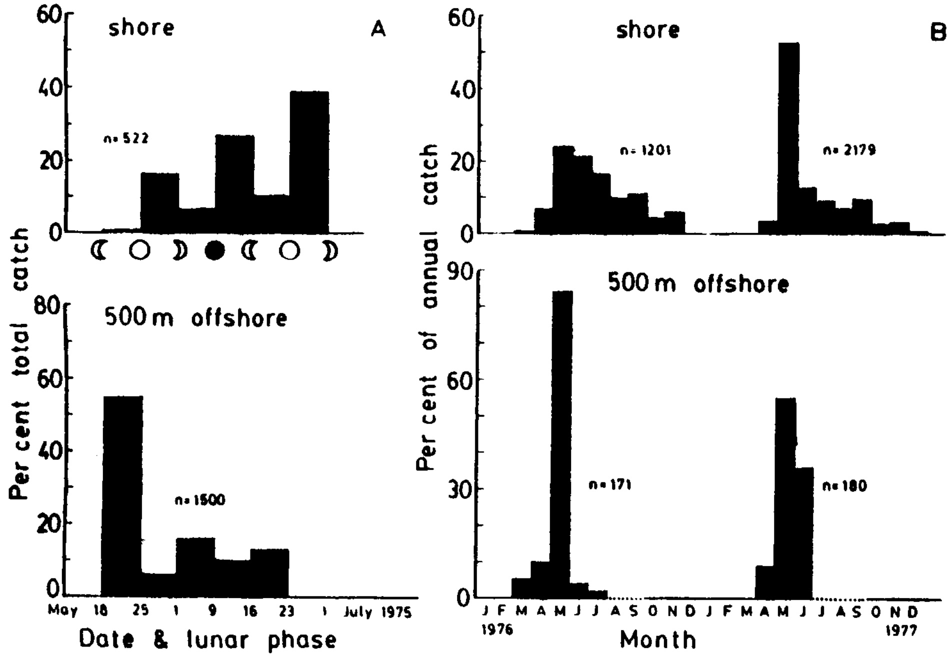


Fig. 11. Occurrence of milkfish fry onshore and larvae and fry 500 m offshore (*otoshi-ami* site) in Pandan Bay, Philippines showing (A) lunar periodicity (Data from Kumagai et al. 1976) and (B) seasonality (Data from Bagarinao & Taki 1986). Catches at the *otoshi-ami* are higher before, and those onshore after the full moon and new moon dates, suggesting movement of larvae onshore with accompanying growth. The shorter "season" at the *otoshi-ami* is partly due to non-operation during the stormy months (dotted abscissa).

(Kumagai 1984). There is no significant variation in mean size of shore-caught fry from month to month, but the size modes increase between the quarter-moon and the full-moon periods (Fig. 12). This suggests either the arrival of fry in shore waters at a relatively small size (minimum 10 mm, 2 wk old) during neap tides and subsequent growth of these fry to mean size (13-14 mm) the following week, and/or arrival of larger, older fry during spring tides. The general uniformity in fry size has raised the question of active versus passive migration (Buri & Kawamura 1983; Kumagai 1984). Apparently, there is a mechanism that enables milkfish larvae to come to shore waters from open-water spawning grounds, and only the larvae that have attained a certain degree of morphological, physiological, and behavioral development (probably 10 mm and 2 wk old) are able to utilize such mechanism.

Kumagai (1984, 1990) discussed the influence of seasons, currents, tides, bottom profiles, and proximity to inland waters on the occurrence and abundance of milkfish fry in shore waters. Contrary to popular belief, milkfish fry do not seek freshwater habitats (salinity preference tests on shore-caught fry showed them staying in seawater). Rather they seek habitats with abundant food, which in the tropics happen to be mainly mangrove-vegetated brackish-

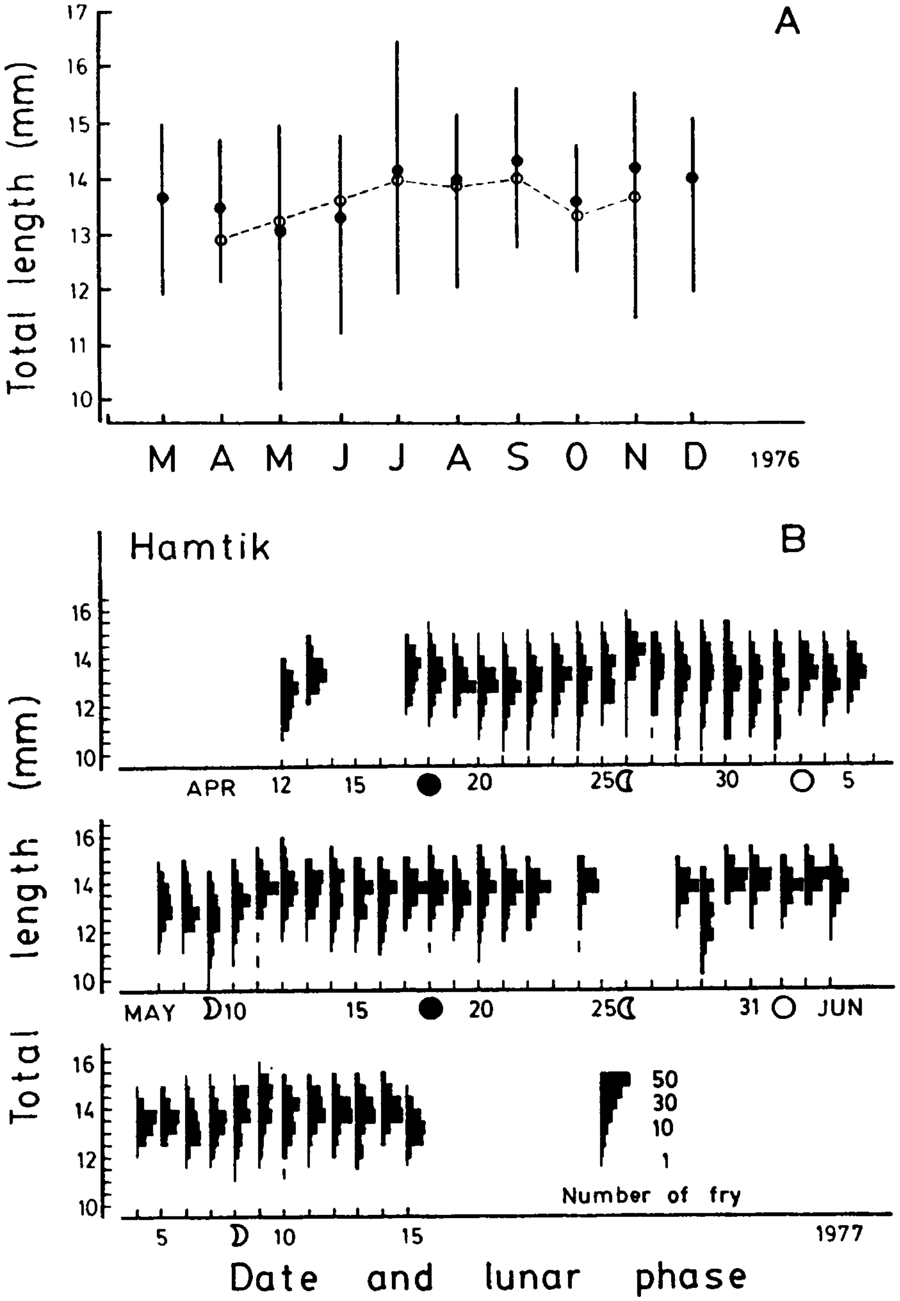


Fig. 12. Monthly variation in size of milkfish fry collected in Panay, Philippines (A): open circles connected by line, means for Hamtik fry; closed circles and bars, means and ranges for Pandan fry (n=53-724); and, daily size frequency distribution of fry in Hamtik, in relation to the lunar phase (B): growth (0.3-0.5 mm/day) in shore waters is indicated by the change in size modes (*Modified* from Kumagai 1981, 1990).

water coastal wetlands. Ingress of milkfish fry into Pulicat Lake, a large brackishwater lagoon in eastern India, was documented by Rao (1970).

Milkfish fry are phenomenally abundant. Total catch potentials are not known, but some 1.35 billion fry were collected in the Philippines in 1974 (Smith 1981), and 700-800 million fry are collected in Indonesia per year (Chong et al. 1984). Taiwan, which has far less coastline but better statistics than either of the former, collected an average 30 million fry a year during the period before 1945 and 130 million fry a year after 1950 (Lin 1968; Smith 1981). These fry go into a grow-out culture industry that produces 285 000 t of milkfish a year in southeast Asia (Smith & Chong 1984).

Figure 13 illustrates milkfish fry with closely similar larvae of other species that often occur together in shore waters and pose identification problems (Bagarinao et al. 1986). Milkfish fry may be easily distinguished by means of size range (10-17 mm), the single line of pigments on the ventral edge of the body, the simple non-striated intestine, and the pigments on the caudal fin. Tarpon (*Megalops cyprinoides*) and tenpounder (*Elops machnata*) larvae have

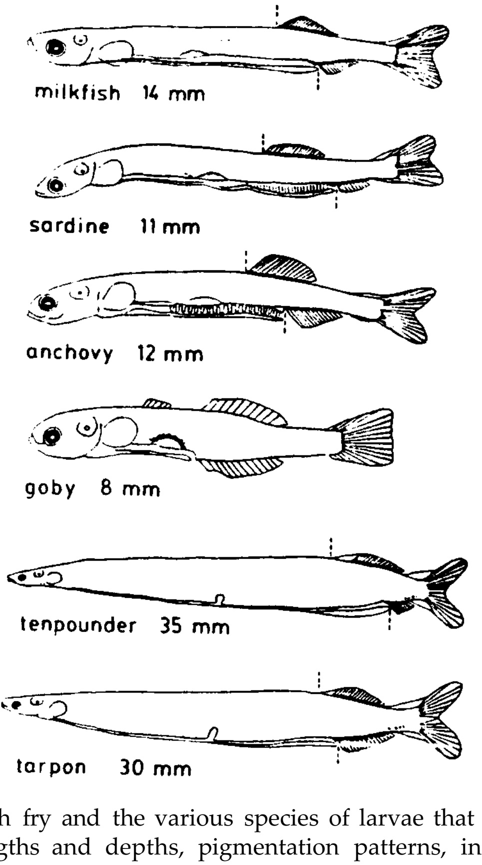


Fig. 13. Milkfish fry and the various species of larvae that occur in collection grounds. Body lengths and depths, pigmentation patterns, intestine length and striations, and the relative positions of the dorsal and anal fins (indicated by the broken lines) are the more prominent and useful characters in distinguishing among these species/taxa (*After* Bagarinao et al. 1986).

deeper, flatter (ribbon-like), and longer (25-35 mm) bodies; anchovy (*Stolephorus* spp.) and sardine (*Sardinella* spp.) larvae have striated intestines; and goby larvae have 2 short dorsal fins and a prominent inflated swim bladder.

The transformation stage, also termed the "metamorphic stage," is a complex of morphological developments accompanied by many physiological and behavioral changes (Kawamura & Hara 1980a). Stage V has never been recorded from the open sea, but has occasionally been taken from the coastal wetlands in the Philippines and in large numbers in Sri Lanka, India, and Kiribati (Kumagai et al. 1985; Ramanathan 1969; Dorairaj et al. 1984; J. Juario, pers. comm.). The culture industry employs special facilities and techniques to pass this transition from fry to the early juvenile stage (fingerlings) with minimum mortality (Baliao 1984).

Juveniles

Milkfish larger than 20 mm acquire the characteristic shape and morphology of the adult of the species and are considered juveniles. Juveniles <10-cm long are usually called fingerlings. They bear complete fin-ray complements, forked caudal fin, scales, and silvery coloration. Juvenile milkfish have been found in such diverse habitats as coral lagoons, mangrove lagoons, estuaries, marsh flats, tidal creeks, and tide pools that share the common characteristics of rich food deposits and protected, relatively shallow waters (Buri 1980; Kumagai & Bagarinao 1981; Dorairaj et al. 1984; Kumagai et al. 1985).

Dorairaj et al. (1984) described a milkfish nursery habitat in Manoli Island in the Gulf of Mannar (India). Three main tidal creeks lead into waterlogged mangrove areas (<0.5 m-deep), varying in configuration with the tides, and leaving small pools (6-65-cm deep) behind during the lows of spring tides. Milkfish fry and transformation stage juveniles (12-27 mm TL) could be collected along the banks of the creek and in tide pools, while juveniles (30-170 mm TL) could be collected in the waterlogged areas. Temperatures in the creeks and tide pools vary (29-41 °C), as do dissolved oxygen (0.2-10.4 ml/1), salinity (34-41 ppt), and gross production (300-430 mg C/m^3/d). Other accounts of natural habitats of juvenile milkfish include Tampi (1959), Kumagai et al. (1985), Pinto (1985), and Blaber & Milton (1990).

Habitat area, depth, and connection with the sea apparently determine the maximum size and duration of stay of juvenile milkfish in natural nursery grounds where food is too abundant to be limiting. Where habitats are small or temporary, only small juveniles up to 25 cm fork length (FL) are found (Ramanathan 1969; Kumagai & Bagarinao 1981; Krishnamurthy & Jeyaseelan 1981; Dorairaj et al. 1984). In a 1.6-ha mangrove lagoon in Naburut Island, milkfish fry were found to enter with the high tides of spring tide periods (i.e., every 2 wk), grow into juveniles, stay there for 4-5 months until they are about 20 cm, and then leave, again with the high spring tides (Kumagai et al. 1985). Occasionally juveniles find themselves in large coastal lagoons, lava ponds, atolls, and freshwater lakes. There they stay and grow for several years until they reach adult sizes only slightly less than their kin in the open sea (Angeles 1971; Therezien 1976; Nash & Kuo 1976; Oceanic Institute 1977,1980; Castro-Aguirre 1978; Reyes 1978; Muench 1978) in many of these large habitats, the adult females fail to reach full sexual maturity, but in the hypersaline lagoons in Christmas Island, gravid stunted females have been found.

In countries where coastal wetlands have been extensively converted into culture ponds, wild juvenile milkfish are relatively hard to find and could be collected only in small numbers (Kumagai & Bagarinao 1981; Kawamura et al. 1983). In contrast, wild juveniles 2-25 cm TL can be collected in large numbers in Sri Lanka, India, Kiribati (Villaluz et al. 1982; Dorairaj et al. 1984; J. Juario, pers. comm.), and similar places where wetland areas are still mostly in the natural state and fishing pressure on milkfish fry is negligible. Of course, exploitation is not the only reason for the observed difference in occurrence and abundance. Juvenile milkfish is not reported in some undeveloped coastal wetland where investigators have conducted extensive collections, e.g., in the Kretam estuary in north Borneo (Inger 1955), in the Ponggol estuary in Singapore (Chua 1973), and in the Labu estuary in eastern Papua New Guinea (Quinn & Kojis 1986). Many aspects of the ecology of wild milkfish remain to be investigated.

FOOD AND FEEDING HABITS

Morphology and Development of the Digestive System

The morphology of the digestive system of adult and juvenile milkfish (Fig. 14; Chandy & George 1960; Kinoshita 1981) suggests that it is mainly an herbivore with generalist tendencies. It has a small toothless mouth, fine closely laid gill rakers, and a pair of muscular raker-lined epibranchial organs. The esophagus is long and thick-walled, with 20-22 spiral folds (like in shark intestines) and many mucus cells. The stomach is large, the cardiac region characteristically bent or doubled-over, and the pyloric region has a spherical gizzard with very thick walls and a mucus membrane (or cuticle in fish > 10 cm). The cardiac stomach has gastric glands; the gizzard has none and seems to function in trituration of coarse food materials. Numerous pyloric caeca cluster behind the gizzard. The intestine is convoluted and extremely long.

Ferraris et al. (1987) conducted a detailed histological and histochemical study of the development of the digestive tract in milkfish. The esophagus and the intestine begin to differentiate 3 d after hatching. In 3 wk, the cardiac and pyloric stomach become histologically distinct and goblet cells develop in the intestine. Acid- and pepsin-secreting glands develop in the cardiac stomach during the transformation stage. Mucosal folds develop secondary branching during the juvenile stage.

Milkfish fry from shore waters (2-3 wk old) have well differentiated esophagus and a straight stomach-intestine; 28 d after capture, the pyloric caeca appears and the stomach differentiates into the cardiac and pyloric

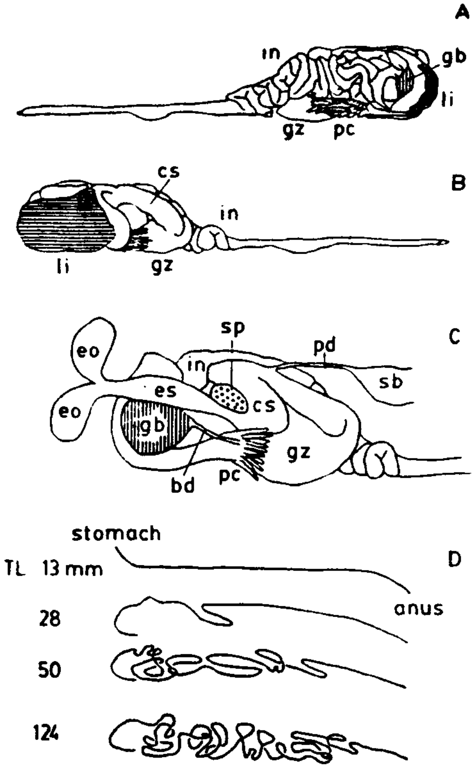


Fig. 14. Digestive system of milkfish: A, right side showing intestine mass; B, left side with liver and stomach; C, with liver removed and other organs exposed; D, elongation and convolution of the intestine between the fry and juvenile stages [in, intestine; gb, gall bladder; pc, pyloric caeca; li, liver; gz, gizzard (pyloric stomach); cs, cardiac stomach; eo, epibranchial organ; es, esophagus; sp, spleen; sb, swimbladder; pd, pneumatic duct; bd, bile duct] (*Modified* from Kinoshita 1981).

regions (Kinoshita 1981). A rudimentary epibranchial organ and 14 gill rakers are present in 14 mm shore-caught fry; the former becomes fully elaborated and the latter come to number 177 in 19 mm juveniles (Kafuku & Kuwatani 1976). The intestine-to-body length ratio (I) increases with growth. I is about 0.5 in the fry, increases to about 1.0 at 20 mm body length, about 2.0 at 50 mm, and exceeds 3.0 at 80 mm (Kinoshita 1981). Kumagai & Bagarinao (1981) obtained the relationship: In I = 3.7 + 0.0023 FL for the increase in intestine length with growth of juvenile milkfish (100-180 mm FL) in Naburut Island (Philippines). Adult milkfish (50-100 cm TL) in Indonesia have 1 ratios of 3.3-7.2 (Poernomo 1976); values up to 12 have been reported (Schuster 1960). Aside from increasing with fish size or age, the I ratio also shows adaptation to the predominant food type in the habitat. I ratios vary from 4 to 6 among juvenile milkfish from different habitats around Panay Island and tend to be higher in fish with more plant food than those with more animal food (Kumagai & Bagarinao 1981)

Feeding of Larvae and Fry

Feeding commences shortly after the eyes become fully pigmented and the mouth opens (54 h from hatching) and before the yolk is completely resorbed (120 h); unfed larvae all die about 150 h from hatching at rearing temperatures of 26-30°C (Bagarinao 1986). Eda et al. (1990) found the onset of feeding at 80 h after hatching, and all unfed larvae dead at 170 h at rearing temperatures of 25-27°C. Mouth of milkfish larvae measures 225 μm in width and 200 μm in jaw length at the onset of feeding (Kumagai 1990). Larvae are particulate visual feeders, i.e., they snap up prey one by one and swallow them whole. Small live prey such as the rotifer (*Brachionus*), water flea (*Moina*), harpacticoid copepod (*Tisbintra*), and brine shrimp (*Artemia*) have been successfully used as feed for rearing milkfish larvae and fry at SEAFDEC/AQD. When milkfish larvae are about 2 wk old, they begin to be able to take non-live feed; about 40% can be weaned to the juvenile stage using various finely ground artificial diets (Duray & Bagarinao 1984).

Milkfish fry in shore waters feed mainly on copepods and diatoms (Banno 1980; Kinoshita 1981). Copepods appear to be taken mostly head on, probably the easiest way for the fry with mouth size about 1-mm wide to feed on prey with long appendages. Large copepods such as *Calanus* occurred about 1 /gut, while small ones such as *Oithona* and harpacticoids occurred in greater numbers (Kinoshita 1981). The proportion of shore-caught fry with food in the guts varies from 3-11 % (Banno 1980), up to 65% but with small amounts per gut (Buri 1980), and 0-68% with average 12% (Kinoshita 1981). The fry probably void their gut contents when agitated at capture.

Feeding behavior of milkfish larvae has been studied in the laboratory. Kawamura & Hara (1980b) observed that shore-caught milkfish fry could not feed on *Artemia* nauplii in the dark, but the newly transformed juveniles could. Hara et al. (1983) studied hatchery-reared larvae and found that they exhibit a diurnal feeding habit (Fig. 15). Day 9 and day 15 larvae could not feed in the dark, but day 21 larvae could. The illumination level required for active feeding in the morning decreases with age of the larvae: 1500 lux at day 9, 130 lux at day 15, and 0.1 lux at day 21. The average number of rotifers taken by each larva during the daylight hours is about 10 at day 9, 25 at day 15, and 100 at day 21. Satiation occurs after 2-3 h of feeding and digestion takes about 5 h. Eda et al. (1990) estimated the satiation level for milkfish larvae 6-11 d from hatching by the equation: number of rotifers = 190 - 35 TL. Villaluz & Unggui (1983) found that feeding activity of milkfish fry varied with temperature, with guts filling up within 15-60 min of introduction of food, and digestion taking 1-3 h.

The physiological and nutritional effects of various food types have been studied in milkfish fry. Fry grow well on rotifers fed a mixture of phytoplankton (*Chlorella, Isochrysis,* and *Tetraselmis*), but not on rotifers grown on each of the phytoplankton alone, or when fed the phytoplankton directly (Acosta & Juario 1983). Electron microscope studies indicate that milkfish fry can not directly utilize *Chlorella* which has a rigid cell wall (Juario & Storch 1984), and that *Chlorella*-fed rotifers commonly used in hatcheries are nutritionally inade-

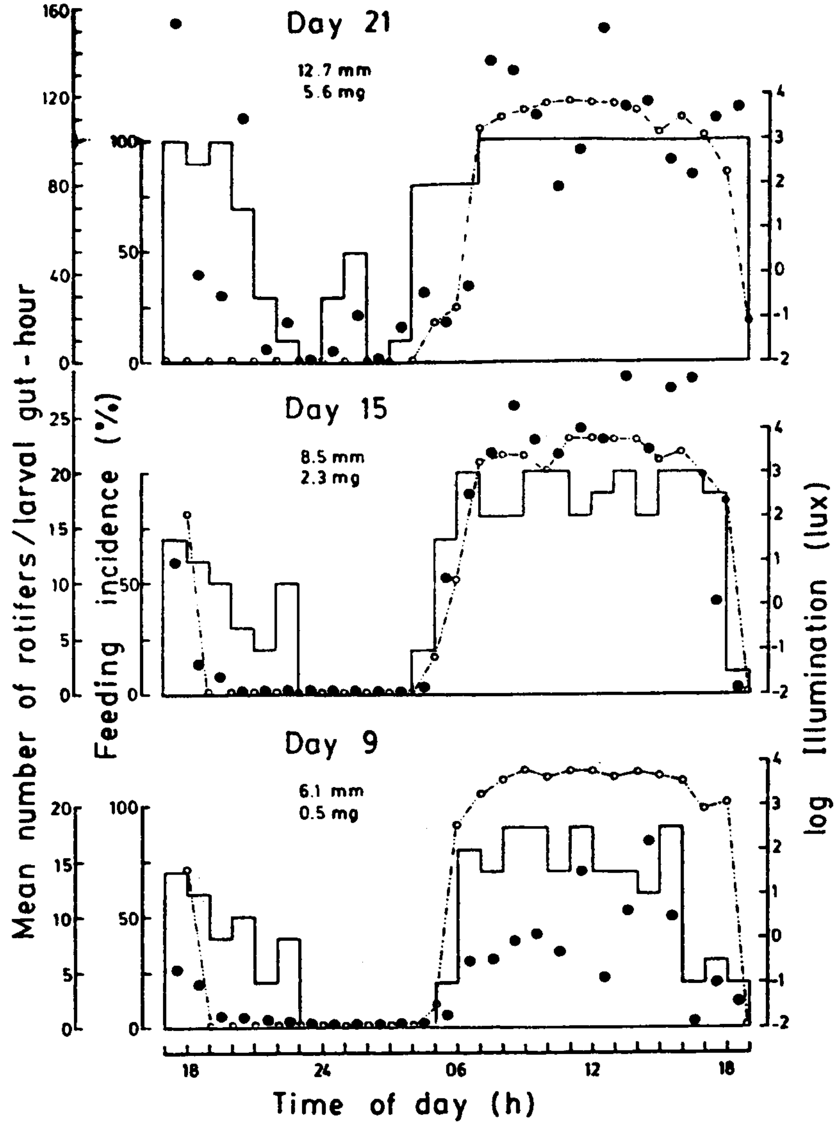


Fig. 15. Diel feeding pattern of milkfish larvae in laboratory in terms of % larvae feeding (histogram) and mean number of rotifers taken (closed circles), as influenced by the illumination cycle (open circles connected by line) and larval age (Hara et al., unpubl.).

quate (Segner et al. 1984). In freshwater, milkfish fry given the cyanobacteria *Oscillatoria* and *Chroococcus* showed higher growth, survival, and assimilation rates than those fed *Navicula, Chlorella*, and *Euglena* (Pantastico et al. 1986). Milkfish fry grow well on artificial diets with about 40% protein (Santiago et al. 1983; Alava & Lim 1988). Fry reared in brackishwater ponds show better growth on formulated diets than on natural feeds, the cyanobacteria *Oscillato-*

ria and *Spirulina.* At the practical level, milkfish fry dealers store fry for 1 -4 wk on a diet of uncooked pounded rice, wheat flour, and hard-cooked chicken egg yolks (Schuster 1960; Villaluz 1984).

Carreon et al. (1984) reared milkfish fry in raceways of freshwater recirculating systems, feeding them natural plankton or artificially produced detritus supplemented with rice bran and mung bean meal. Detritus (containing 8-12 x 10^6 bacteria and various species of cyanobacteria, diatoms, rotifers, and protozoans) was produced by aging for 10-15 d finely ground rice straw and rice hull suspended in water with powdered chicken manure and maintained at pH 6.5-7.8. Milkfish fry showed 3-32% survival and poor growth (4-6 mg BW, emaciated) on detritus, and 40-60% survival and good growth (13-28 mg, healthy) on natural plankton. The fry elected to feed on cyanobacteria, diatoms, copepods, cladocerans, and protozoans. This result indicates that shore-caught milkfish fry may be too young to feed on detritus and that detritus may not be appropriate for use in raceways with water currents at speeds of 10 cm/s.

Feeding of Juveniles

Juvenile milkfish take food mainly from the bottom. The kinds of food ingested vary by habitat and fish size (Sunier 1922; Hiatt 1944; Schuster 1952; Tampi 1958; Lin 1968; Nair et al. 1974; Therezien 1976; Vicencio 1977; Whitfield & Blaber 1978; Kumagai & Bagarinao 1981; Bagarinao & Thayaparan 1986). Juveniles from natural habitats around Panay Island and elsewhere most commonly eat cyanobacteria, diatoms, and detritus, along with filamentous green algae and invertebrates such as small crustaceans and worms. The food items of milkfish in culture ponds are very similar to those in natural nursery grounds. Lin (1968) found that pond fish ingest about 65% algae and 35% animals during the day and 54% animals and 46% algae at night, probably due to the diel change in availability of food organisms.

Milkfish is characterized as being iliophagous, ingesting the top layer of bottom sediments with the associated micro- and meiofauna, as mullets do (Whitfield & Blaber 1978; Blaber 1980). A great deal of this material is detritus, which is rich in protein due to its high complement of bacteria, fungi, and protozoans and has been shown to be important in tropical shallow-water food chains (Odum & Heald 1975). Detritus is probably utilized by juvenile milkfish as soon as they reach their depositional-type habitats.

Although juvenile milkfish are capable of feeding in the dark in the laboratory (Kawamura & Hara 1980b), juveniles in the wild or in ponds do not necessarily feed at night. Gut content analyses of milkfish from natural habitats show empty guts in the morning and loaded guts during the day (Kumagai et al 1985; Bagarinao & Thayaparan 1986). Pond-grown juveniles show peak feeding around noon when digestive enzyme activity, dissolved oxygen, and water temperature are highest; feeding occurs in the dark when oxygen levels are > 3 ppm (Chiu & Benitez 1981; Chiu et al. 1986). Gut content as per cent body weight is positively correlated with dissolved oxygen and water temperature (Lin 1969)

The intestinal passage time is 10-15 min in 20 g juveniles (I = 2.1) and 27-50 min in 60 g juveniles (I=3.0) (Ferraris et al. 1986). The rate of food movement is significantly higher in juveniles kept in seawater (13-19 mm/min) than in freshwater (10-11 mm/min). Digestibility of fish meal and soybean meal is lower in seawater than in freshwater. Lower digestibility in seawater is due in part to the higher rate of food movement, reducing the opportunity available for complete digestion and absorption of nutrients. Because of this, food conversion efficiency in milkfish may decrease and protein requirements increase under seawater culture conditions (Ferraris et al. 1986).

The digestive enzymes of juvenile milkfish have been characterized. High amylase activity is seen in the intestines, pancreas, pyloric caeca, and liver, but there is no cellulase activity (Chiu & Benitez 1981). Protease and lipase activity is high in the pyloric caeca, intestines, and pancreas, and is present also in the esophagus (Benitez & Tiro 1982; Borlongan 1990). These enzymes have different pH optima, but all show maximal activity around 50°C. That the activities of all digestive enzymes of milkfish increase with temperature up to 50°C is consistent with the observation that milkfish feed and grow well in ponds during the warm months and not as well during the cold months.

In the Philippines and elsewhere in Asia, milkfish culture depends on the utilization of 2 natural food bases: *lablab* (also called *klekap* and *tay-ayer* in Indonesia), a complex of cyanobacteria, diatoms, and associated invertebrates; and *lumut,* consisting mainly of filamentous green algae. On the basis of faster growth and higher yields, *lablab* is considered by most fish farmers as a better food for juvenile milkfish in ponds. Floating *lablab* has 15% protein, 2 kcal/g, and 57% ash; attached *lablab* has 6% protein, 1 kcal/g, and 80% ash (Jumalon 1978). Milkfish appears to prefer *lablab* over *lumut* and would not gain weight if provided the latter alone (Schuster 1952). *Lumut,* particularly the dominant species *Chaetomorpha,* has a low protein digestion coefficient of 3% when fresh, or 66% when decayed; in contrast, the protein digestion coefficients are 87% for diatoms and 69% for cyanobacteria (Tang & Huang 1967). Recent work likewise explains the observed unsuitability of *lumut* for milkfish. Juvenile milkfish do not have cellulase and can not digest the tough filaments of fresh *lumut* (Chiu & Benitez 1981). *Chaetomorpha brachygona* in *lumut* has a trypsin inhibitor that blocks protein digestion if not destroyed (Benitez & Tiro 1982). Protease and lipase activities tend to be higher in milkfish grown on *lablab* than in those grown on *lumut* (Benitez & Tiro 1982; Borlongan 1990).

Tang (1972) estimated that 2.5 g juvenile milkfish consume benthic algae equivalent to 60% of their body weight per day while 100-300 g juveniles need about 25%. Some 25 000 kg/ha of benthic algae is needed to support 2000 kg of milkfish (Tang & Chen 1967). To increase *lablab* production in ponds, fertilizers are applied and additional surfaces for attachment and growth (e.g., nylon screens and rice straws) are provided (Fortes 1984).

Rice bran and commercial pellets are accepted by juvenile milkfish in ponds (Baliao 1984). Considerable research has been conducted on the nutritional requirements and feeds of juvenile milkfish (see Benitez 1984 for review; Teshima et al. 1984; Ferraris et al. 1986; Coloso et al. 1988; Shiau et al. 1988).

Table 7. Food of adult milkfish

Locality	Gear	n	Fish TL (cm)	Major food items
Philippines [1, 2, 3]				
Cigantes Is.	gn	4	102-104	*Lucifer*
	gn	1	107	*Acetes*
Panagutan Cays	gn	1	102	*Squilla*
Jintotolo Channel	h&l	1	92	sardine juveniles
Tigbauan	fc	1	88	anchovy larvae (others: isopods, crab megalopa, cumaceans, fish eggs & larvae, ostracods)
Pandan Bay	on	9b	85-103	copepods, diatoms, cyanobacteria, detritus, fish eggs and larvae, green and red algae, other small crustaceans
western Luzon	fc	3	90-150	diatoms (*Coscinodiscus, Pleurosigma, Chaetoceros, Navicula*), dinoflagellates
Indonesia [4, 5]				
Java	s, fc	8	76-93	diatoms (planktonic and benthic), copepods, salps, amphipods, ostracods, lamellibranchs, higher algae, *Globigerina*
Karimun Jawa	gn	8	59-99	copepods, foraminiferans, vascular plants, *Lucifer,* gastropods, ostracods, amphipods, *Coscinodiscus,* filamentous algae
India [6, 7]				
Gulf of Mannar				*Lucifer,* mysids, diatoms, copepods, larval bivalves, appendicularians, *Trichodesmium*
Pudumatom		7	108-126	lamellibranchs (*Pteria*), copepods, nematodes, polychaete larvae, small gastropods, diatoms, red algae (*Gracitaria, Hypnea, Polysiphonia*), vascular plants
Christmas Is.[8]				
hypersaline ponds	gn		40-50	Algal mats composed of halophilic bacteria, cyanobacteria, fungi, diatoms; *Artemia*

gn, gill net; h&l, hook and line; fc, fish corral; on, *otoshi-ami* (Japanese nylon set net); s, seine. [1]Kumagai 1981, 1990; [2]Villaluz et al. 1976; [3]Vicencio 1977; [4]Sunier 1922; [5]Poernomo 1976; [6]Chacko 1949; [7]Tampi 1958; [8]Crear 1980.

Feeding of Adults

Both planktonic and benthic plants and animals occur in the guts of adult milkfish (Table 7). Specimens from around Panay have been found with large quantities of zooplankton and larval and juvenile clupeoids. There is usually 1-2 dominant kind of food in a gut, suggesting that adult milkfish feed by swimming through plankton masses or larval fish schools. In Rangiroa Atoll, adult milkfish have been observed to move with the plankton mass drifting from one area in the lagoon to another (K. Muench, pers. comm.). Adults are also reported to graze on rock surfaces and on floating algae. They have been found gorged with lamellibranch (*Pteria*) spats that cluster on seaweeds, indicating browsing near the bottom (Tampi 1958). Thus, adult milkfish, like the juveniles, are opportunistic generalists. Many investigators have found specimens with empty guts or with a white mucoid material (Tampi 1958; Poernomo 1976; Vicencio 1977). One reason for this, at least for fish caught by stationary gear, is the time lapse between impoundment and hauling during which the fish digest whatever they have eaten.

Adult milkfish can be kept in captivity on a diet of commercial pellets with about 42% protein given at 1.5-2% of body weight twice daily (Marte & Lacanilao 1986). Kawamura & Castillo (1981) observed that adults take pellets from a feeding tray both day and night but more actively during the day.

AGE, GROWTH, AND MORTALITY

Figure 16 shows the composite growth curve for milkfish around Panay Island (Philippines).

Growth of Larvae and Fry

Milkfish larvae trace a sigmoid growth curve (Liao et al. 1979). Growth as TL (mm) over 30 d from hatching (D) at 25-27°C in Hawaii is expressed by the equation: $\ln TL = 1.627 + 0.039\ D$ (Eda et al. 1990).

Tzeng & Yu (1988) examined the otoliths of reared milkfish larvae in Taiwan and found that the first growth increment was formed during the yolk-sac reabsorprion period about 2 d from hatching and that increment formation continued on a daily schedule regardless of growth rate. The relationship between the number of growth increments (N) in the otoliths and the age in days from hatching is: $D = N+1$. The relationship between size and age is best expressed by the equations:

$\ln TL = 1.229 + 0.071D$ (in April; water temp, 26-31°C)

$\ln TL = 1.383 + 0.057D$ (in August; water temp, 29-33°C)

In a subsequent study, Tzeng & Yu (1989) validated the otolith daily increments in shore-caught milkfish fry by the oxytetracycline method, and

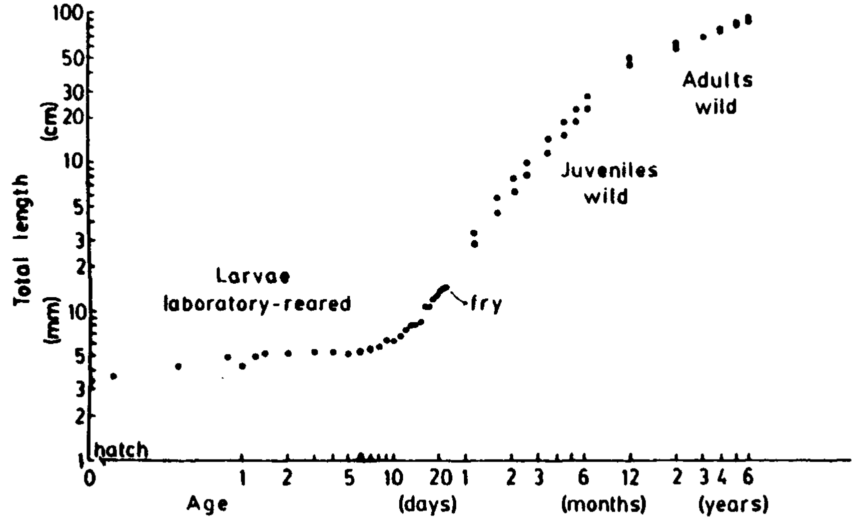


Fig. 16. Composite growth curve of milkfish larvae, juveniles, and adults (Data from Liao et al. 1979; Kumagai 1981, 1990; Kumagai et al. 1985; Bagarinao 1986). Note that both axes are logarithmic.

confirmed that the increments are formed at the rate of about 1 per day, and that the formation is unaffected by growth rate. In an earlier study, Kawamura & Washiyama (1984) found 18-20 increments in the otoliths of shore-caught fry from southern Japan. Thus the otolith method indicates that shore-caught fry are about 3 wk old.

Based on the size frequency distribution of about 10 000 milkfish fry (Fig. 12B), Kumagai (1981, 1990) estimated that fry in shore waters grow at a rate of 05 mm/day. The equation: TL (mm)=5.0+0.5 (D-4) estimates growth during the linear phase following the post-yolk sac stage (larvae remain at 5 mm for about 4 d from hatching). Using this equation, shore-caught fry of mean TL = 13.5 mm are estimated to be 3 wk old, while the smallest ones of mean TL = 10 mm are about 2 wk old.

Hatchery-reared milkfish fry tend to be heavier and morphologically more advanced (heavily pigmented, with pelvic fins present) than shore-caught fry of similar length (Vanstone et al. 1977; Liao et al. 1979). However, Taki et al. (1986) did not find differences in the osteological development of wild and hatchery-reared fry in the 11-12 mm size range. Growth and survival performance in nursery ponds in the Philippines did not differ between wild and hatchery-reared fry (Baliao et al. 1980). But Lin (1985) observed that hatchery-reared fry in Taiwan have better survival, growth, and ability to resist cold temperatures.

Villaluz & Unggui (1983) found that growth of shore-caught milkfish fry is temperature-dependent: they enter the transformation stage within 5 d of rearing at 30°C, 7 d at 27°C, and 15 d at 21°C. Shore-caught fry treated with the hormone thyroxine by immersion in a 0.5 ppm bath showed accelerated growth and metamorphosis compared to unexposed fry and fry exposed to 0.1 ppm thyroxine (Lam et al. 1985). Growth of milkfish fry varies with other factors as well, the effects of diet and feeding level being the most studied (Villegas & Bombeo 1981;Santiago et al. 1983, 1989; Carreon et al. 1984; Alava & Lim 1988).

Growth of Juveniles

There are few data on growth of juvenile milkfish in nature. Kumagai et al. (1985) obtained monthly samples from the lagoon in Naburut Island and computed growth equations from the size frequency distribution. Growth rates of 8.7, 7.6, 7.4, and 7.0 mm/wk were found for batches of milkfish fry that entered the lagoon in late March, mid-April, mid-May, and late May, respectively. These rates are comparable with those found for pond-cultured and wild milkfish in other localities (Rabanal et al. 1953; Villaluz et al. 1982; Teroroko 1983). Dorairaj et al. (1984) showed size frequency distribution of juvenile milkfish from collection grounds in India, but provided no growth estimates. In Pillaimadam lagoon, milkfish collected on different days in June-July ranged 21-209 mm TL, with 4 size groups. The size groups probably correspond to the batches of fry that enter the lagoon at 2-wk intervals, i.e., during the highs of spring tides.

On the other hand, Blake & Blake (1981) used check marks on the scales and the opercular bones to determine the age of juvenile milkfish in a coastal lagoon in Mexico. For milkfish 75-355 mm SL, the relationships between SL (mm) and length of the scale (X_s, mm) or opercular bone (X_o, mm) are:

$$SL = 29.6 + 117.4\ X_s \text{ and } SL = 12.0 + 96.0\ X_o.$$

A check mark is formed on or close to the scale margin during July-October with the heavy rains, and another during February-March when evaporation is high, and salinities and temperatures rise. Milkfish 16-cm long have 2 check marks; those 30-cm long have 4.

Milkfish grows very well in ponds, compared to many other fish and crustacean species (Grover et al. 1976; Eldani & Primavera 1981; James et al. 1984); this is why it has been so successfully cultured for centuries. Growth rates of juvenile milkfish vary considerably depending on (1) generic factors, which have not been studied; (2) environmental factors such as food, competitors, pests, predators, dissolved oxygen, temperature, salinity, pH, and toxicants; and (3) stock manipulation techniques such as initial stock size, stocking density, feeding, duration of culture, mono- or polyculture with other species. Growth and survival parameters are among the tools used to evaluate culture techniques and innovations, so data for juvenile milkfish abound (Rabanal et al. 1953; Schuster 1960; Juliano et al. 1970; Gopalakrishnan 1972; Pudadera & Lim 1980; Eldani & Primavera 1981; Gerochi et al. 1988).

In nursery ponds in Iloilo (Philippines), the growth curve of early juveniles is generally sigmoidal at stocking densities of 10-100/m^2 with *lablab* as food; in grow-out ponds, growth is linear at densities <2000/ha, but linear to logarithmic at 3000-5000/ha, with steeper slopes where *lablab* is the food base (Juliano & Hirano 1986). Pudadera & Lim (1980) found that increasing the stocking density from 2000 to 4000/ha reduces the weight gain of juvenile milkfish to about 50%. Juveniles could be stocked at 6000-9000/ha if supplementary feed is provided (Sumagaysay et al. 1990). In floating cages, juvenile milkfish grow faster in 5-m diameter cages than in 3-m diameter cages at stocking densities of 1, 2, and 4 kg/m^3; likewise faster at 4 kg/m^3 than at 1-2 kg/m^3 in both cage sizes (G. Quinitio, pers. comm.).

Growth of Adults

Kumagai (1981, 1990) examined the vertebral centra of captive adult milkfish known to be 1, 2, 3, 4, and 5 yr old, and found 1, 2, 3, and 5 growth rings. He aged 60 wild adult milkfish using vertebral rings (Table 8), and from the corresponding lengths, inferred the growth rates. Females grow slightly faster than males. Between ages 4 and 6 yr, females grow roughly 7 cm/yr and males 5 cm/yr. Other estimates of age of wild adult milkfish using scale markings are also indicated in Table 8. There is disagreement among the data; obviously, more work is necessary.

There is no data on longevity, but Schuster (1960) mentioned pond-reared milkfish 12 yr of age and 5-6 kg in weight. A large population of 10-11 yr old milkfish are maintained in Taiwan ponds for spawning (Lin 1985). At present, there are 12-yr old milkfish held in floating cages at SEAFDEC/AQD (A. Emata, pers. comm.).

Adult milkfish collected around Panay Island (n = 527) measured 60-100 cm FL (mean, 75 cm) or 75-120 cm TL (mean, 95 cm), and 4-14 kg BW (mean, 7 kg), with condition factors ($CF = BW/FL \times 10^3$) of 14-16 (Table 9). The size composition of Pandan Bay adults is shown in Figure 17. Adults from Naujan Bay are slightly smaller but more robust, probably because they are younger and had just come from the lake growing area. Adult milkfish from Indonesia, Taiwan, India, and Rangiroa Atoll (Table 9) are similar in size to those in the Philippines. Ocean-caught adult milkfish from Hawaii are smaller and less robust than the Philippine specimens; those inhabiting the large lava ponds in Kona are even smaller but fatter. Compared with the Philippine milkfish, the most divergent group is that from Christmas Island. In this group, the adults from the open ocean are larger than those from the hypersaline lagoons,the deviation increasing with salinity of the lagoon (Table 9).

Compared to milkfish from the wild, adults raised in captivity tend to be smaller (Table 9). Adults grown from juveniles in floating cages in the Philippines measure 56 cm FL and 3 kg on average (Marte & Lacanilao 1986). Those grown in concrete tanks in Indonesia measure 69 cm TL and 3.3 kg (Poernomo et al. 1985a). However, specimens 17-19 kg have been reported from culture ponds (Chen 1952; Schuster 1960).

Poernomo et al. (1985a) raised 2-yr old milkfish (mean 63.5 cm TL, 2 kg BW) for a year in tanks of different shapes and capacities and fed a formulated diet and trash fish at 2% body weight (dry basis) daily. Their data show that growth depends on mobility of the fish. Annual growth is 12 cm and 2.3 kg in tanks with 21 water/fish, 6-10 cm and 1.5 kg in tanks with 31 water/fish, and 3.5 cm and 0.7 kg in tanks with 9 t water/fish. With a ration of 2% body weight daily.

Table 8. Estimated age of adult milkfish from the Philippines and Taiwan

No. of rings in vertebrae = age (yr)	Philippines (Pandan Bay, Panay)				
	Sex	FL range (cm)	FL mean ±	2SE	n
4	M	66.2-79.5	73.0	1.5	21
4	F	65.2-79.9	74.8	4.1	8
5	M	71.5-85.0	78.2	2.4	10
5	F	73.8-91.0	82.2	3.5	12
6	M	82.5-83.2	82.3	1.5	2
6	F	79.7-93.5	88.6	4.3	7

No. of sets of discontinuous lines on scales = age (yr)	Philippines (Pandan Bay, Panay)				
	Sex	FL range (cm)	FL mean ±	2SE	n
3	M	67.4-78.0	75.3	2.4	9
3	F	72.5-77.3	75.6	1.7	5
4	M	68.7-80.5	74.6	1.0	26
4	F	74.5-85.5	79.1	2.4	9
5	M	74.2-78.0	76.1	3.8	2
5	F	84.5			1

No. of rings on scales = age (yr)	Taiwan (Tungkang)				
	Sex	FL range (cm)	FL mean ±	2SE	n
5	F	62.7-71.1	67.9	3.9	4
6	F	64.7-85.0	74.9	14.4	2
6	M	65.5			1
7	F	77.6-81.1	79.4	2.5	2

Modified from Kumagai 1981, 1990; Tiro et al. 1976; and Liao 1971, respectively. SE is standard error of the mean; 2SE, 95% confidence interval.

milkfish in small tanks grow faster than those in large tanks, probably because the former have less room to move about and thus save more energy. The situation seems to be analogous to cattle feedlots, or poultry farms, where the animals are crowded together, fed to satiation, and harvested big and fat.

Length-Weight Relationships

Computed length-weight relationships for milkfish fry, juveniles, and adults from various localities are given in Table 10. The L-W relationship allows computation of weights where only lengths are given and vice-versa. With proper statistical tests, it may also indicate variation among samples from different localities.

Table 9. Size and condition factor of wild adult milkfish in the Indo-Pacific

Locality	Sex	n	Length range (cm)	Length mean ±SD (cm)	Weight mean+SD (kg)	Mean CF based on	
						FL	TL
Philippines							
Pandan Bay[1, 2]	M	196	FL 61-85	74.0±4.4	5.9+1.1	14.5	
	F	162	62-95	79.4±5.4	7.2+1.5	14.3	
Hamtik[1]	M	44	FL 64-80	73.8±4.4	65+1.3	16.2	
	F	30	66-90	76.1±6.4	7.3±1.9	16.0	
Tigbauan[1]	M	46	FL 66-97	75.6±6.2	6.3±1.4	15.0	
	F	49	63-94	79.9+6.6	8.0+2.2	15.3	
Naujan Bay[3]	M	37	TL 65-94	84.4+7.0	4.8+1.1		8.1
	F	21	65-95	91.1+8.0	5.9+1.8		8.1
Cages[4]	M	125		FL 55.1±1.9	3.0+0.3	18.0	
	F	119		56.4+1.9	3.2+0.5	17.8	
Indonesia[5, 6]	M	20	TL 68-98	88.9+5.4	5.5+1.1		7.7
	F	31	59-105	89.3+10.0	6.1+2.2		8.3
Tanks[7]	both	122		TL 69.1±3.8	3.3+0.8		10.0
Taiwan[8, 9]	M	3	TL 81-100	93.0+10.3	6.7+2.7		8.3
	F	10	78-104	90.3+9.1	5.7+2.7		7.9
India[10]	M	3	TL 75-114	99.0+2.0			
	F	16	50-126	88.1+2.9			
Hawaii Is.[11, 12]							
Oahu coast	M	297	FL 50-88	68.9+6.6	45+1.3	13.7	
	F	159	44-93	70.2+7.3	5.0+1.4	13.7	
Kona ponds	M	47	FL 44-72	61.4+4.6	4.1+1.0	17.2	
	F	37	44-69	61.8±4.6	4.0+0.9	16.4	
Christmas Is.[12, 13, 14]							
Main camp	M	7	FL 63-79	70.4+7.6	5.0+1.6	13.9	
ocean		61			4.6*		
Te Bati	M	3	FL 54-69	62.0+73	4.4+2.1	175	105
56 ppt	F	7	36-72	53.8+11.6	3.1+2.2	16.9	8.6
Pelican	M	10	31-38	36.1+2.2	0.8+0.1	17.4	9.5
Lagoon	F	19	36-41	37.5+1.7	1.0±1.6	18.0	10.0
76 ppt		30			0.9*		
Isles Lagoon	M	30	35-42	37.0+1.6	0.9+0.1	16.8	
125 ppt	F	8	37-46	40.1+2.9	1.1+0.2	17.4	
		309			1.1*		
Tahiti							
Rangiroa	M	28	TL 67-97	89.6+6.1	5.4+0.7		7.5
Atoll[15]	F	11	85-95	93.1+3.1	5.8+0.5		7.2

Condition factor CF = 1000W/L, where W is body weight (kg) and L is fork length FL or total length TL(cm). Values are computed from data of various authors: [1]Bagarinao, unpubl.; [2]Tiro et al. 1976; [3]Angeles 1971; [4]Marte & Lacanilao 1986; [5]Martosudarmo et al. 1976; [6]Poernomo 1976; [7]Poernomo et al. 1985a; [8]Liao 1971; [9]Liao & Chang 1976; [10]Tampi 1958; [11]Nash & Kuo 1976; [12]Oceanic Institute 1977; [13]Oceanic Institute 1980; [14]Crear 1980 for values denoted by *; [15]Muench 1978.

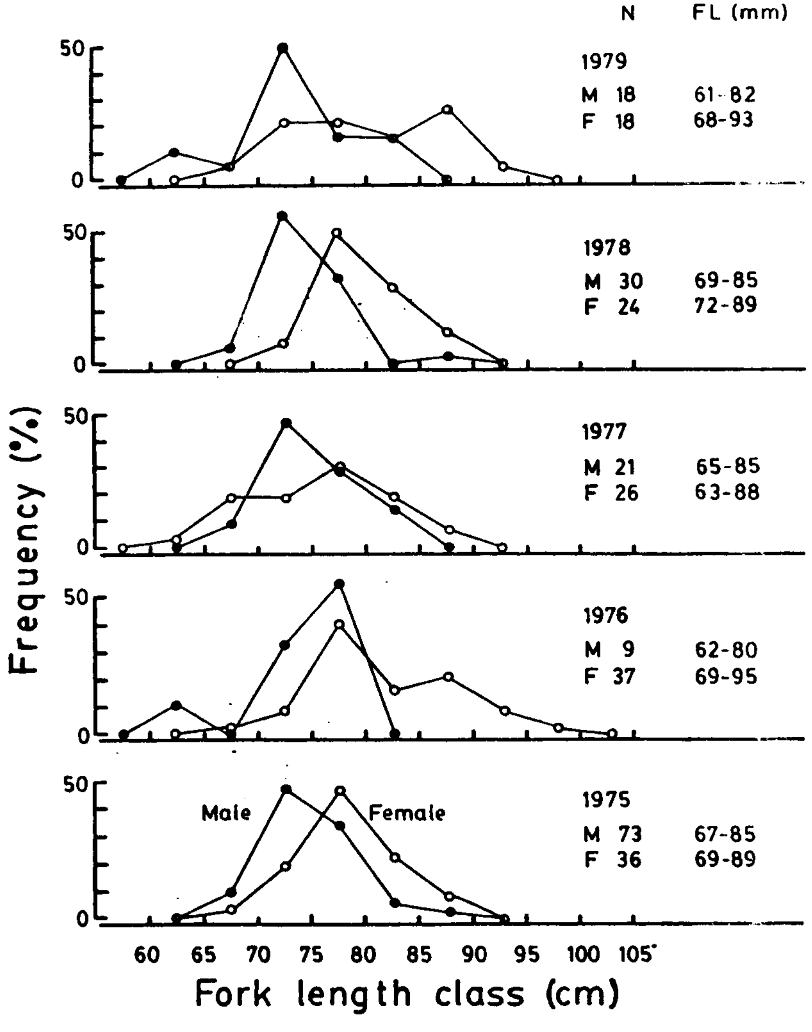


Fig. 17. Size frequency distribution of male and female milkfish in Pandan Bay, Philippines. In 3 years out of 5, females are significantly larger than the males (*Modified* from Kumagai 1981, 1990).

Change in Isozyme Patterns With Growth

A yet uncommon approach in growth studies is the use of biochemical indices. Metabolic and physiological requirements change with growth and these would be reflected in what the fish can and can not do, and in the levels of expression of gene products such as enzymes. For example, the enzyme lactate dehydrogenase (LDH), important in anaerobic glycolysis, can change its activity or expression of its isozymes (variants) depending on the needs of the animal at different stages or under various oxygen conditions. Requintina

Table 10. Length-weight relationships in milkfish, log BW = log a + b log FL*

Locality	Stage	log a	b	r	n
Philippines					
Pandan Bay[1]	adults	-4.0311	2.5810		
Libertad[2]	adults	-4.0052**	2.4169	0.90	32
Hamtik[1]	adults	-4.4683	2.8234	0.86	72
Hamtik[3]	adults	-3.8371**	2.3503	0.84	17
Tigbauan[1]	adults	-4.5051	2.8316	0.81	95
Tigbauan[3]	adults	-5.3542**	3.1117	0.97	27
Naujan Bay[4]	adults	-4.7555**	2.8213	0.85	58
Naburut Is.[5]	juveniles	-5.2991	3.2388		225
Pagbilao[6]	juveniles	-1.9970**	2.9185	0.97	57
Ponds[7]	juveniles	-5.2120	3.1831		240
	juveniles	-5.1505**	3.0299		240
Ponds[8]	juveniles	-5.0463**	2.9890		6304
Ponds[9]	fry-juveniles	-5.9684**	3.5656	0.96	36
Panay Is.[1]	fry	-3.9332	4.1641		20
Taiwan					
Tungkang[10]	fry (early)	-4.1867	4.3623	0.89	39
	fry (late)	-4.1118	4.3067	0.96	48
Ponds[11]	juveniles	-6.0083	3.0730		
Indonesia[12, 13]					
Karimun Jawa	adults	-5.1662**	3.0248	0.98	48
	adults	-5.1816**	3.0354	0.98	15
Sri Lanka					
Negombo[14]	juveniles	-5.6083	3.2598	0.95	31
India[15]					
Gulf of Mannar	fry-juveniles	-5.3348	3.0724		30
Hawaii[15, 16]					
Oahu coasts	adults	-4.4470	2.7811	0.98	177
Hopeia pond	adults	-5.5755	3.4618	0.95	45
Christmas Is.[16, 17]					
Main camp-ocean	adults	-4.5825	2.8509	0.99	7
Isles Lagoon	adults	-4.7190	2.9667	0.97	38
Pelican Lagoon	adults	-4.5956	2.9010	0.87	29
	adults	-4.2881**	2.5634	0.81	29
TeBati	adults	-5.1497	3.2211	0.99	17
		-5.5163**	3.2612	0.99	17
14 Pond	adults	-3.5778	2.2985	0.93	15
		-3.7591**	2.2832	0.90	15

*BW, body weight is kg for adults, g for juveniles, mg for fry; FL, fork length is cm for adults, mm for juveniles and fry. **BW-TL relationship. Most equations were derived by the author from data of various authors:[1]Bagarinao, unpubl.; [2]IFPP 1976;[3]IFPP 1974a; [4]Angeles 1971;[5]Kumagai et al. 1985;[6]Pinto 1985;[7]Arroyo et al. 1976; [8]Grover & Juliano 1976; [9]Rabanal et al. 1953; [10]Liao et al. 1977; [11]Lin 1969; [12]Martosudarmo et al. 1976; [13]Poernomo 1976; [14]Bagarinao & Thayaparan 1986; [15]Viswanathan & Tampi 1952; [16]Nash & Kuo 1976; [17]Oceanic Institute 1977 et al. (1981) examined LDH isozyme patterns in milkfish fry, younger and older juveniles, and adult males and females. They found A and B LDH expressed in all organs examined. The A4 isozyme is the most dominant in skeletal muscle of all stages, while the B4 isozyme is dominant in heart, liver, and eye. The A3B1 and A1B3 isozymes are expressed at all stages. Heart tissue shows different isozyme patterns with growth. The adult heart expresses all 4 isozymes, suggesting that the heart requires A4 LDH that can function at low oxygen concentrations. An unknown isozyme called X4 is expressed in the fry and gonads of females, suggesting a maternal influence. An anodally migrating isozyme called L4 occurs in the liver of juveniles and adults. (X4 is suggested to switch to L4 with growth.) This isozyme was also observed in milkfish liver by Mok et al. (1988) and identified as C4, the product of LDH-C gene. Requintina et al. (1981) further found that stunting of juvenile milkfish for 6 and 11 months does not change the LDH pattern, but affects the development of the liver, heart, and muscle, but not the eye.

Mortality at Different Stages

Natural mortality rates of milkfish are unknown. S. Kumagai (pers. comm.) estimated larval mortality based on the number of eggs and larvae of various stages collected in the Culasi-Maralison-Batbatan-Lipata waters. He estimated 0.04% survival from the egg to the fry stage (15-21 d in the plankton), a rate that presumably reflects the combined effects of dispersion, predation, starvation, and net avoidance. In the hatchery, survival of larvae from spawning to 21 d is about 15%; from hatching to 21 d, 30% on average (Liao et al. 1979; Juario et al. 1984b; Marte & Lacanilao 1986). Obviously the protective hatchery environment keeps the mortality down. In intensive larval rearing trials in Hawaii, Eda et al. (1990) obtained 19-46% (mean, 33%) survival over 30 d at stocking densities of 12-32 larvae/1. In Indonesia, Prijono et al. (1988) reported survival rates of 2-52% from hatching to fry stage (12.7 mm TL), 64% from fry stage to the end of the first year (195-360 g BW), and growth to 1-1.5 kg after the second year.

Mortality of milkfish fry during collection was found to be 15% (Kumagai et al. 1980). Milkfish fry that survive capture are phenomenally hardy. Survival > 80-90% is readily obtained during storage and transport (Quinitio & Juario 1980; Baylon 1983; Villaluz 1984). Survival during the nursery period tends to be lower (40-70% over 35-45 d) (Villegas & Bombeo 1981; Carreon et al. 1984) than during the grow-out period (75-100% over 90-120 d) (Pudadera & Lim 1980; Eldani & Primavera 1981; Otubusin & Lim 1985; Gerochi et al. 1988). Mass kills of juvenile milkfish in ponds sometimes occur, associated with rains and attributed to low dissolved oxygen levels, low pH, and other factors.

Smith (1981) estimated that for every 100 fry collected from shore waters and stocked in ponds in the Philippines, 38 are harvested at market size (200-300 g). In Taiwan, 70% survival of fry to market size is obtained with improved methods (Chen 1952). In culture systems, survival rates of milkfish are very much a function of experience and the culture techniques used.

REPRODUCTION

Milkfish reproduction in nature is discussed in great length by Kumagai (1981, 1990). Artificial propagation, both by environmental and hormonal manipulation, has been the subject of recent reviews and studies (Lam 1984; Juario et al. 1984b; Marte & Lacanilao 1986; Lee et al. 1986). Studies in milkfish reproductive endocrinology not discussed below include Marte & Crim (1983), Tan (1985), Sherwood et al. (1984), Lacanilao et al. (1985), Marte et al. (1988b), and Tamaru et al. (1988).

Sexuality and Sex Ratio

Sexes are separate in milkfish, but females are difficult to distinguish from males without handling the fish. In the anal region, there are 2 openings externally visible in mature males, and 3 in mature females (Chaudhuri et al. 1976). Females maturing for the first time may have only 2 openings (J. Juario, pers. comm.). Milt oozes out of ripe males when pressure is applied to the abdomen. The abdomen may appear distended in gravid females. The ovaries and testes are symmetrically developed, suspended in the coelom from the dorsal side by mesenteries. The ovaries are each half-exposed to the peritoneal cavity. The oocytes are released from the ovary into the cavity, enter the oviducts through a funnel, and are then expelled through the genital pore. Egg samples can be obtained from the ovary, but the cannula sometimes ruptures membranes and organs. The testes are each covered by a smooth tunica. Although often large in mature fish, they produce limited amounts of highly viscous milt.

In schools of adult milkfish caught around Panay, the males tend to be smaller than females (Table 8-9; Fig. 17). There is little size difference between the sexes in the populations in the lava ponds in Hawaii and in the hypersaline lagoons in Christmas Island (Table 9).

The sex ratio varies widely among groups of milkfish occurring together in fishing gear hauls (Table 11); of 576 specimens, 62% are males.

Maturation and Spawning

The stages of gonadal maturation in milkfish have been described and classified (i.e., immature, developing, mature, gravid, and spent) according to gross morphology of the gonads, gonadosomatic index (GSI, gonad weight as % of body weight), oocyte diameter, and histological appearance of the gonads (Tampi 1957; Kuo & Nash 1979; Liao & Chen 1984; Tan 1985; Kumagai 1990). The milkfish ovary undergoes a series of group-synchronous type of maturation (Tamaru et al. 1988). At some point, there is a fairly uniform clutch of large eggs in addition to a more variable clutch of smaller oocytes from which larger eggs are recruited. Female milkfish become most receptive to LHRHa (luteinizing hormone-releasing hormone analogue) induction of spawning when oocyte diameter is 0.75 mm or more, when vitellogenesis is nearly complete

Table 11. Sex ratio of milkfish groups caught around Panay Island (Philippines), 1975-1979 (*Modified* from Kumagai 1981,1990 and Bagarinao, unpubl.)

Ratio	Frequency of occurrence		
male/female	Pandan Bay	Hamtik	Tigbauan
No males	3	3	1
0.5	5	-	3
1	3	3	19
1.5	1	-	1
2	1	3	5
3	2	2	-
4	1	1	-
5	1	-	-
>5	4	1	1
No females	2	2	13
No. groups*	23	15	43
Total males	230(61%)	45 (56%)	83 (69%)
Total females	146(39%)	35 (44%)	37 (31%)
All fish	376	80	120

*For Pandan Bay, only groups with >4 milkfish caught in one haul of the *otoshi-ami* were used in the analysis of sex ratio. Hamtik and Tigbauan catches were lower, and groups with >2 milkfish caught in one haul of the fish corral were considered.

(Tamaru et al. 1988). On the contrary, Marte et al. (1988a) found that maturing milkfish administered human chorionic gonadotropin or gonadotropin-releasing hormone analogues ovulate or spawn when the oocyte diameter is 0.67 mm or greater.

Records and estimates of first sexual maturity vary with locality and whether fish are wild or captive (Table 12). It is not clear whether first sexual maturity is related to age or size (Lam 1986).

Figure 18 shows the distribution of GSI values over a range of adult weights. Both male and female milkfish caught around Panay Island (Philippines) show high GSI > 5, i.e., mature, at 5 kg body weight (Fig. 18A). GSI values of 16-20 are recorded for females 8-14 kg, but the mode is around 10. During March to June, a high proportion of females collected from Tigbauan and Hamtik have higher GSI (mature) than those collected from Pandan (spent). Males from these 3 places have similar GSI. This is suggestive of a possible south-to-north spawning migration. Figure 18B shows data for other milkfish populations. Indonesian fish have similar GSI- body weight distribution as the Philippine fish. Hawaiian fish have very low GSI except during July-August when 3 kg fish have GSI > 5. Christmas Island fish have GSI > 5 at weights of only 1 kg. There are also differences between wild and captive broodstock. For example, captive females in the SEAFDEC/AQD floating cages are smaller (3.5 kg) and have lower GSI (mean, 4.5) at maturity, i.e., when the average oocyte diameter is 0.70 mm (Marte & Lacanilao 1986).

Contrary to the situation up till the 1970s, milkfish now mature and spawn under various conditions of captivity. The first instance was in August 1980

Table 12. Records or estimates of first sexual maturity in milkfish

Locality/conditions	Sex	Total length (cm)	Body weight (kg)	Age (yr)
Philippines				
Panay				
Cage-reared[1, 2]	both	60-70	2-5	3.5-5.5
Wild[3]	both	75-85	4-5	3?
Naujan Bay				
Wild[4]	both	80-85	4-5?	3?
Taiwan				
Pond-reared[5]	females	66-80	3.5-7	8-10
Tank-reared[5]	males	70	2.5	4
	females			5
Indonesia				
Wild[6]	females		>3.5	>6
Tank-reared[7]	males	69-77	x=3.8	8-9
	females	64-79	x=3.2	8-9
Hawaii				
Wild[8]	both	75*	7*	4
Pond-reared*	males	65	2.5-5	
Tank-reared[9]	both			6-7
India				
Wild[10]	females	110	11	4-5
	males	108-114		

Given by C.M. Kuo in Lam (1986). [1]Lacanilao & Marte 1980; [2]Marte & Lacanilao 1986; [3]BW estimated from Fig. 18; TL and age computed from equations in the text; [4]Based on data of Angeles 1971 on the assumption that the adults in Naujan Bay had mostly come from the lake growing area and were maturing for the first time; [5]Liao & Chen 1984; [6]Schuster 1960; [7]Poernomo et al. 1985a; [8]Nash & Kuo 1976; [9]Lee 1985; [10]Tampi & Bensam 1976.

when the milkfish broodstock in floating cages at SEAFDEC/AQD spawned spontaneously (Lacanilao & Marte 1980). Ten natural spawnings occurred during the subsequent year and 17000 eggs were collected (Marte & Lacanilao 1986). The first generation cycle of milkfish in captivity was completed when the offspring of a wild female induced to spawn in 1978 (Liao et al. 1979) in turn spawned in 1983, with 14 spawnings between May and June and 315 000 eggs collected (Marte & Lacanilao 1986). In 1985, 41 natural spawnings were recorded from April to October (Marte et al. 1986); in 1986, 54 spawnings were observed between May and October (Marte 1988). Pond- and tank-reared milkfish have matured and spawned in Taiwan, Hawaii, Indonesia, and the Philippines (Liao & Chen 1984; Lam 1984; Lee 1985; Lin 1985; Poernomo et al. 1985a, b; Lee et al. 1986; Prijono et al. 1988; Emata & Marte 1990). In Taiwan, 62 natural spawnings were recorded in April- September 1984 in a population of 110 pond-reared milkfish, producing a total of 62 million eggs (Lin 1985).

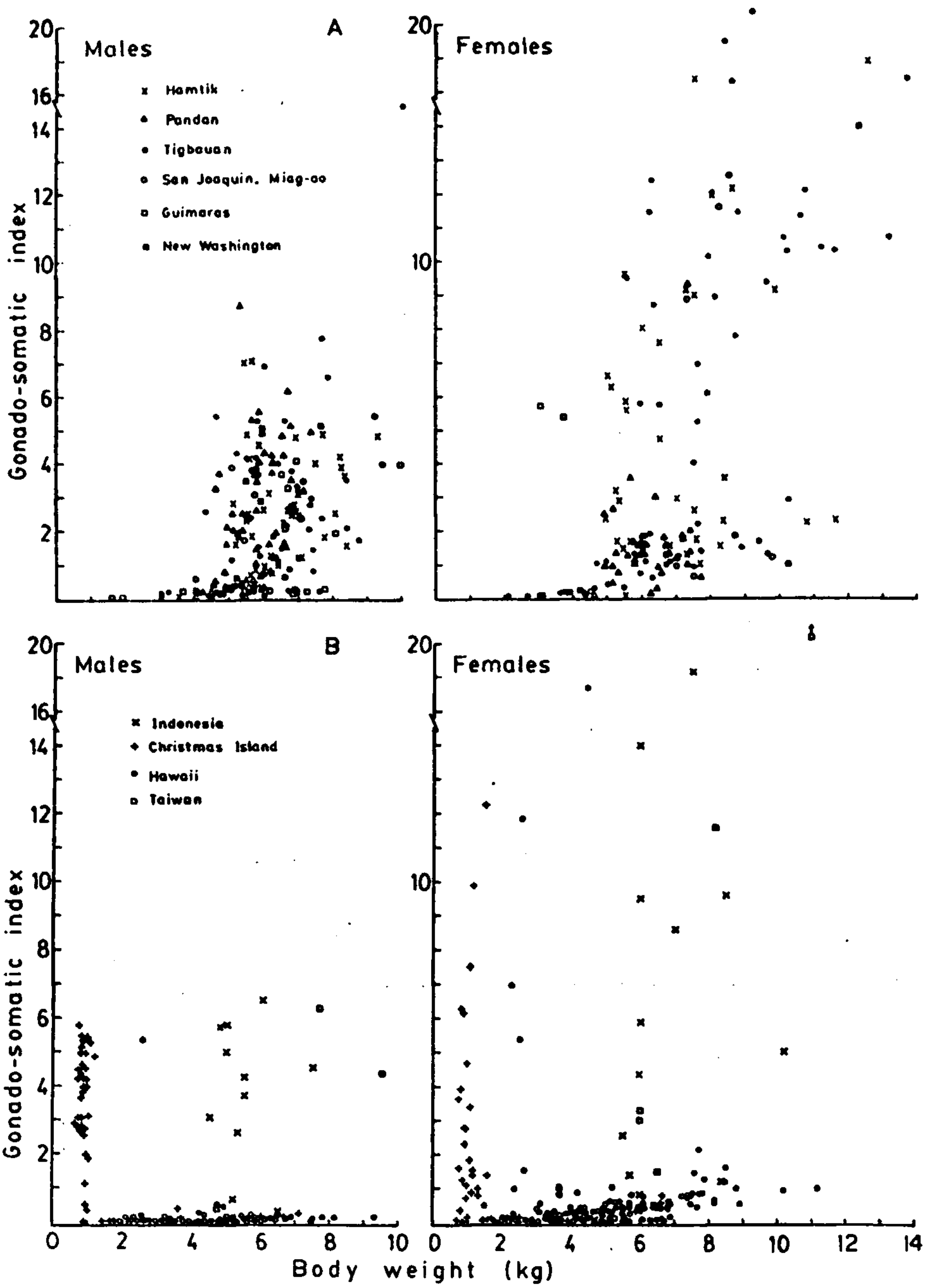


Fig. 18. Distribution of gonadosomatic indices against body weight in milkfish: A, fish around Panay Island, Philippines caught March-June (GSI >5 observed for females >5 kg); B, fish from other localities show similar (Taiwan and Indonesia) or different (Christmas Island and Hawaii) distributions as Panay (Data from Liao 1971; Nash & Kuo 1976; Martosudarmo et al. 1976; Tiro et al. 1976; Oceanic Institute 1977, 1980; Bagarinao, unpubl.).

The environmental determinants of maturation and spawning of milkfish in captivity have been discussed by Lam (1984, 1986) and Lee (1985). Milkfish have been observed to spawn at water temperatures of 24-33°C (Lam 1984). Milkfish do not spawn in freshwater as evidenced by adults leaving Naujan Lake to spawn at sea (Delmendo & Angeles 1971). However, they mature and apparently spawn in the landlocked hypersaline lagoons in Christmas Island (Crear 1980). Reproductive readiness in these fish seems to be determined by the interaction of diet and salinity, with the effect of diet prevailing. A diet of brine shrimp and microbial mat (similar to *lablab*) results in maturation even at high salinities; without a brine shrimp diet, maturation occurs only at lower salinities (Crear 1980). On the other hand, the rapid gonadal development of milkfish in the floating cages at SEAFDEC/AQD seems to coincide with rising water temperatures and lengthening photoperiod (Marte & Lacanilao 1986). Hormone-induced milkfish (8-9 yr old) spawn spontaneously in 5-200-t tanks, but the eggs from the spawnings in 5-11-t tanks do not hatch (Emata & Marte 1990). In Indonesia, Poernomo et al. (1985a) found that size and shape of tanks do not affect milkfish maturation but influence the amount of fat deposition; a feeding rate of 2% of body weight is too high for milkfish held in 40-t and 60-t tanks, but adequate for those in 400-t tanks.

Fecundity and Spawning Frequency

Milkfish producesa tremendous number of eggs. When mature, the ovary is usually around 10% of body weight, but could be nearly 25% (Fig. 18; Liao 1971). Some 1-6 million eggs may be produced by females 5-13 kg in weight (Fig. 19), equivalent to some 300 000 eggs/kg. Milkfish in the floating cages at SEAFDEC/AQD are smaller and produce fewer eggs (200 000 eggs/kg) (Marte & Lacanilao 1986; Fig. 19).

In the wild, milkfish probably spawns more than once a year. Around Panay (Philippines), milkfish specimens have 3-4 batches of oocytes at a time (Fig. 20). A female caught in Okinawa waters had 3 batches of oocytes, including a 0.85-0.90 mm batch about to be spawned (Kanashiro & Asato 1985). In Taiwan ponds, 33 spawnings were recorded in a pond with 15 females (Lin 1985). Gonad maturation was not uniform among this stock; usually a single female spawned in a day, occasionally 2 or 3 (Lin 1985). In Hawaii, females induced to mature by hormone implantation spawn repeatedly over several months(Leeet al. 1986; Tamaru et al. 1988). At SEAFDEC/AQD, individually tagged females kept in floating cages and concrete tanks can spawn up to 3 times (Marte & Lacanilao 1986; A. Emata, pers. comm.).

Spawning Grounds

Delsman (1926, 1929) collected 15 milkfish eggs during his 10-year survey in the Java Sea, and Chacko (1950) apparently did so around the Krusadai Island. Various accounts by fishermen and investigators in several countries suggested possible spawning of milkfish in locations with clear shallow water above a bottom of sand or corals situated at a distance of not more than 30 km

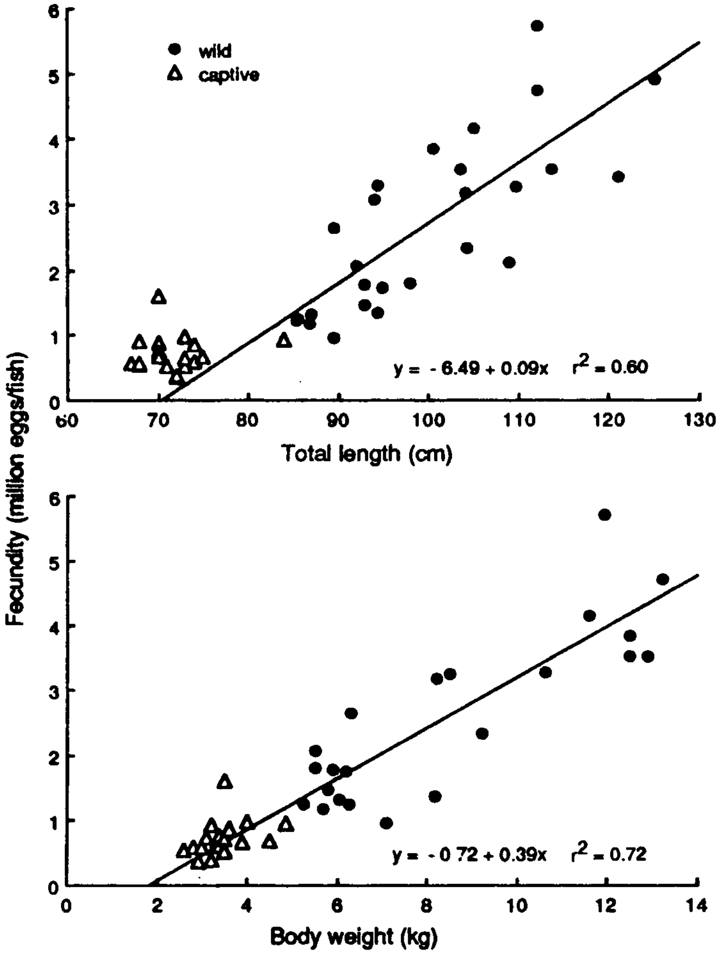


Fig. 19. Fecundity of wild and caged milkfish as a function of total length and body weight; regression lines and equations shown are for wild milkfish (Data from Tampi 1957; Schuster 1960; Liao 1971; Siu & Muench 1979; Kumagai 1981, 1990; Kanashiro & Asato 1985; Marte & Lacanilao 1986).

from shore (Schuster 1960; Johannes 1978). Schmittou (1977) suggested that the milkfish fry occurring in western Panay come from spawning grounds in the Cagayan Islands in the Sulu Sea. The western Panay coast is one of the most productive milkfish fry collection grounds in the Philippines (Villaluz 1975; Smith 1981), and survey efforts by SEAFDEC/AQD were concentrated in this area in 1976-1980.

During the 1976-1979 survey, 544 milkfish eggs were collected in 90 of the 1304 plankton net tows in Cuyo East Pass, mostly around the islands of Batbatan, Maralison, Maniguin, and Seco (Fig. 21; Senta et al. 1980a). A few eggs were also collected around the Cagayan Islands in the Sulu Sea, a single one near Zapato Island in the Sibuyan Sea, but none from the Panay Gulf nor

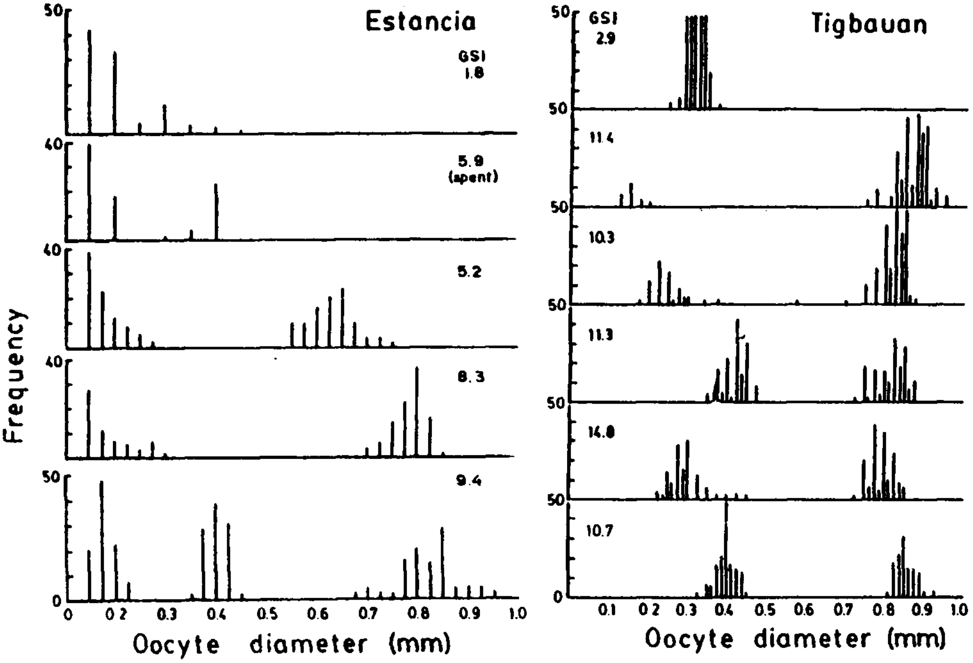


Fig. 20. Oocyte diameter distribution of milkfish from Estancia in northeastern Panay (*Modified* from Kumagai 1981, 1990) and Tigbauan on the southern coast (Almendras, unpubl.). One to 3 diameter modes are seen in individual fish, depending on the stage of maturity (GSI), but 4 modes are seen for the Panay milkfish as a group. Plotted are representative specimens (total n = 18); 100 oocyte measurements/Estancia fish and 150 measurements/Tigbauan fish.

the Visayan Sea. The eggs occurred in small numbers, <10/tow, with the maximum catch of only 33 eggs in a tow. The stations where milkfish eggs were collected were mostly within 5 km of land in waters <200 m deep, although eggs that probably drifted from the actual spawning grounds were also collected at stations up to 23 km from land and up to 900-m deep.

In 1980, the survey was concentrated in the waters bounded by Maralison, Batbatan, and Lipata (Fig. 21; Kumagai 1981, 1990; Bagarinao & Kumagai 1987). This time, 1149 milkfish eggs were recovered in 98 of a total 594 plankton net tows during 17-day cruises in March to June. The maximum number obtained by a single tow was 156 eggs, 5x greater than the previous record. The most productive area was the vicinity of Maralison Island. The waters off Lipata, though second most productive, was way behind in the catch. Still fewer eggs were obtained from stations off Batbatan, and least productive were the relatively deep offshore stations. Eggs were collected 3x from a station merely 500 m off Culasi beach. The water currents were estimated to be 0.3-0.4 m/s due N-NW during the survey period. Most of the eggs were apparently spawned near the reefs around Maralison and some of these drifted from the

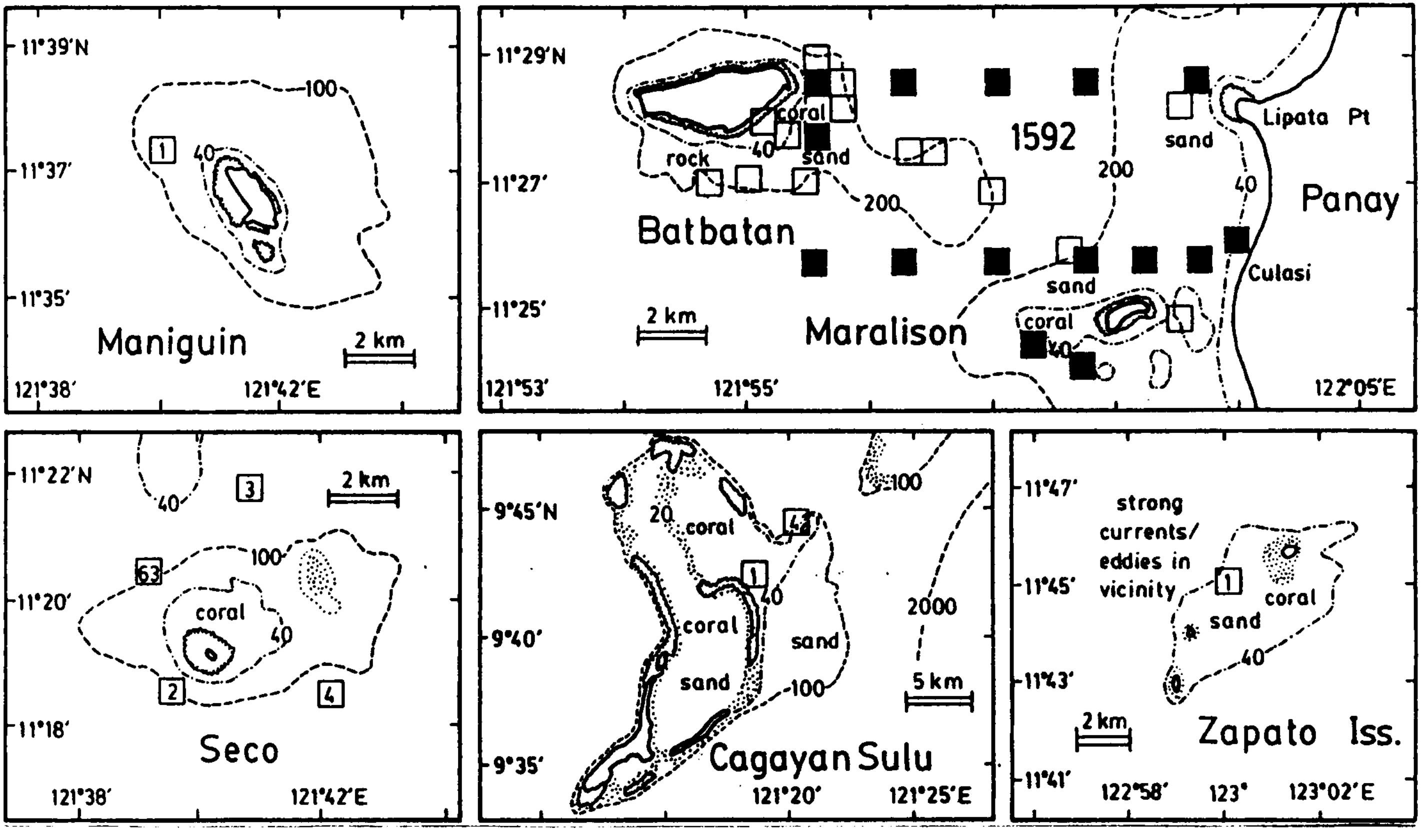


Fig. 21. Locations off west, north, and south Panay, Philippines where milkfish eggs were collected. Stations of successful tows (squares with number of eggs indicated) are mostly over shallow water (20-200 m) close to small islands and coastal promontories. Closed squares, stations in the April-May 1980 survey. Total egg catch from the Batbatan-Maralison-Culasi-Lipata spawning ground, 1592; other locations, 29.

stations to the north-northwest (Fig. 21). Another explanation for the egg distribution is that milkfish spawns within or along the 200-m depth contour, and that the lower catch in the northern stations could have been due to the later sampling times.

Thus, milkfish appears to spawn in the vicinity of shoals or otherwise clear, shallow waters around islands and promontories. From the spawning ground surveys, it also appears that the population of adult milkfish is relatively small and scattered in small schools, which partly explains why an extensive survey is less effective in sampling eggs than one concentrated in time in a particular area.

Leis & Goldman (1987) collected young milkfish larvae near reefs from waters <30-m deep. Spawning locations of milkfish in Palau are 4-10-m deep waters over fringing reefs 100-200 m from shore near the edge of a steep drop-off (Johannes 1981). Spawning locations are thought to be selected by the need to position the eggs and larvae over water deep enough to minimize predation by benthic planktivores like corals, and near enough to the coast to facilitate return of larvae to inshore habitats (Johannes 1978).

Time of Spawning

Milkfish spawning has never been directly observed at sea, although fishermen in the Philippines and in Palau report seeing schools of milkfish massing together at certain areas in the reefs or lagoon at particular times (author's interviews; Johannes 1978). Off western Panay, spawning occurs around midnight, based on the developmental stages of eggs collected by plankton tows (Fig. 22). In SEAFDEC/AQD floating cages and in ponds in Taiwan, spawnings take place around midnight (Marte & Lacanilao 1986; Lin 1985) although daytime spawnings (1100-1300 H) have been known to occur less frequently. In Palau, spawning is reported to occur during the day, but efforts to verify this failed (Johannes 1981).

On days when spawnings occur in SEAFDEC/AQD floating cages, increased swimming activity, chasing, and occasional leaping and slapping of water is observed from late afternoon to early evening, becoming more pronounced from 2000 H (Marte et al. 1986). Milkfish in Taiwan ponds circulate around the pond and feeding decreases 3 d before spawning (Lin 1985).

Lunar Periodicity of Spawning

Off western Panay, milkfish eggs are more abundant during the quarter moon periods than during the full or new moon (Fig. 23). Delsman (1926, 1929) collected milkfish eggs on 24, 25, and 27 September 1928, days which also fell within the first and last quarter periods. Spawning during the neap tide periods probably minimizes flushing of eggs and helps ensure that the larvae remain near the coast, as suggested by Johannes (1978) for tropical marine species with pelagic eggs. The estimated spawning time around midnight coincides with the low tides of quarter moon periods during the milkfish

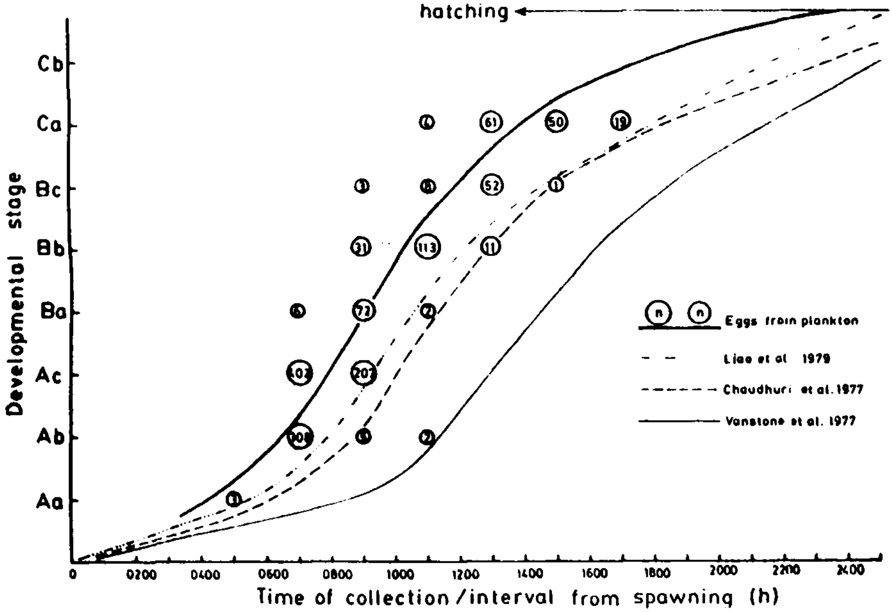


Fig. 22. Numbers and developmental stages of eggs collected off western Panay, Philippines at different times of day. Eggs taken to the laboratory hatched in 1900-2000 H. Incubation period (18-24 h) at sea is shorter than in the laboratory. Milkfish apparently spawns around midnight between 2200 and 0200 H (*Modified* from Kumagai 1981, 1990).

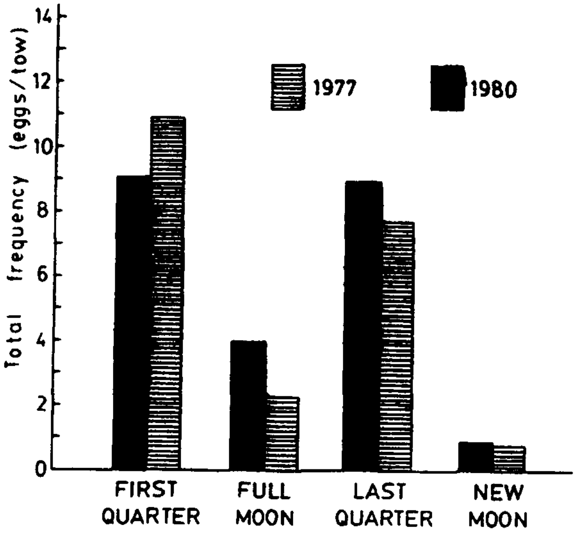


Fig. 23. Lunar periodicity of milkfish egg occurrence (i.e., spawning activity) off western Panay, Philippines. Differences among lunar periods (each reckoned as 3 days before and after the phase date) are significant (x^2 test, $p<0.05$ in 1977 and $p<0.01$ in 1980) (*Modified* from Kumagai 1981, 1990).

season in Panay.

Younger larvae tend to be more abundant during the quarter moon periods, and older larvae during the full moon and new moon periods (Table 13). Milkfish fry are more abundant during the full moon and new moon periods in western Panay, as well as in many other localities (Kuronuma & Yamashita 1962; Rao 1970; Kumagai 1984). Since the fry are on average 3 wk old, it follows that they are abundant on the full moon and new moon 3 wk after the quarter moon when they were spawned. The fry caught during the quarter moon periods have a higher percentage of smaller, younger (2-wk old) individuals (Fig. 12).

Spawning of milkfish in SEAFDEC/AQD floating cages occurs mostly during the first quarter and full moon periods, with more days of spawning and more eggs per spawning than the other 2 periods (Marte et al. 1986). On the contrary, spawning in Taiwan pond is most frequent (with the greatest egg production) during the last quarter period and about equally spread out during the rest of the month (Lin 1985). Milkfish spawning is reported to occur for 3 d around the full moon and new moon periods in Palau, and the fry migrate into mangrove areas during rising spring tides 2 wk later (Johannes 1981). It is not known what exactly determines the lunar periodicity of milkfish spawning in the wild and in captivity.

Seasonality of Reproduction

There is a marked seasonality in the spawning activity of milkfish. Along the coasts of Panay, mature fish appear starting March, and spent fish become more frequent in May to June (Fig. 6). The GSIs are highest in March in Tigbauan, and in April in Pandan (Fig. 24). The monthly egg occurrence off the western coast shows a relative high in April (Senta et al. 1980a; Table 14). Fry occurrence in Pandan and Hamtik peaks in May although extending from

Table 13. Occurrence of milkfish larvae off Culasi in western Panay (Philippines) at different lunar periods in April-May 1980 (*After* Bagarinao & Kumagai 1987)

Dates/ lunar phase		No. of tows	No. of larvae by stages (Density/10 000m³)				
			I	II	III	IV	Total
A 16, 17, 18	NM	86	1 (0.7)	1 (0.7)		2 (1.3)	4 (2.6)
A 21, 22, 23	FQ	103	3 (1.6)	1 (0.5)			4 (2.2)
A 26		38		2 (2.9)			2 (2.9)
A 29, 30; M 1	FM	132			4 (1.7)		4 (1.7)
M 4		44		2 (2.5)			2 (2.5)
M 7, 8, 9	LQ	125	10 (4.4)	4 (1.8)	1 (0.4)		15 (6.7)
M 12, 13, 14	NM	66	7 (5.9)	5 (4.2)	1 (0.8)		13 (10.9)
Total		594	21 (2.0)	15 (1.4)	6 (0.6)	2 (0.2)	44 (4.1)

A, April; M, May; NM, new moon; FQ, first quarter; FM, full moon; LQ, last quarter.

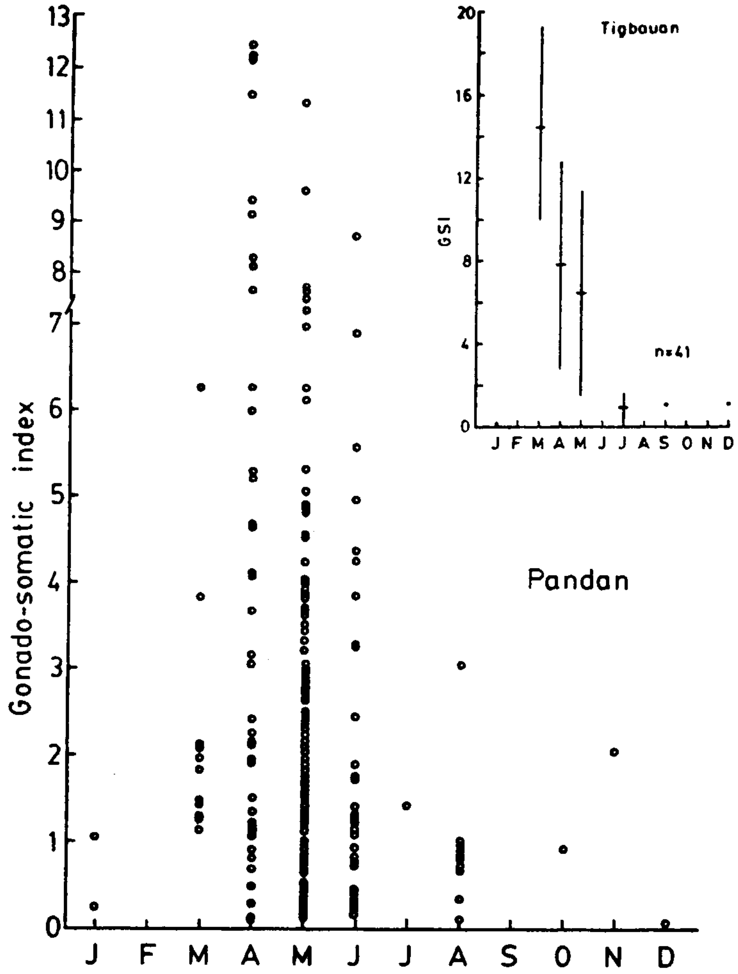


Fig. 24. Seasonal pattern in the GSI of female milkfish in Pandan (*Modified* from Kumagai 1981, 1990) and Tigbauan (Bagarinao, unpubl.) showing values >5 (mature) between March and June, and peak values in April and March, respectively.

March to December (Kumagai 1984). There is a lag of about a month between peak spawning and peak fry occurrence which is reasonable given the age of the fry (3 wk).

Spawning of milkfish in the SEAFDEC/AQD floating cages occurs at various times within April to October, with peaks in May-July and September-October (Marte et al. 1986; Marte 1988). GSI and percentage of mature fish show peaks in April to June and occasionally in August to September (Marte & Lacanilao 1986). These periods coincide with the natural spawning season in Panay waters. Spawnings of milkfish in the ponds in Taiwan and in tanks in Indonesia also coincide with the natural season (Lin 1985; Prijono et al. 1988). Table 15 shows the spawning seasons of milkfish in various localities.

Table 14. Monthly occurrence of milkfish eggs off western Panay (Philippines)

Month	Total eggs		Total tows		Eggs/tow		Eggs/10 000 m^3	
	A*	B	A	B	A	B	A	B
February	0		25		0		0	
March	72		160		0.45		25	
April	323	631	443	315	0.73	2.00	41	111
May	123	518	416	279	0.29	1.86	16	103
June	26		196		0.13		7	
July	0		4		0		0	
August	0		22		0		0	
September	0		10		0		0	
October	1		23		0.04		2	
November	0		5		0		0	
Total	545	1149	1304	594	0.42	1.93	23	107

*A, plankton surveys extensive over a wide area and collected few eggs (1976-79); B, survey limited to particular spawning areas (1980) *(Modified* from Senta et al. 1980a and Kumagai 1981, 1990).

Table 15. Spawning seasons of milkfish in different localities

Locality	Spawning season	Peak(s)	Basis
Philippines			
Panay (11-12°N)[1]	Feb-Nov	Apr,Sept	Egg collection, high GSI, and fry collection pattern
Igang cages[2]	Mar-Nov	Apr-June, Aug-Sept	High GSI, % mature fish
Igang cages[3]	Apr-Oct	May-July, Sept-Oct	Actual spawnings
Taiwan			
Tungkang(22°N)[4]	May-Aug	July	High GSI, yolky oocytes
Ponds[5]	Apr-Sept	May	Actual spawnings
Hawaii			
Oahu (20°N)[6]	June-Aug	July	High GSI, yolky oocytes
Tanks[7]	Mar-Sept		Actual spawnings
India			
Mandapam (9°N)[8]	Mar-Nov	Apr, Sept	Fry and fingerling occurrence
Pichavaram (11°N)[9]	Jan-Sept		Juvenile recruitment
Indonesia			
Java (7-8°S)[10]	Jan-Dec	Sept,Apr	Egg collection, high GSI
Tanks[11]	Jan-Apr		Actual spawnings

[1] From Table 14, Fig. 24,26B;[2]Marte & Lacanilao 1986;[3]Marte et al. 1986, Marte 1988; [4] Liao & Chen 1984;[5]Lin 1985;[6]Kuo & Nash 1979;[7]Lee et al. 1986, Tamaru et al. 1988; [8]Tampi 1959, Dorairaj et al 1984;[9]Krishnamurthy & Jeyaseelan 1981; [10]Delsman 1926, Martosudarmo et al. 1976;[11]Poernomo et al 1985a, Prijonoetal. 1988.

Milkfish eggs were collected at temperatures of 27-31°C and salinities of 33-35 ppt, conditions that occur between March and November off western Panay (Fig. 25). Kuronuma & Yamashita (1962) considered 27°C as the threshold for milkfish spawning. However, spawning in Taiwan ponds also took place at temperatures of 25°C (Lin 1985).

Seasonality in milkfish reproduction may also be seen in the fry occurrence patterns at different latitudes (Figs. 26 A, B). The fry occurrence season is long and has 2 peaks near the equator. It becomes progressively shorter with a single peak at higher latitudes. The northern hemisphere has the early season (March-June) emphasized, and the southern hemisphere the later (September-December), i.e., during spring in both cases. It can be inferred that the milkfish spawning season would have the same pattern though advanced by about a month. Fry occurrence and abundance patterns, however, are affected by oceanographic and topographic factors which may mask the relationship to spawning seasonality at particular locations. For example, wild adults off Taiwan apparently mature only during June to August, yet fry occur along the coasts as early as April (probably seeded from the south by the *Kuroshio* Current).

Good correlation is seen between fry occurrence patterns and seasonal pattern of insolation, i.e., the radiant energy reaching particular latitudes at

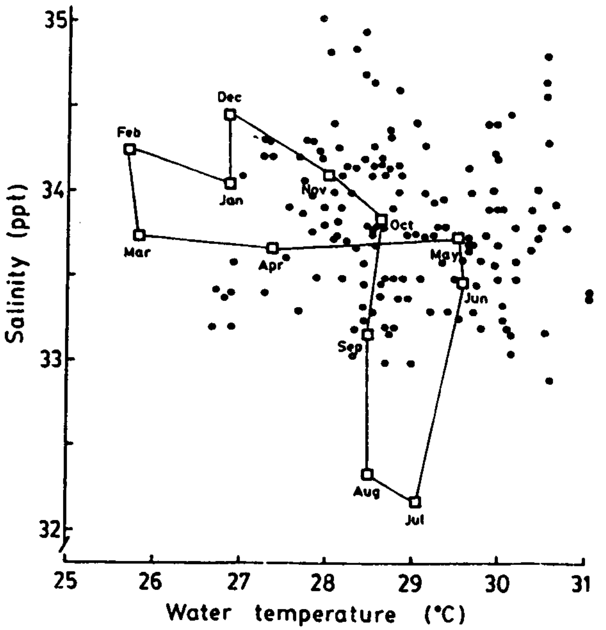


Fig. 25. Water temperatures and salinities at which milkfish eggs (circles) were collected off western Panay, Philippines compared with the T-S polygon for Pandan Bay at 5 m depth (squares). All eggs were collected between March and June except a single one in October, within 27-31°C and 33-35 ppt. A river empties into Pandan Bay, thus, the low salinity in July-August (typhoon season). The bay gets colder than the more open waters where milkfish spawns (*Modifed* from Kumagai 1981).

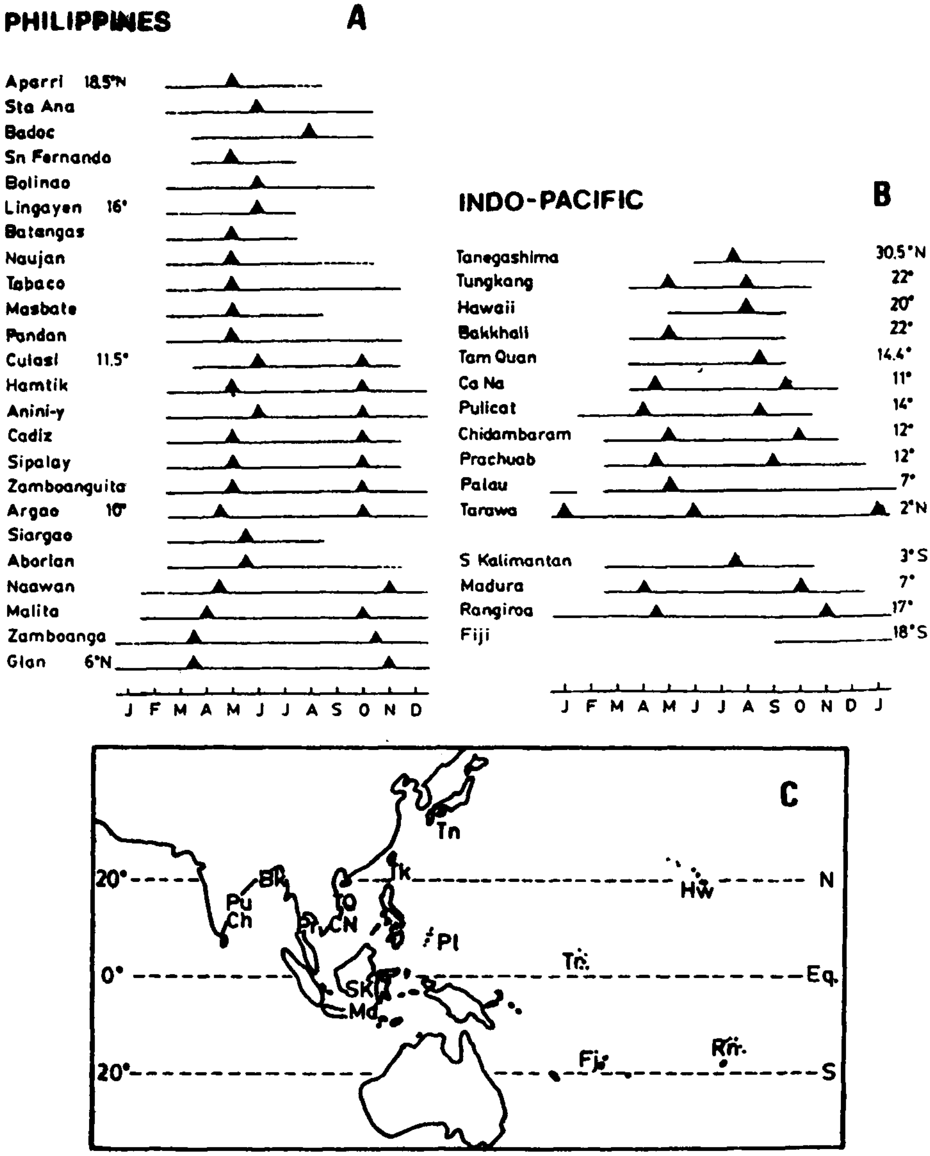


Fig. 26. Milkfish fry occurrence seasons in various localities from north to south in the Philippines (A) (Data from Deanon et al.1974; Kumagai 1984) and the Indo-Pacific (B) (Data from Thiemmedh 1955; Schuster 1960; Kuronuma & Yamashita 1962; Rao 1970; Basu & Pakrasi 1976; Liao et al. 1977; Siu & Muench 1979; Johannes 1981; Senta & Hirai 1981; Wainwright 1982) showing latitudinal variation. Horizontal lines, duration; triangles, peaks of occurrence. Abbreviations in map (C) refer to places in B.

different times of the year (Kumagai 1981, 1990). On the other hand, Wainwright (1982) found that the fry season is longer in areas with higher annual sea surface temperature (SST), with 24°C the apparent minimum temperature required for spawning.

BEHAVIOR

The importance of behavior to fish capture and culture has been well elucidated by Bardach et al. (1980). Certain aspects of the behavior of milkfish have been studied, but for the most part, observations were casual.

Sense Organs

At the time of capture from shore water, milkfish fry have well-developed eyes with regionally differentiated duplex retina (Kawamura & Hara 1980b; Kawamura & Shinoda 1980; Kawamura 1984). Cell density and thickness are highest in the temporal region of the retina (*area temporalis*) indicating highest visual acuity for objects directly in front of the snout. Although rod density in newly caught fry is low (R ratio of nuclei to cone ellipsoids is 1.4-2.1), retinomotor response is observed and both photopic and scotopic vision must be possible; rod density increases in about 2 wk from capture (R becomes 2.6-3.3). A tapetum lucidum is present in the pigment epithelium and probably functions under subdued light. The adipose eyelid in milkfish is not formed at the fry stage but appears during the transformation stage. The adipose eyelid in fishes has been shown to be birefringent and to aid in polarotaxis, or to increase the focusing power of the eye (Stewart 1962). The retinae of juvenile milkfish (12.5-14.0 cm FL) show spectral sensitivity with peaks at 492-522 run (blue-green) and 582-621 nm (yellow-orange) which suggest that milkfish has color vision (Kawamura & Nishimura 1980). Behaviorally, juveniles can recognize white, red, and green light (Durve 1968).

The inner ear, olfactory organ, lateral line, and taste buds are likewise well-developed in the fry. and become further elaborated in juveniles (Kawamura 1984). Juveniles have well-developed gustatory and olfactory perception (Durve 1968).

The importance of vision is well known in studies on feeding behavior, optomotor reaction, phototaxis, and response to fishing nets (Kawamura & Hara 1980a,b; Kawamura & Shinoda 1980; Kawamura 1984). It may be presumed that the fry make use of their sense organs to find their way from the spawning grounds to the fry collection grounds.

In common with other ostariophysans, milkfish has alarm substance cells in the epidermis (Pfeiffer 1977). These are club cells not connected to the surface and distinct from mucus cells in general morphology, staining reaction, and position of the nucleus. Skin injury releases the cell's alarm substance (a pheromone) that elicits the fright reaction among other members of the group. Fishes that show the fright reaction are mostly freshwater species, social (schooling), lacking in defensive structures, and non-predatory.

Swimming Speeds

Swimming speeds of fry and juveniles measured in the laboratory (Kumagai 1981, 1990) are given by the following equations, where V is the swimming speed (cm/s) and t is the swimming time (in seconds, s).

Fry (mean , 14 mm *TL*, n = 38)	$V = 30.05\ t^{-0.1469}$
Transformation larvae (mean 21 mm TL, n = 31)	$V = 25.40\ t^{-0.1205}$
Juveniles (mean, 24 mm TL, n = 15)	$V = 30.44\ t^{-0.0957}$

Using 5 s as the standard length of time for burst speed V_b, and 60 min for cruising speed V_c, the following values are obtained:

	V_b (cm/s)	V_c (cm/s)	V_c (TL/s)
Fry	23.7	9.0	6.5
Transformation larvae	20.9	9.5	4.5
Juveniles	26.1	13.9	5.8

Fry appear to have better swimming ability (as body length/s) than early juveniles. While the vertebral column is already completely ossified in the fry, the body remains flexible enough to be laterally undulated in swimming as in eel. Burst speed is reduced during the transformation stage presumably due to the increasingly rigid body and the forward migration of the dorsal fin. Swimming ability is thereafter improved in the juveniles as the caudal fin becomes more powerful with further ossification of its bony elements. Other measurements of swimming speeds in milkfish fry fall within the range 9-11 cm/s (Komaki 1981; Kawamura 1984). In comparison, larvae of other fish species have cruising speeds of 2-3 body length/s and burst speeds of 10 body length/s (Blaxter & Staines 1971).

Milkfish fry collectors in Panay operate the fry sweeper at speeds of roughly 40 cm/s which is unnecessarily too fast. Injury results from such manner of collection and it is suggested that gear operation be at slower speeds of 10-20 cm/s (Kumagai et al. 1980).

Schooling

When the dorsal, anal, and caudal fins differentiate (day 10), larvae begin to swim in groups and show strong rheotaxis in daytime (Liao et al. 1979). Schooling is bound to start early in rearing tanks because of the proximity of neighbors. At sea, however, there is greater dispersion, and until the fry reach shore waters, they probably do not school. Kawamura (1984) showed high correlation in the catch of 2 fry gear operated simultaneously but independently within the same length of beach and concluded that milkfish fry in shore waters are only loosely aggregated. Kumagai (1984) likewise suggested that milkfish fry arrive in shore waters in patches (i.e., pulses in time) but are distributed homogeneously along considerable stretches of beach. Kept in containers after capture, milkfish fry typically swim round and round in the same direction, this behavior an indication that the fry are in good condition (Villaluz 1984). This circling behavior, however, is not exhibited in darkness (author's obs.).

Juveniles tend to hover in one place for long periods, make abrupt dashes when disturbed, then go back to hovering. At night, activity is even less; they stay close to the bottom almost motionless (Buri 1980). In ponds, juveniles school in groups of tens to hundreds. Those larger than 150 mm can be observed to become very excited on days when high tides can be expected to reach the ponds (Schuster 1960). Hours before the advancing tide reaches the pond, the fish swim close to the surface of the water, all in the same direction, circling the pond again and again. When water is allowed into the pond, the fish swim against the current and accumulate in front of the pond gate. Efforts to swim against the current are so violent that many fish hurt themselves. This behavior is utilized in pond harvesting. Based on observations in natural nursery grounds, Kumagai et al. (1985) suggested that the fish probably want to leave the ponds at this time and use the tide to go back out to sea. Large milkfish in the Molii pond in Kaneohe Bay attempt to go through the gates out to sea during the high tides of the new moons; at other times, these fish are not seen near the pond gates (Nash & Kuo 1976).

Adult milkfish school, and school size probably depends on the activity, whether feeding, spawning, or migrating. Schools of 10-20 fish, as well as of hundreds of individuals have been reported. Milkfish schools could be recognized by the caudal fins breaking the water as the fish swim near the surface, and also by the frequent jumping. In Indonesia, schools of milkfish are repeatedly observed in the mouths of the rivers which flow into the Gulf of Poso; they are supposed to swim up the rivers at noon and go back out to sea in the afternoon (Tjiptoaminoto 1956).

Response to Capture

The fry collection gears presently used in various localities in the Philippines (Fig. 27; Kumagai et al. 1980), Indonesia, and Taiwan operate by filtration of water in similar manner as plankton nets. Marine fish larvae avoid plankton nets towed slowly in daytime (Clutter & Anraku 1968). Having good vision, milkfish fry may respond toward the collection gear either negatively (avoidance) or positively (may be driven or herded). Experiments in tanks showed that milkfish fry blocked by a stationary net (twine 053 mm in diameter, mesh 5-20 mm) hesitated going through the mesh and were retained by a black net longer than by a white net; similarly, fry were herded well by moving nets, with black nets slightly more effective (Kawamura et al. 1980). These results indicate that milkfish fry gear may be designed to function in herding, not mere filtering(Kawamura 1984). Young juvenile milkfish can be collected from tidal wetlands using nets with scarelines (Dorairaj et al. 1984).

Nash & Kuo (1976) observed that success in the capture of adult milkfish with a 200 m x 8 m gillnet of 6.6 cm mesh was related to water turbidity. In turbid waters the net is invisible and the fish do not struggle too much. In clear waters, the net is visible and fish struggle to avoid it.

Adult milkfish trapped in fish corrals struggle violently when the net closes, usually jumping out, and sometimes bursting through the side nets (IFPP 1976) Trapped fish swim continuously in a single school in midwater 6-30 m deep As the net closes in, the fish swim more rapidly and excitedly still in a school When the net forms a bag 10-15 m in diameter, 10-12 m deep at the center, the fish break school and individuals swim in all directions and jump

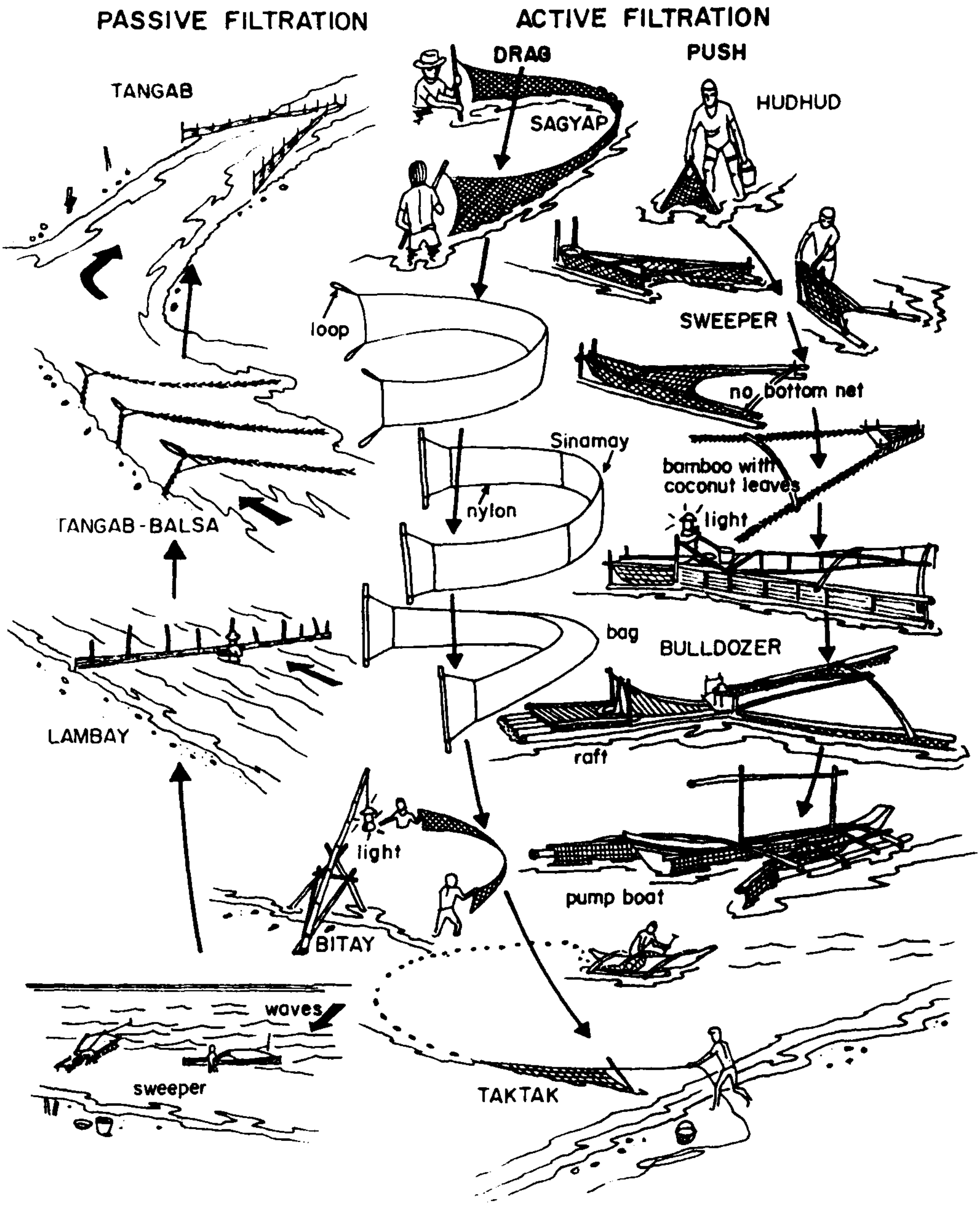


Fig. 27 Variety in the collection gear used for milkfish fry around Panay, Philippines: 1) operation in shore waters and at entrances to coastal wetlands, 2) use of fine mesh nets and lamps, 3) utilization of currents and waves or motor power to move the gear, and 4) other adaptations of structure, materials, and methods according to fry behavior and conditions of fry grounds (*After* Kumagai et al. 1980).

out of the bag. No fish is left inside when the bag is 3-4 m in diameter and 1-m deep unless a net cover is used. The jump starts from about 2 m below the surface, the swimming fish turning upward and leaving the water in one motion. The jump is made with enough power to hurl the 5-8 kg fish an estimated height of 8 m and a horizontal distance of 10 m (IFPP 1976).

Adult milkfish are extremely timid and wary, but may be speared if carefully approached from below (Bagnis et al. 1974). They offer the least resistance when speared near the tail (since the tail provides the greatest power for swimming in milkfish). They are capable of towing a spearfisherman for some minutes. When hooked, milkfish makes repeated runs at tremendous speed. Milkfish is "the most powerful fish in Palau" (Johannes 1981).

When captured, the fish turn from dark blue to black above the lateral line, or from silvery to gunmetal blue (Muench 1978; Johannes 1981; Lam 1986). The pineal region becomes very dark and sometimes becomes a depression. The adipose eyelids become opaque shortly after capture or handling, but clear up in 1-2 wk. Blinded fish swim singly but otherwise move among other fish and avoid obstacles as easily as normal fish (IFPP 1976; Muench 1978).

Migration and Movements

Figure 5 shows that the life history of milkfish is one big migration. While a great deal of study has been done in the laboratory and under semi-natural conditions on various aspects of milkfish biology, little is yet known about its migration habits. Three large areas need study:

(1) the period after the juveniles leave the nursery grounds until they appear along the coasts for spawning (where do the juveniles go?)

(2) the period following spawning of adults in nature (where do the adults go?)

(3) the period during which larvae move from open-water spawning grounds to onshore collection grounds (how do the larvae come to shore?)

It is difficult to study the migration of milkfish because the juveniles and adults are not fished in quantity. Ultrasonic tracking of adult milkfish off Panay shows the fish heading for shore after release 2 km offshore, and swimming parallel to shore at average speeds of 1-2 km/h (maximum 6 km/h) for periods of 2-24 h (Groot 1976).

Drift card experiments (Fig. 28) conducted to determine whether surface currents affected transport or migration of larvae onshore had inconclusive results. During March and April when milkfish fry begin to appear along the western Panay coast, the surface currents flow generally away from the coast; between June and October, the currents move north along the coast. Further studies need to be conducted to determine the mechanism of larval transport. This is relevant to natural recruitment of fry in shores close to the National Bangus Breeding Project maturation cage sites in the Philippines. It is necessary to know whether the cages are properly located relative to currents and whether and how larvae use such currents.

Kumagai (1984, 1990) discussed in great detail the influence of seasons, currents, tides, substrate, bottom profile, and proximity to inland waters on the

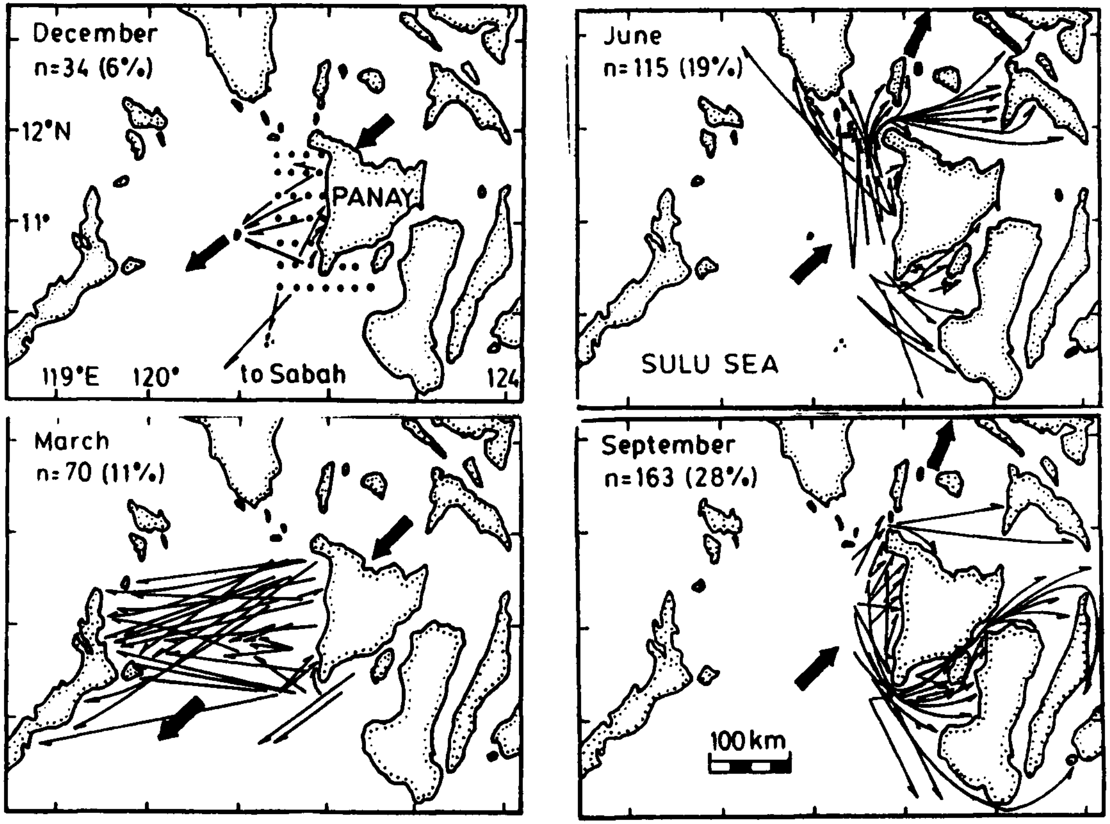


Fig. 28. Surface currents off western and southern Panay, Philippines as determined by drift cards (trajectories indicated by thin arrows) and influenced by the prevailing winds (bold arrows). Cards recovered, 6-28% (90% within a month of dispatch). Drift speed mode in December and March, 0.1 -0.2 m/s; June and September, <0.1m/s (*Modified* from Kumagai & Bagarinao 1979).

occurrence and abundance of milkfish fry in shore waters. The seasonality, lunar periodicity, and location of fry occurrence and abundance are determined directly by the seasonality, lunar periodicity, and location of spawning but may be modified by other factors. Fry are more abundant (i.e., the catch is better) at flood tide and high tide due to the greater strength and the concentrating effect of the water current during these periods. Fry abundance is not related to time of day nor to wind velocity. The most productive collection grounds are usually sandy beaches with gentle slopes, but some are gravelly-rocky with steep inclines. The greatest catches are obtained right at the surf zone. There is no clear trend of increasing fry abundance closer to creek or river mouths. It seems that milkfish fry arrive in the surf zone in small batches and are subsequently transported by longshore currents. Such movement of fry is essentially passive, governed by physical factors (Kumagai 1984). In contrast, Buri & Kawamura (1983) and Kawamura (1984) argued that fry in shore waters are in active migration to inshore nursery grounds. They marked 4060 shore-caught milkfish fry with alizarin red, released them 150-160 m offshore, and recovered them in collection gears inshore. The question of active versus passive migration is not yet resolved; the truth is probably not either-or but both.

ENVIRONMENTAL PHYSIOLOGY

Table 16 shows the environmental conditions that milkfish might experience, particularly in ponds.

Salinity

Milkfish is remarkably euryhaline. Except during spawning and the early larval stages, they can be found from freshwater lakes to hypersaline lagoons. In brackishwater ponds, wide salinity fluctuations usually occur during the growing season (Table 16). Because milkfish obviously has to confront a wide range of salinities, many physiological studies have concentrated on the effects of salinity.

Tolerance. The salinity tolerance range during 48-h exposure periods is 4-38 ppt for very young milkfish larvae, and 0-70 ppt for 21 -d old larvae (Dueñas & Young 1983). Shore-caught fry have similar tolerance limits as hatchery-bred 21 -d old larvae. Milkfish fry may be transferred abruptly from 30 ppt to 0 ppt without mortality, but newly transformed juveniles (fingerlings) all die (Juliano & Rabanal 1963). These fingerlings tolerate abrupt changes in salinity as long as the change is not direct to freshwater. Dead fingerlings show hemorrhagic areas on the ventral side and around the operculum. The maximum lethal salinity for juvenile milkfish was found to be 109±8ppt (Lin 1969), but adult milkfish occur in hypersaline lagoons of up to 158 ppt (Crear 1980).

Osmoregulation in fry. Shore-caught milkfish fry abruptly transferred

Table 16. Environmental conditions in milkfish ponds

Pond size	Season	Water temperature (°C)	Salinity (ppt)	Dissolved oxygen (ppm)	pH
Panay Island					
[1]500 m^2 90-cm deep	Nov-Mar	24-35	22-47	3.0-7.4	6.9-8.9
[2]1 ha	Apr-Jun	28.5	42	6.9	8.2
[2]1 ha	Sept-Nov	28.2	21	6.9	7.7
[2]1 ha	Dec-Feb	27.3	26	7.3	8.1
[3]490-580 m^2 80-cm deep	Mar-May	23-32	36-68	0.6-15	8.0-9.5
[4]144 m^2	Oct-Nov	26-33	13-35	0.8-5.3	6.0-8.8
[4]144 m^2	May-Jul	28-32	17-41	0.9-8.7	4.2-9.1
[5]144 m^2 30-cm deep	Oct-Dec	26-29	1-28	-	6.9-8.5* 5.6-6.8**
[6]0.18-8 ha (n=19)		24-34	13-40	4-11	6.5-9.5* 4.7-7.9**
[7]503 m^2 30-cm deep	Apr	28-38	31-55	1.6-7.9	4.0-8.6
[7]549 m^2 70-cm deep	Apr	28-35	32-43	2.1-7.7	4.1-8.5
Mandapam, India					
[8]ponds	whole year	25-33	16-42	1.6-7.3	7.2-8.4

Values are ranges or means. [1]Eldani & Primavera 1981; [2]Gerochi et al. 1988; [3]Otubusin & Lim 1985; [4]Villegas & Bombeo 1981; [5]Bombeo-Tuburan et al. 1989; [6]Baticados et al. 1986; [7]IFPP 1974b; [8]James et al. 1984. *Water pH; **soil pH. 1 ha=10 000 m^2. For 0_2, 1 ppm = 1 mg/1.

from 32 ppt to 0, 8, 16, 32, and 45 ppt are able to regulate and return their plasma osmolalities and chloride values to near-control levels in about 24 h; the isotonic point is equal to 13.8 ppt (Almendras 1982). Freshwater-acclimated milkfish fry (F-fry) abruptly transferred to 32 or 45 ppt show increased chloride cell density and size; so do fry from ambient seawater (S-fry) transferred to 45 ppt (Young, unpubl.). Cell density and size are lowest in S-fry transferred to 16 ppt. Different populations of chloride cells function under different conditions. The characteristic apical pits observed in chloride cells of S-fry totally disappear 12 h after abrupt transfer to freshwater. Apical pits are absent in chloride cells of F-fry, but appear 12 h after abrupt transfer to 32 or 45 ppt.

Osmoregulation in juveniles. Larger milkfish are more efficient at handling osmotic stress than smaller ones (Ferraris et al. 1988). Juveniles of 40, 120, and 240 g sizes were acclimated to 32 ppt, then abruptly transferred to 0, 16, 32, and 48 ppt. Plasma osmolalities and chloride values deviate from the initial and control values immediately after transfer, but are subsequently tightly regulated. The isotonic point is 350 mOsm and 180 mEq/1 chloride, equal to 11 ppt. Regardless of fish size, plasma osmolality changes by < 0.1 mOsm for every mOsm change in environmental salinity. The summed deviations from the control values indicate that small milkfish tend to adapt better to fresh than to hypersaline water, while larger milkfish are more likely to find freshwater more stressful than hypersaline water. Survival rate is independent of fish size and salinity.

Metabolic effects. Salinity has been shown to affect oxygen consumption rates (Lin 1986; Swanson 1990), growth rates (Hu & Liao 1976), and transport of nutrients, digestibility of proteins and movement of food in the gut of juvenile milkfish (Ferraris & Ahearn 1983; Ferraris et al. 1986).

Swanson (1990) found that at equivalent activity levels, routine metabolic rates (RMR) are significantly higher in fish acclimated in 35 ppt than in either 15 or 55 ppt. At uniform food intake rates, growth rates are lowest in 35 ppt. Low RMR and high growth rates in 15 ppt reflect reduced osmoregulatory costs at this salinity, which is near isosmotic with blood. The equally low RMR and high growth rates at 55 ppt are unexpected and not yet explained. Examination of the gills shows that fish in 55 ppt have reduced gill surface area (fusion of adjacent secondary lamellae and reduction in lamellar length).

Maturation and spawning of milkfish in captivity have been observed in a wide range of salinities: 14-40 ppt in Taiwan, 8-42 ppt in Hawaii, 25-38 ppt in the Philippines, 16-130 ppt in Christmas Island (see Lam 1984 for review).

Temperature

Temperature affects oxygen solubility and all rate processes and is therefore very important. However, few studies have been conducted on temperature effects on milkfish. Given the relatively small temperature fluctuations in tropical waters, it has generally been assumed that these effects are minimal. In the future, more temperature studies would have to be conducted because of their important applications in milkfish culture. Temperature is critical and must be regulated during storage and transport of eggs (Garcia & Toledo 1988) and fry (Villaluz 1984). In the hatchery, the outdoor or indoor location of rearing tanks makes a difference in the rate of larval growth and development (Lin 1985). Temperature fluctuations can be a significant factor in the growth of milkfish in nursery and culture ponds that are small or shallow.

Tolerance. Fertilized milkfish eggs do not tolerate 20°C during transport in plastic bags. While 65-75% hatch following transport at 28°C, <1% hatch at 20°C (Garcia & Toledo 1988). Pannikar et al. (1953) found the heat-death temperature to be 43°C for milkfish fry and 39°C for fingerlings, and the minimum temperature tolerated, 14-18°C. Juvenile milkfish are able to tolerate temperatures up to 38-41°C in ponds and lagoons, but are sensitive to low temperature, becoming sluggish at 15°C, paralyzed at 13°C, and dead at 12°C (Chen 1952). Lethal temperatures for juvenile milkfish are >42.7°C and <8.5°C (Lin 1969).

Metabolic effects. Milkfish larvae grow to the fry stage in 21-24 d at 26-30°C (indoors) and in 13-18 d at 28-33°C (outdoors) (Lin 1985). In freshwater raceways, growth of milkfish fry varies with the season, being high in June-July (hot and dry) and low in August-September (cool and rainy) (Carreon et al 1984). Low temperatures <23°C decrease activity, responsiveness, food intake, growth, and development of milkfish fry and juveniles; high temperatures have the opposite effect (Villaluz & Unggui 1983). At 24-35°C, the fry feed and defecate throughout the day provided there is enough light and dissolved oxygen is >1 ppm; at 17-23°C, they feed very little. Survival after 9 wk is 97-100% at 26-30°C, but only 77% at 21°C Mean lengths of juveniles at higher temperatures were 2x greater and mean weights 10x greater than those at lower temperatures. Feeding of juveniles is likewise affected by temperature (Lin 1969; Chiu et al. 1986).

Maturation and spawning of adult milkfish have been observed at temperatures between 24 and 33°C (Lam 1984).

Dissolved Oxygen

Tolerance to hypoxia. For juvenile milkfish, the lethal minimum level is 0.1-0.3 ppm oxygen (Lin 1969). They show signs of asphyxia when oxygen levels drop to 1 ppm in ponds; about 50% die with about 0.1 ppm (Job 1957; Gerochi et al. 1978). Milkfish survives low oxygen levels that kill mullets (James et al. 1984), *Elops, Terapon, Cerres,* tilapia, prawns, and crabs (Dorairaj et al. 1984).

Oxygen consumption rates. Milkfish fry of body weight about 5-8 mg uses oxygen at the rate of 0.011 mg/h at 20°C and 0.056 mg/h at 32°C (Millamena & Villaluz, unpubl). At 24°C and 18 ppt, milkfish fry may be transported for 4-7 d at densities of up to 1000 fry/1 when the air-to-water ratio is 5:1; dissolved oxygen decreases from 7.5 to 4 ppm during this period (Oceanic Institute 1980).

Viswanathan & Tampi (1952) determined the relationship between oxygen consumption rates (Q, ml Q_2/h) and body weights (W, g) of juvenile milkfish 0.01-50 g in size in freshwater at 28-30°C:

$$Q= 1.829\ W^{0.8342}.$$

Lin (1986) measured oxygen consumption rates of milkfish 26-156 mg in body weight in relation to salinity (0, 15, 30, 45 ppt). The standard rates vary between 0.1 and 0.3 units (1 unit = 1 ml 0_2/g-h) during the diel cycle, being highest during the day. Milkfish rates are lower than those of carp (0.3-1.0 units) and tilapia (0.4-0.9 units). Oxygen consumption rates following transfer from acclimation salinities to test salinities vary significantly with both and decrease over time. At 2 h post-transfer, rates are between 0.4 and 0.8 units, depending on salinity

Ammonia and Nitrite

Ammonia is the waste product of protein metabolism in fishes and is toxic in high amounts. The 96-h LC_{50} (median lethal concentration) of un-ionized ammonia (NH_3) to milkfish fry is 28-30 ppm (Jumalon 1979), values far above the 0-6 ppm ammonia seen in ponds (Batirados et al. 1986; Bombeo-Tuburan et al. 1989). For 2-4 g juvenile milkfish. the 96-h LC_{50} is 21 ppm (Cruz 1981).

Thus, observed mortalities of milkfish under culture conditions are not due to ammonia toxicity. Gill damage in exposed fry and juveniles is reversible after 10 d in ammonia-free water.

Nitrite is an intermediate product in the oxidation of ammonia and is notorious as a methemoglobin (mtHb) former. MtHb is non-functional in oxygen transport. For juveniles 32 g in weight, the 48-hLC_{50} of nitrite is 12 mg/1 (=ppm) in freshwater and 675 mg/1 in 16 ppt brackishwater (Almendras 1987). After 48 h in 0.88 mg/1 nitrite in freshwater and 14 mg/1 nitrite in brackishwater, mtHb levels increased significantly above the control (5% of total Hb). Levels rose to 70-80% at the LC_{50}s. The fish are able to reduce mtHb to normal levels within 24-36 h after removal of the toxicant. The high tolerance of milkfish to nitrite in brackishwater rules out nitrite toxicity as a factor in mass kills in ponds where nitrite levels are 0-1 ppm (Baticados et al. 1986; Bombeo-Tuburan et al. 1989; Borlongan 1990). Environmental chloride exerts a protective effect against nitrite toxicity by competing with nitrite for the same active transport mechanism across the gill membrane (Tomasso 1986).

Acidity

The optimum pH for milkfish seems to be about pH 8, the pH of seawater. Low survival of fry is obtained after 96 h of storage in all salinity-temperature combinations when the pH is 5 (Baylon 1983).

In brackishwater ponds, pH values do not usually go below pH 7 because of the buffering effect of seawater. However, ponds with acid sulfate soils are characterized by water near pH 4 (Singh & Poernomo 1984). Low water pH has been implicated in mass kills of milkfish in brackishwater ponds following heavy rains (IFPP 1974b; Singh & Poernomo 1984). The runoff from the dikes can be strongly acidic, the dike soil being excavated mud whose sulfides (mostly pyrite) have been oxidized to sulfate. Fresh wet mud is only slightly acidic (pH 6.5), but become strongly acidic (pH 4.1) after exposure to air till drying.

In one case of milkfish kill following an 8.6 cm rainfall, IFPP (1974b) found no correlation between severity of the fish kill and the measured water temperature, salinity, and dissolved oxygen levels. Water temperatures stayed around 28-30°C before and after the rain. Salinities decreased from 55 to 32 ppt in the shallow ponds, and from 42 to 33 ppt in the deep ponds. Dissolved oxygen within 10 cm of the surface dropped from an average of >5 to 4 ppm during the 3 d following the rain. However, severity of the fish kill was correlated with decrease in pH and increase in carbon dioxide. Water pH dropped from 8 to 5, and even lower (pH 4) at the base of the dikes. Free carbon dioxide levels increased from nearly zero to 10-100 ppm due to reduced photosynthesis, and might have contributed to decrease in pH.

Sulfide

While the mass kills of milkfish that occasionally occur in ponds may be due to low pH (IFPP 1974b), they may also be due to hydrogen sulfide, a compound ubiquitous in marine sediments. Sulfide is obviously present in milkfish ponds, particularly toward the later part of the growing season, as indicated by the pungent "rotten egg" odor of the mud. However, of the multitude of measurements made of water and sediment characteristics of ponds and milkfish natural habitats, there is none of sulfide (Baticados et al. 1986; Bombeo-Tuburan et al. 1989; Table 16). Tampi (1959) noted the presence of sulfide in a milkfish natural habitat but discounted its importance. IFPP (1974b) recognized that toxic gases (hydrogen sulfide, methane, carbon dioxide), abundant in pond soils, may be released at lethal levels by a hard rain or wind in shallow ponds. However, they made no measurements of sulfide during their investigation of a fish kill.

Hydrogen sulfide inhibits cytochrome *c* oxidase and stops aerobic respiration. Fishes that are normal residents of coastal wetlands have higher tolerance to sulfide than those that live in more open water (Bagarinao & Vetter 1989). Sulfide concentrations in sediment pore water are typically 1 mM or greater, part of which diffuses into the water column; 0.01 mM is sufficient to kill most fishes and invertebrates. Of the total sulfide present, the fraction that exists in the toxic form, H_2S, increases with decrease in pH. Where ponds are shallow, the organic load high, the water stagnant, or the bottom disturbed, sulfide levels in the water can be quite high. Milkfish kills occur in ponds 30-cm deep but not in 70-cm deep (IFPP 1974b). Kills also occur after rains in ponds fertilized with chicken manure and MASA fertilizer (processed from agricultural wastes), but not in those with ammonium phosphate and urea (Bombeo-Tuburan et al. 1989). There has been no study yet of milkfish tolerance to sulfide.

Toxicants and Xenobiotics

Mercury. Cuvin-Aralar (1990) determined mercury levels in monthly water, sediment, and fish samples from a heavily industrialized section of Laguna de Bay (the biggest freshwater lake in the Philippines), where milkfish is cultured in net pens. Sediments contain 26-117 ppb mercury (dry weight basis), while the total body burden of milkfish is 5-56 ppb (n=29). Mercury levels are lower in milkfish than in tilapia and bighead carp. The maximum permissible mercury level set by the World Health Organization (WHO) for fish samples is 50 ppb. Water samples have low mercury levels ranging from non-detectable to 0.6 ppb.

Anaesthetics. Murai & Catacutan (1981) determined the susceptibility of young juvenile milkfish (0.05-5 g; mean, 1 g BW) to 2 commonly used anaesthetics. At concentrations of 80, 120, 160, and 200 ppm, 2-phenoxyethanol fails to immobilize fish within 5 min, and causes no mortality in 2 d. MS-222 (metaaminobenzoic acid ethylesther methanesulfonate) at 100 ppm immobilizes fish in 1 min and allows recovery in 1 min; 200 ppm is effective within 30 s but causes 50% mortality. Anaesthesia may not be absolutely necessary during handling of young juveniles, but if so, 100 ppm MS-222 is adequate.

Antiseptics. Potassium permanganate ($KMnO_4$) and formalin are sometimes used to rid milkfish of ectoparasites, epiphytic fungi, and bacteria. For milkfish fingerlings, the median lethal concentration (LC_{50} of $KMnO_4$ is 1.5 mg/l at 96 h (Cruz & Tamse 1986). The LC_{50} for formalin in 24-, 48-, 72-, and 96-h exposure periods are 322, 260, 241, and 232 ppm (Cruz & Pitogo 1989). In both cases, histopathological changes occur in the gills, liver, and kidney even at sublethal concentrations: hyperplasia, epithelial separation, and necrosis of the gills; cloudy swelling, hemorrhage, deposition of pigments, and necrosis in liver parenchyma; and degeneration of renal tubules. Tissues partially recover after 10 d in antiseptic-free seawater.

Surfactants. Chen & Chang (1979) studied the effects on milkfish fry of some surfactants used in oil spill clean-up operations. Milkfish fry are less susceptible than *Penaeus monodon* fry. The higher the concentration of surfactant used, the shorter the median lethal time for the animals. Low concentrations inhibit feeding and growth. A concentration inhibiting food consumption by 20% in milkfish fry is ultimately lethal. Biological safe concentrations for milkfish are 0.2 ppm Dunall O.S.E., 5 ppm BP1100, and 10 ppm Seagreen 805. Of the surfactants tested, Seagreen 805 and BP1100 are the least toxic and can be applied on a limited basis.

Pesticides. Various pesticides have been tested against chironomid larvae, the highly effective competitor of milkfish in ponds. Among these are the organophosphorothioates studied by Tsai (1978). The toxicity (72-h LC_{50}, in mg/kg) of Abate temephos 50% emulsifiable concentrate (EC) to milkfish fry is 0.38; milkfish fingerlings, 2-35; chironomid larvae, 0.0025; mullet, 0.6; tilapia, 3.5; *Penaeus monodon,* 0.04. The toxicities of the other pesticides to milkfish fingerlings are as follows: Abate 1% granule, 103; Dursban 4 EC, 0.15; Lebaycid 50% EC, 1.7; Sumithion 50% EC, 11. Chironomid larvae are effectively killed with Abate temephos 50% EC when it is diluted 1:2000 with seawater and applied to milkfish ponds to establish a concentration of 0.05 mg/1 of the active ingredient. This treatment does not harm milkfish and benthic algae. Residues found in the edible portions of milkfish after 7 applications ranged from 0.02 to 0.08 mg/kg, well below the 1 mg/1 approved by the WHO for human drinking water.

Crowding

Although adult milkfish are fish of the open sea, the fry and juveniles adapt well to crowding. Milkfish eggs tolerate a 2 h simulated transport at 28°C, 35 ppt, and 10 ppm 0_2 when loaded at densities up to 12 000 eggs/1 (Garcia & Toledo 1988). Milkfish fry may be stored in basins at 366 fry/1 at 8-32 ppt for 14 d with 96-98% survival (Quinitio & Juario 1980). Fry are usually stocked in 30-60-cm deep nursery ponds at densities of 30-60/m^2, but densities of up to 1000/m^2 are tolerated (Rabanal et al. 1953; Schuster 1960; Villegas & Bombeo 1981; Santiago et al. 1989). With just enough food for body maintenance, fingerlings can be kept in nursery ponds in a stunted condition for 6 months. When later given more space and food, they achieve good growth not significantly different from the non-stunted fish (Lijauco et al. 1978; Bombeo-Tuburan 1988). The stunting technique allows fish farmers in the Philippines to stock up on milkfish fry during the time of abundance and low prices, and to grow a second crop later in the year when fry supply is low and prices high. Juveniles in grow-out ponds are usually stocked at 2000-5000/ha.

Starvation

Starvation of milkfish fry for 10 d and of juveniles for 2 months results in marked structural alterations in the hepatocytes (Storch & Juario 1983): reduction in cell size and nucleus size, apparent loss of nucleoli, loss of stored glycogen, reduction of endoplasmic reticulum profiles, increase in mitochondrial size, condensation of chromatin material in the fry, and increase in the number of electron-dense bodies containing large amounts of iron in juveniles. These changes are reversible following refeeding of the fry for 2 d and of the juveniles for 4 d.

Histopathological changes in the intestine of milkfish fry starved for 9 d include (Segner et al. 1987): fragmentation of microvilli over the whole length of the intestine, cellular hydration, transformation of mitochondria, and appearance of autolytic vacuoles in the enterocyte cytoplasm. After refeeding with *Artemia* for 1-2 h, the fry show intensive lipid absorption in the midgut, and pinocytotic activity and large supranuclear vacuoles in the hindgut.

General Stress

Stress has been implicated in the common failure of milkfish broodstock to respond favorably to hormonal treatment to induce maturation and spawning (Lam 1986; Marte et al. 1988a,b). However, there has been no study on the problem.

Smith (1980) reported a case of spontaneous thrombus formation in milkfish, resulting in sudden death. This adult milkfish had been maintained with several others in a circulating seawater pond, had been feeding and growing, and appeared externally healthy. All of a sudden, it thrashed around and died within a few minutes. The lethal blood clot was lodged in the heart wall, occluding the lumen between the bulbus arteriosus and the ventricle. One wonders how often thrombus formation has been responsible for death of adult milkfish during handling for breeding purposes.

Smith (1978b) found a high incidence of gastritis, a stomach inflammation, in milkfish in Hawaii. All 57 fish (1-8 kg in weight) examined were outwardly healthy; 65% from Pearl Harbor and 29% from Puako had the inflammation. The high incidence of gastritis is attributed to pollution and to reduced resistance to disease due to genetic uniformity of the isolated populations.

Smith & Ramos (1976) proposed a simple method for early detection of stress in milkfish. Early induced stress may result in the release of free hemoglobin into the skin mucus of fishes, and it could be indicated quickly and simply by the color change of a commercially available hemoglobin test strip. The method uses skin mucus so it is harmless to the fish. It can be used to detect early stress conditions so that efforts may be made to lessen or remove them before debility and overt disease takes over.

Hematological changes are often observed when fish are exposed to stressful conditions. Bhaskar & Rao (1989) measured 19 blood characteristics in juvenile milkfish from different brackishwater farms in India. The farms all use a stocking density of 1500/ha, but differ somewhat in temperature, salinity, dissolved oxygen, and pH. No significant differences are found among fish from the different farms with regard to most blood values. Salinity is significantly correlated with total plasma proteins and plasma sodium and potassium. The number of monocytes was negatively correlated with dissolved oxygen and pH. The estimated normal values of some blood parameters are: RBC count, $2.4 \times 10^6/\mu l$; hematocrit, 43%; hemoglobin, 8 g/100 ml; leucocytes, $4 \times 10^4/\mu l$; lymphocytes, 63%; thrombocytes, 17%; monocytes, 14%; granulocytes, 5%; cholesterol, 220 mg/100 ml; total plasma proteins, 3.7 g/100 ml; Na^+, 180 mEq/1; K^+, 5.6 m Eq/1 (Bhaskar & Rao 1989).

COMMUNITY RELATIONSHIPS

Associated Fishes, Invertebrates, and Vegetation

Table 17 lists the most common species/taxa of fish recorded with milkfish in 4 habitat types in the Philippines, from 500 m offshore, to the surf zone of a sandy beach, to mangrove lagoons, to ponds. Bagarinao & Taki (1986) found some 120 species in 74 families at the offshore station in Pandan Bay (n = 345 day-samples) and 70 species in 47 families at the surf zone (n = 587), with about 60 species common to both stations. Larvae and juveniles caught offshore are generally smaller (<10 mm) than those caught onshore (>10 mm), particularly among species caught at both stations. Adjacent Bugang lagoon is part of an estuarine mangrove-nipa system; its fauna consists partly of larger juveniles of the same species found in the surf zone, and is similar to the fauna of the mangrove lagoon in Pagbilao, Quezon. Pinto (1985) found 128 species (54 families) of mostly juvenile fish in Pagbilao lagoon, the most specious family being the Gobiidae, and the most numerous single species being *Ambassis kopsi*. Ponds in the Philippines harbor at one time or another some 76 species from 68 families (Herre & Mendoza 1929).

The surf zone juvenile fish community in the Philippines has also been studied by Blanco & Villadolid (1951) and Bañada (1980). Kinoshita (1984) has done the same in Tosa Bay (Japan) and Liu & Su (1984) in northern Taiwan. These localities have milkfish and many other species in common. Milkfish and about 78 species of juvenile fish (195 species at all stages) from 34 families occur in the Pichavaram (India) mangrove ecosystem, using the habitat as nursery ground (Krishnamurthy & Jeyaseelan 1981). Many species that adventitiously enter ponds in India (Nair et al. 1974) are similar to those in the Philippines.

Some 91 species occur with milkfish in Trinity, Queensland (Australia), with 70% of the species occurring in the estuary being more abundant as

Table 17. Fish taxa commonly occurring with milkfish larvae and juveniles in the Philippines

500-m offshore[1]	Adjoining sandy beach[1]	Mangrove swamps[2,3]	Natural ponds[4]
Engraulidae	Mugilidae	*Ambassis* spp.	*Ambassis* spp.
Clupeidae	*Ambassis*	Gobiidae	*Butis butis, Periopthalmus*
Apogonidae	*Chanos chanos*	*Lisa* spp.	*Lisa spp., Mugil cephalus*
Schindleria	Leiognathidae	*Leiognathus* spp.	*Leiognathus* spp.
Leiognathidae	Engraulidae	*Chanos chanos*	*Chanos chanos*
Dussumieria	*Sphyraena*	*Sphyraena* spp.	*Sphyraena* spp.
Siganus	*Terapon*	*Terapon* spp.	*Terapon* spp.
Caesio	Hemiramphidae	Hemiramphidae	*Zenarchopterus dispar*
Gobioidei	*Abudefduf*	*Sillago sihama*	*Sillago sihama*
Upeneus	*Siganus*	*Siganus* spp.	*Siganus* spp.
Pomacentrus	*Lutjanus*	*Lutjanus* spp.	*Lutjanus* spp.
Synodontidae	Atherinidae	Atherinidae	*Lates calcarifer*
Gerres	Belonidae	*Megalops cyprinoides*	*Megalops cyprinoides*
Atherinidae	Clupeidae	Bleniidae	*Mollienesia latipinna*
Nemipterus	*Gerres*	*Pomadasys hasta*	*Pomadasys hasta*
Dipterygonotus	Apogonidae	Ophichthidae	*Ophiocephalus striatus*
Benthosema	Syngnathidae	Syngnathidae	*Elops hawaiiensis*
Chanos chanos	*Petroscirtes*	*Scatophagus argus*	*Scatophagus argus*
Lutjanus	*Fistularia*	*Monodactylus*	*Anabas testudineus*
Sphyraena	*Lobotes*	*Gerres* spp.	*Gerres* spp.

[1]Pandan Bay, Panay Island (Bagarinao & Taki 1986);[2]Bugang lagoon adjoining the sandy beach of the second column (Bagarinao, unpubl.); [3]Pagbilao, Quezon (Pinto 1985);[4]Ponds throughout the country, not highly managed (Herre & Mendoza 1929). Columns 1,2 taxa are arranged in order of abundance. Columns 3,4 list the most common taxa, but no order of importance/abundance implied. Columns 1,2 specimens are larvae or early juveniles and could only be identified to the nearest taxa. Columns 3,4 species are identifiable but are given as spp. when conspecifics occur together; family names given when several genera are present.

juveniles than as adults, and 54% of those occurring in the bay being more abundant as adults than as juveniles (Blaber 1980). Blaber and his colleagues have studied south African, Australian, and Solomon Island estuaries and adjoining habitats. In a series of papers, they discussed species composition, biomasses, community structure, and zoogeographic affinities of fishes in different habitats of tropical estuaries, as well as the factors affecting the distribution of juvenile estuarine and inshore fish (Blaber 1980; Blaber & Blaber 1980; Blaber et al. 1985, 1989; Blaber & Milton 1990). Milkfish does not appear to be abundant in these estuaries, and is merely incidental in the studies. The role of milkfish in the community structure of tropical coastal wetlands has yet to be investigated.

A host of crustaceans, molluscs, and other invertebrates occur with milkfish in all habitats. The more conspicuous of these include penaeid shrimps, crabs, mysids, sergestids, copepods, amphipods, ostracods, nematodes, and gastropods (Herre & Mendoza 1929; Tampi 1959; Gomez 1980), many of which are potential prey or predators. An indeterminate number of species of phytoplankton, benthic micro- and macroalgae, seagrasses, and mangrove vegetation (Vicencio 1977; Gomez 1980; Pinto 1985) form the basis of the various food webs of which milkfish is a part.

The luminous bacteria *Vibrio harveyi* and *V. fischeri* are found associated with the gut of pond-cultured milkfish (Ramesh et al. 1986).

Predators

Most of the fish and crustacean species that occur with milkfish in shore waters are in the transformation or juvenile stages and are larger than milkfish fry. Depending on body size, mouth size, behavior, and availability of alternative prey, they are potential predators. Almost any one of them will feed on milkfish fry if placed with it in an aquarium (author's obs.). Among those found with milkfish fry in the guts (1-15 fry/gut) were 7-66 mm specimens of *Ambassis* sp., *Terapon* spp., *Epinephelus* sp., *Lutjanus* sp., *Sphyraena* sp., *Chaetodon* sp., *Meracanthus grammistes, Oxyurichthys microlepis,* and *Scatophagus argus* (Buri 1980). It is possible that milkfish fry in shore waters are occasionally eaten by mugilids and siganids <20 mm in length before these latter have assumed the permanent herbivorous/iliophagous habit.

In ponds and in coastal wetlands like estuaries and lagoons, large voracious carnivores like gobiids, eleotrids, ophichthyids, blenniids, *Sphyraena* spp., *Lutjanus* spp., *Channa* spp., *Epinephelus* spp., *Lates calcarifer,* and *Megalops cyprinoides,* as well as water snakes and birds, have been reported to prey on juvenile milkfish (Herre & Mendoza 1929; Schuster 1960), but quantitative evidence is lacking. Although *Elops machnata* has been implicated as a milkfish predator in ponds, examination of 164 specimens of various sizes failed to show any milkfish (Hiatt 1944). In a study comparing the fish fauna of the Trinity (Australia) estuary and its adjacent bay, Blaber (1980) noted that this and other tropical estuaries in the Indo-Pacific are dominated by juvenile marine fish, have a high number of planktivores, and few piscivores (mostly represented by juveniles); he suggested that the significantly lower numbers of piscivores in estuaries relative to open waters increase their advantage as nursery grounds.

Adult milkfish at sea probably fall prey to sharks and not very many other predators considering its large size, swimming ability, and schooling habit. On the other hand, predation on milkfish eggs spawned in the SEAFDEC/AQD floating cages appears to be considerable, with apogonids, engraulids, atherinids, the milkfish breeders themselves, and several other species taking hundreds to thousands of milkfish eggs per individual (Marte 1988).

Competitors

Milkfish and mullets (Mugilidae) almost always occur together in coastal wetlands, have very similar food habits, and are potential competitors (Hiatt

1944; Whitfield & Blaber 1978; Buri 1980). Other species found to feed on microbenthos and detritus are tilapias (*Oreochromis* spp.), rabbitfishes (*Siganus* spp.), the scat (*Scatophagus argus*), and clupeids (*Nematalosa* spp.) (Whitfield & Blaber 1978; Blaber 1980; Pinto 1985). The small, prolific-breeding fishes *Oreochromis mossambica, Mollienesia latipinna,* and *Gambusia affinis* often become very abundant in ponds and cause reduction in milkfish yield. At least in St. Lucia Lake (south Africa), potential competition between milkfish, mullets, and tilapia is reduced by resource segregation: the percent frequency of food items, feeding method, and temporal distribution change with growth of the 3 species (Whitfield & Blaber 1978).

Various crabs, snails, barnacles, oysters, polychaetes, and chironomid (fly) larvae are considered pests in milkfish ponds because of their fast growth and multiplication and because their fouling, boring, and burrowing activities destroy the pond bottom and dikes and interfere with the development and maintenance of the algal pasture (Herre & Mendoza 1929; Lin 1968; Pillai 1972). Counts of 700-7000 and a weight of 3.4 kg/m^2 have been recorded for cerithiid snails (Pillai 1972), and counts up to 24 $250/m^2$ for chironomid larvae (Padlan et al. 1975). Chironomid larvae compete seriously with milkfish for *lablab;* in Taiwan in June-August, chironomids eat 60-90 kg/d when the milkfish stock needs 100 kg/d (Lin 1968). Both biological control (stocking shrimps with milkfish) and pesticides have been used to control chironomids in ponds, the latter being more successful (Padlan, unpubl.; Tsai 1978).

Polyculture with prawn (*Penaeus monodon*) does not adversely affect growth and production of milkfish in ponds (Pudadera & Lim 1980; Eldani & Primavera 1981).

Parasites and Diseases

Milkfish is relatively resistant to parasitic infestations and diseases (Lio-Po 1984; Velasquez 1984). Acanthocephalan worms have been found in the intestines of adult milkfish, as many as 45-658 worms in one fish (Poernomo 1976). The frequently observed opacity of the eye cover is due to injury and infection with a *Vibrio* sp. (Muroga et al. 1984). Diseases and parasites often break out when milkfish are stocked at very high densities, or stressed for long periods. Probably the single most important factor in health maintenance among juveniles in ponds and coastal wetlands is the regular and frequent change in salinity which is lethal to most parasites and bacteria (Lin 1968).

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