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FEEDING LARVAL MARINE FISHES IN THE LABORATORY: A REVIEW

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INTRODUCTION

Interest in rearing marine fishes under laboratory conditions has intensified during the past decade, and there is every reason to believe that this trend will continue. The larval stages of marine fishes are being investigated experimentally because of their inherent biological interest, their importance in determining recruitment in adult fish populations, and their central place in problems associated with large-scale fish culture. The greatest difficulty in attempts to rear marine fishes through the larval stage has frequently been to provide a suitable food—that is, a food which the larvae will consume and grow on and which can be supplied in sufficiently large quantities. The literature on rearing marine fishes is scattered, in several languages, and in some cases not readily accessible, and a comprehensive review emphasizing feeding has not appeared until now. This review summarizes the attempts to feed larval marine fishes in the laboratory which have been described in the literature from 1878 through 1969, in the hope that such a review will aid persons who undertake similar work in the future.

Several previous reviews contain information relevant to the problem of feeding larval fishes. Hertling's treatise on rearing marine fishes (Hertling, 1932) includes a section on feeding, but investigators now will find his discussion of little help, partly because at the time he was writing, relatively little work had been done on rearing beyond the yolk-sac stage under laboratory conditions. Morris (1955) confined his discussion of nutrition in marine fish larvae to a consideration of Pütter's theory that dissolved organic matter is an important source of nutrition for fishes, an hypothesis which has so far not been definitively tested in larval fishes. Morris (1956) described rearing experiments with 17 species of California fishes and included a lengthy discussion of various food types. Hirano and Oshima (1963) reviewed methods of feeding the larvae of a variety of marine animals, including selected examples of attempts to feed larval fishes, and supplied valuable data on the sizes of various potential food organisms. Shelbourne (1964) described his extensive work with the plaice and gave an account of the historical development of marine fish culture. Blaxter (1965) discussed the feeding ecology of herring larvae, integrating data from the laboratory and the field, and Blaxter and Holliday (1963), reviewing the biology of the clupeids, summarized information on the larvae of this well-studied family of predominantly marine fishes.

The present review will summarize previous attempts to feed the larvae of marine fishes in the laboratory by presenting 1) a list of all food types used in the studies reviewed, and 2) a general discussion of the major food types. Only reports describing the rearing of larvae hatched from eggs in the laboratory are considered here, and reports of rearing in large, uncontrolled bodies of water such as ponds, are excluded. Also excluded, of course, are studies dealing with the rearing of fishes which have no free-swimming larval stage. A number of papers have appeared during the 1960's concerned with the physiology and behavior of marine fish larvae; although they frequently include mention of feeding in the laboratory, most of them have been omitted here since the methods used are usually described in greater detail in other papers more specifically concerned with rearing techniques.

One of the drawbacks of reviews of this kind is that they necessarily oversimplify the original work and thus may be misleading if not used properly. When dealing with reports—many of which are sketchy almost to the point of uselessness—of experiments conducted under vastly different conditions with a variety of species, comparisions are difficult and generalizations risky. If a particular food type was used in the past without success, it is still possible that it will prove useful for another species of fish or for the same species under different conditions. Also, several different approaches to the problem of feeding may prove equally fruitful. A case in point is the rearing of the sole, *Solea solea*: Fabre-Domergue and Biétrix (1905) reared sole using a flagellate as first food and, later, wild plankton from which the larvae selectively preyed upon other fish larvae and ignored copepod nauplii; nevertheless, Flüchter (1965) obtained excellent results by feeding larvae of this species only *Artemia* nauplii.

The emphasis of the present review on feeding is not meant to imply that other factors are not important for the successful rearing of larval fishes, or that larval survival in the studies reviewed was solely dependent upon the choice of food. Providing a suitable food is a sine qua non in any rearing attempt, but a host of other significant factors are operating in the complex artificial environment of the larvae. The importance of such factors is evident, for example, in Blaxter's (1968a) observation that although over 90% of the herring larvae in his experiments were feeding well, only 25–35% survived yolk-ab-

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sorption. Also, it is not uncommon to find dead larvae with food in their guts. A discussion of factors other than food is beyond the scope of the present review, and persons interested in the details of the studies reviewed here must consult the original papers.

LIST OF FOOD TYPES

Table 1 lists the food types which have been used in all papers included in the review. For convenience the living organisms other than wild plankton have been arranged taxonomically under four main headings: *Protista: planktonic forms; Protista: nonplanktonic forms; Metazoa: planktonic forms;* and *Metazoa: nonplanktonic forms.* In a few cases the designations *planktonic* and *nonplanktonic* are somewhat arbitrary. Nonliving foods and "prepared aquaria" have been placed under the heading *Miscellaneous.*

TABLE 1

Foods Used in Attempts to Rear the Larvae of Marine Fishes

Food	References
WILD PLANKTON	Antony, 1910; Blaxter, 1968, 1969; Blaxter and Hempel, 1961; Budd, 1940; Cunningham, 1893–95a & b; A. Dannevig, 1948; H. Dannevig, 1897; Dannevig & Hansen, 1952; David, 1939; Fabre-Domergue & Biétrix, 1897, 1905; Garstang, 1900; Ivanchenko & Ivanchenko, 1969; Kramer & Zweifel, 1970; Lebour, 1925; Meyer, 1878; Mito et al., 1969; Morris, 1956; Okamoto, 1969; Orcutt, 1950; Richards & Palko, 1969; Schach, 1939; Schumann, in Bardach, 1968; Yamamoto & Nishioka, 1952
PROTISTA: PLANKTONIC FORMS	
Chlorophyta	
Loxophyceae	
Platymonas subcordiformis	Orcutt, 1950
Halosphaera minor	Blaxter, 1969
Chlorophyceae	
Chlamydomonas sp.	Bishai, 1961; Blaxter, 1962, 1969; Gross, 1937; Qasim, 1955, 1959
Dunaliella primolecta	Blaxter, 1969
Dunaliella salina	Fabre-Domergue & Biétrix, 1905
Dunaliella sp.	Blaxter, 1962; Budd, 1940; Delmonte et al., 1968; Morris, 1956
Chlorella stigmata	Qasim, 1955
Chlorella sp.	Blaxter, 1962
Stichococcus sp.	Morris, 1956
Pyrrophyta	
Cryptophyceae	
Cryptomonas maculata	Blaxter, 1969
Desmophyceae	
Prorocentrum micans	Blaxter, 1969; Gross, 1937, Lasker et al., 1970; Qasim, 1955
Dinophyceae	
Gymnodinium splendens	Lasker et al., 1970
Oxyrrhis marina	Morris, 1956
Oxyrrhis sp.	Kasahara et al., 1960
Protoceratium reticulatum	Lasker et al, 1970
Fragilidium heterolobum	Lasker et al., 1970
Crysophyta	
Xanthophyceae	
Olisthodiscus sp.	Blaxter, 1969
Chrysophyceae	
Isochrysis galbana	Qasim, 1955, 1959
Monochrysis lutheri	Forrester, 1964
Chromulina pusilla	Qasim, 1955

TABLE 1—Continued

Foods Used in Attempts to Rear the Larvae of Marine Fishes

Food	References
Bacillariophyceae	
Coscinodiscus concinnus	Hertling, 1932
Coscinodiscus radiatus	Gross, 1937
Skeletonema costatum	Blaxter, 1962; Forrester, 1964; Gross, 1937; Kurata, 1956, 1959
Thalassiosira sp.	Gross, 1937
Lauderia borealis	Blaxter, 1969
Rhizosolenia sp.	David, 1939
Chaetoceros sp.	David, 1939
Biddulphia mobiliensis	Hertling, 1932
Ditylum brightwellii	Blaxter, 1969
Nitzschia closteium	Orcutt, 1950
Nitzschia sp.	Bishai, 1961; Blaxter, 1962; Budd, 1940
"Diatoms"	David, 1939; Rubinoff, 1958
Eumycophyta	
Ascomycetes	
"Yeast"	Klima et al., 1962; Morris, 1956
Taxonomy uncertain	
"Natural and cultured phytoplankton"	Klima et al., 1962
"Raw cultures of phytoplankton"	Dannevig, 1948
"Cultures of single species of green algae and naked flagellates"	Dannevig, 1948
"Phytoplankton"	Bishai, 1961; Ivanchenko & Ivanchenko, 1969
"Plankton algae"	Runnström, 1941
"Algae"	Fabre-Domergue & Biétrix, 1897
"Monadinen"	Kotthaus, 1939
"Vegetarian diet"	Soleim, 1942
PROTISTA: NONPLANKTONIC FORMS	
Cyanophyta	
"une nostocacee"	Fabre-Domergue & Biétrix, 1897
Chlorophyta	
Enteromorpha sp.	Kotthaus, 1939
Chrysophyta	
"Filamentous brown diatom"	Fabre-Domergue & Biétrix, 1897
Ciliophora	
Ciliata	
Euplotes sp.	Fabre-Domergue & Biétrix, 1897
Philaster digitiformis	Fabre-Domergue & Biétrix, 1897
Stylonychia sp.	Kasahara et al., 1960
Taxonomy uncertain	
"Filamentous algae"	Delmonte et al., 1968
"Cultured infusorians"	Fabre-Domergue & Biétrix, 1897
METAZOA: PLANKTONIC FORMS	
Aschelminthes	
Rotifera	
Brachinous plicatilis	Hirano, 1969; Mito et al., 1969; Okamoto, 1969
Mollusca	
Gastropoda	
Crepidula sp. "larvae"	Rubinoff, 1958
Bulla gouldiana veligers	Lasker et al., 1970
Haminoea vesicula veligers	Lasker et al., 1970
Navanax inermis veligers	Lasker et al., 1970
"Nacktschnecken" (? nudibranch) larvae	Kotthaus, 1939
Pelecypoda	
Mytilus californianus "larvae"	Morris, 1956
Mytilus sp. trochophores	Blaxter & Hempel, 1961; Okamoto, 1969; Schach, 1939
Mytilus sp. "larvae"	Dannevig, 1948; Kotthaus, 1939; Kurata, 1956
Ostrea edulis "larvae"	Dannevig, 1948
Crassostrea gigas "larvae"	Hirano, 1969
"Oyster" trochophores	Okamoto, 1969
Annelida	
Polychaeta	
Chone teres trochophores	Kurata, 1959
Pomatoceros sp. "larvae"	Dannevig, 1948
Nereis sp. eggs	Cunningham, 1893–95b
"Minced worms"	Cunningham, 1893–95a

TABLE 1—Continued

Foods Used in Attempts to Rear the Larvae of Marine Fishes

Food	References
METAZOA: PLANKTONIC FORMS —Continued	
Arthropoda	
Crustacea	
Artemia salina nauplii	Bishai, 1961; Blaxter, 1962, 1968; Blaxter & Hempel, 1961; Budd, 1940; Chirinos de Vildoso & Chuman, 1964; Dannevig, 1948; Dannevig & Hansen, 1953; Delmonte et al., 1968; Fahey, 1964; Fishelson, 1963; Flüchter, 1965; Forrester, 1964; Fujita, 1957, 1965, 1966; Gross, 1937; Hirano, 1969; Joseph & Saksena, 1966; Kasahara et al., 1960; Klima et al., 1962; Kramer & Zweifel, 1970; Kurata, 1956, 1959; McHugh & Walker, 1948; McMynn & Hoar, 1953; Mito et al., 1969; Molander & Molander-Swedmark, 1957; Morris, 1956; Okamoto, 1969; Orcutt, 1950; Qasim, 1955, 1959; Richards & Palko, 1969; Rollefsen, 1939; Rubinoff, 1958; Schumann, in Bardach, 1968; Shelbourne, 1964; Shojima, 1957; Soleim, 1942
"Cladocera"	Gross, 1937
Daphnia pulex eggs	McMynn & Hoar, 1953
Daphnia sp.	Blaxter, 1965; Bückmann et al., 1953
"Copepods"	Bishai, 1961; Bückmann et al., 1953; Fishelson, 1963; Gross, 1937; Hirano, 1969
"Copepod nauplii"	Kasahara et al., 1960; Kotthaus, 1939
Tigriopus californicus nauplii	Fahey, 1964
Tigriopus fulvus nauplii	Bishai, 1961; Budd, 1940; Orcutt, 1950
Tigriopus fulvus adults	Blaxter, 1965, 1968; Morris, 1956
Tigriopus sp. "young stages"	Blaxter, 1962
Tisbe sp.	Blaxter, 1962
Balanus balanoides nauplii	Blaxter, 1962, 1968; Dannevig, 1948; Qasim, 1955, 1959; Shelbourne, 1964; Soleim, 1942
Balanus glandula nauplii	Morris, 1956
Balanus amphitrite albicostatus nauplii	Hirano, 1969; Kasahara et al., 1960
Neomysis japonicus "young"	Kasahara et al., 1960

TABLE 1—Continued

Foods Used in Attempts to Rear the Larvae of Marine Fishes

Food	References
Echinodermata	
Echinoidea	
Dendraster excentricus eggs or larvae	Morris, 1956
Strongylocentrotus purpuratus eggs or larvae	Budd, 1940; Morris, 1956; Orcutt, 1950
Tripneustes esculentus eggs or larvae	Richards & Palko, 1969
Arbacia sp. eggs or larvae	Deuel et al., 1966; Rubinoff, 1958
"Fertilized sea urchin eggs"	Fujita, 1965
Asteroidea	
Asterias sp. eggs	Blaxter, 1962
Urochordata	
Ascidian larvae	Fabre-Domergue & Biétrix, 1897
Chordata	
Fish larvae	Fabre-Domergue & Biétrix, 1905
METAZOA: NONPLANKTONIC FORMS	
Aschelminthes	
Nematoda	
Anguillicula sp.	Blaxter, 1962
MISCELLANEOUS	
Prepared aquaria	Bishai, 1961; Delmonte et al., 1968; Heuts, 1947; Klima et al., 1962; McHugh & Walker, 1948
Finely ground trout food	Richards & Palko, 1969
Powdered fish foods	Rubinoff, 1958
Commercial fish-fry foods	Blaxter, 1962; Delmonte et al., 1968; Klima et al., 1962
Cooked chicken egg yolk	Bückmann et al., 1953; Fabre Domergue & Biétrix, 1897; Fishelson, 1963; Fujita, 1966; Heuts, 1947; Ivanchenko & Ivanchenko, 1969; Klima et al., 1962; Kurata, 1959; Morris, 1956; Nikitinskaya, 1958
Water-soluble vitamin compounds	Klima et al., 1962
Liver of shore crab, *Carcinus maenas*	Bishai, 1961
Minced shrimp and crab meat	Kurata, 1959
Crushed mussel	Fabre-Domergue & Biétrix, 1897
Homogenates of *Mytilus*, periwinkle, *Fucus* and kelp	Ivanchenko & Ivanchenko, 1969
Liver-skim milk	McMynn & Hoar, 1953
Human blood	Klima et al., 1962

DISCUSSION OF THE MAJOR FOOD TYPES

Wild plankton. One of the most widely used sources of food for larval fishes has been plankton taken from natural waters, referred to here as wild plankton. Wild plankton is usually collected by tows with a plankton net, although Schumann (work described in Bardach, 1968) collected plankton at night with a submerged pump to which plankters were attracted by a light, and concentrated the plankton with a series of filters. Prior to feeding the plankton to the larvae, it is common practice to strain it through netting of a mesh size which passes only those organisms which the larvae can feed upon. This performs the additional function of removing most potential predators from the plankton. Meyer (1878), however, noted poor survival and growth among herring larvae which were given plankton strained through cloth and found that normal growth was resumed when unstrained plankton containing large numbers of copepods was administered. It would seem obvious that as the larve grow the size range of the plankton used as food should be increased. The plankton supplied to larval fishes usually contains a mixture of organisms, and authors who describe the use of wild plankton in rearing experiments, often list the dominant organisms in the plankton. Some also give information on which plankters were eaten by the larvae, based either on analyses of gut contents or on observations of feeding behavior. Copepods, copepodites and copepod nauplii frequently dominate in wild plankton and often constitute the main food of the larval fishes (Garstang, 1900; Lebour, 1925; Schach, 1939; Blaxter, 1969), but many other types of organisms may be present (*cf.* Blaxter and Hempel, 1961; Blaxter, 1968a), and herring and plaice larvae are reported to have selectively fed upon larval molluscs in wild plankton (Meyer, 1878; Dannevig, 1897). Blaxter (1969) had more success with offshore than with inshore plankton in rearing experiments with larval sardines.

Wild plankton has proved to be an excellent source of food for larval fishes in the laboratory, as might be expected since it contains the same food which fish larvae feed on under natural conditions. Plankton collected in the sea was the mainstay of the successful early attempts to rear marine fishes (Meyer, 1878; Dannevig, 1897; Garstang, 1900; Fabre-Domergue and Biétrix, 1905; Anthony, 1910) and is still being used in rearing for experimental purposes (Schumann, in Bardach, 1968; Blaxter, 1968, 1969; Ivanchenko and Ivanchenko, 1969; Richards and Palko, 1969; Kramer and Zweifel, 1970).

However, despite the proven effectiveness of wild plankton as a food source, its use has serious disadvantages which make it unsuitable in many instances. Among these disadvantages are: 1) the seasonality and highly variable quality and quantity of wild plankton; 2) the dependence of plankton collection on weather conditions; 3) the time-consuming nature of collecting plankton; 4) the mixture of food types in the plankton which makes controlled feeding experiments difficult; and 5) the difficulty of removing from the plankton all organisms which may prove harmful to the fish larvae. Because of such drawbacks, much effort has been expended in the search for larval-fish foods that can be cultured in the laboratory. The long list of food types presented in Table 1 testifies to this fact.

Phytoplankton. Of the many attempts described in the literature to feed phytoplankton to larval fishes (Table 1), very few have met with any success. In several experiments various types of phytoplankters were ingested by fish larvae, yet the larvae survived no longer than starved controls (Gross, 1937; Orcutt, 1950; Qasim, 1955, 1959; Bishai, 1961; Blaxter, 1969); this suggests that at least certain types of phytoplankters are nutritionally inadequate for larval fishes. Schach (1939) found that yolk-sac herring larvae kept in water thick with phytoplankton acquired a "green mass" in their guts, presumably from ingesting phytoplankton, but these larvae did no better than larvae kept in clear water, and both groups began feeding on zooplankton 4 days after yolk-absorption.

In the first successful attempt to use phytoplankton as a larval fish food, Fabre-Domergue and Biétrix (1905) found that newly-hatched sole larvae, *Solea solea,* ate *Dunaliella salina* cultured from salt marshes but soon switched to carnivorous feeding. Hertling (1932) stated that the armed bullhead, *Agonus cataphractus,* could be reared by feeding the early larvae on diatoms, and Runnström (1941) claimed to have kept herring larvae alive for 6 weeks on "plankton algae," but these authors supplied few details. Kasahara *et al.* (1960) fed early larvae of the black porgy, *Mylio macrocephalus,* on the naked dinoflagellate *Oxyrrhis* but soon changed over to animal foods. Lasker et al. (1970) gave the only detailed description of rearing for prolonged periods using phytoplankton alone. They reared the northern anchovy, *Engraulis mordax,* for 19 days (when the experiments were purposely terminated) with good growth and survival, using the naked dinoflagellate *Gymnodinium splendens* as the sole food, and in one experiment kept a larva alive for 34 days on this phytoplankter. Growth and survival were somewhat better, however, when molluscan larvae were supplied along with the *Gymnodinium.*

Artemia nauplii. Perhaps the greatest breakthrough in feeding techniques was the discovery by Rollefsen (1939, 1940) that the plaice, *Pleuronectes platessa,* could be reared from hatching through metamorphosis with nauplii of the brine shrimp, *Artemia salina* L., as the only food. This is an extremely convenient source of food, since the nauplii hatch readily when the dried eggs are placed in water, and the eggs can be stored for long periods and used when needed. Unfortunately, not all fish larvae are able to take *Artemia* nauplii as a first food because of their relatively large size (length 0.4 mm, width with appendages folded 0.35 mm; from Blaxter, 1962). Hirano and Oshima (1963) pointed out that larvae of different fish species begin taking *Artemia* nauplii at different sizes. For example, the puffer, *Fugu rubripes,* eats *Artemia* nauplii when it is 4.1 mm long; *Mylio macrocephalus* and the flatfish, *Liopsetta obscura* at 5 mm; the halfbeak, *Hemiramphus sajori,* at 6–6.5 mm; and the Pacific herring, *Clupea pallasii,* at 9–10.5 mm (Hirano and Oshima, 1963). Fishelson (1963) reported that *Blennius pavo* of 3.5 mm total length will consume *Artemia* nauplii, and Flüchter (1965) found that *Solea solea* larvae 3 to 4 days old, i.e., ca. 5 mm total length, began to eat this food. These differences are undoubtedly related to differences between species in morphometry and mouth size (see Schumann, in Bardach, 1968), and perhaps also to the use of different strains of *Artemia* with different sized nauplii. Rosenthal and Hempel (1970) wrote that among young herring, the success of prey-catching maneuvers was higher with *Artemia* nauplii than with wild plankton, and they attributed this to the greater visibility of *Artemia* (Blaxter, 1968b) and to its sluggish escape response.

Certain flatfish larvae appear to do very well on an exclusive diet of *Artemia* nauplii. Shelbourne (1964) reported good survival (66%) through metamorphosis for plaice larvae feeding on *Artemia* alone, and Flüchter (1965) fed sole larvae on *Artemia* and obtained 80% survival through metamorphosis, and growth comparable to that of larvae in the sea. *Artemia* nauplii alone have also been used successfully to feed larval *Fundulus heteroclitus* (Joseph and Saksena, 1966), *Fundulus majalis* (Fahey, 1964), *Aulorhynchus flavidus* (Morris, 1956), *Sebastes pachycephalus nigricans* (Fujita, 1957), two cottid species (Morris, 1956), four species of artherinids (McHugh and Walker, 1948; Morris, 1956; Chirinos de Vildoso and Chuman 1964), and *Fugu pardalis* (Shojima, 1957). They have frequently been used to supplement other food types (e.g. Dannevig and Hansen, 1952; Blaxter and Hempel, 1961; Blaxter, 1962, 1968a; Fishelson, 1963) or to feed older larvae (e.g. Dannevig, 1948; Kasahara *et al.,* 1960; Schumann, in Bardach, 1968; Okamoto, 1969; Kramer and Zweifel, 1970).

Riley (1966) has shown in a controlled experiment that the survival and growth of plaice larvae feeding on *Artemia* nauplii are markedly affected by the amount of food available. He found that surplus food increased the survival beyond first feeding; but very high feeding levels were detrimental to the larvae after feeding had become established, since they caused fouling of the water and promoted the growth of bacteria and ciliates. Flüchter (1965) recommended extremely high concentrations of nauplii (20,000 per liter) for first-feeding sole larvae. The necessity of high concentrations of food for young larvae is also strongly suggested by Rosenthal's (1969b) finding that first-feeding herring larvae were successful in only 1% to 10% of their strikes at prey.

A rather substantial body of evidence indicates that *Artemia* nauplii alone will not sustain the growth and survival of clupeid larvae over long periods. Dannevig and Hansen (1952) found that older larvae of the Atlantic herring, *Clupea harengus,* did not grow on an exclusive diet of *Artemia.* Blaxter and Hempel (1961) and Blaxter (1962) also had little success using only *Artemia* to feed *C. harengus,* and Blaxter (1968a) was unable to rear herring beyond 25 mm on *Artemia.* McMynn and Hoar (1953) and Kurata (1959) reared the Pacific herring *Clupea pallasii* only to 10.2 and 14.5 mm, respectively, on *Artemia* alone. An explanation for this phenomenon may be that the digestive system of the larval clupeid is incapable of fully digesting the nauplii of *Artemia.* Rosenthal's (1969a) observation that *Artemia* nauplii are much more resistant to digestion by larval *C. harengus* than are copepods supports this explanation. Attempts to feed *Artemia* nauplii on phytoplankton in order to make them more nutritious (Dannevig and Hansen, 1952; Morris, 1956; Blaxter, 1962) appear to have met with little success, although Rosenthal (1969b) fed herring larvae of 15 mm total length and larger on *Artemia* which had been reared on cultured *Dunaliella* to ca. 1.8 mm in length. Despite the evidence for the nutritional inadequacy of *Artemia* nauplii for clupeid larvae, Blaxter (1962) found that 10–12 mm herring which had previously fed on *Artemia* nauplii survived up to twice as long without food as larvae which had fed on *Balanus* nauplii.

Certain technical problems are associated with the use of *Artemia* nauplii. Care must be taken to avoid placing eggshells in rearing containers along with the nauplii, as they may be eaten by fish larvae in place of nourishing food and the larvae may starve as a result (Morris, 1956). Rosenthal (1969a) observed one herring larva which took almost nothing but *Artemia* eggs. Blockage of the gut by *Artemia* eggshells has been reported in young seahorses (Herald and Rakowicz, 1951). As *Artemia* nauplii grow, they may become too large for the fish larvae to eat; they also become less nutritious as their yolk is consumed, a change which is indicated by transition from a deep orange to a whitish coloration (Morris, 1956). Morris stated that fish larvae which fed on older *Artemia* nauplii "did not prosper," and he recommended that uneaten nauplii be removed from rearing tanks each day.

Other crustaceans. Nauplii of the barnacle *Balanus* sp. are smaller than *Artemia* nauplii (Hirano and Oshima, 1963) and have been used to feed larval *C. harengus* (Soleim, 1942; Dannevig, 1948; Blaxter, 1962, 1968a), *Pleuronectes platessa* (Shelbourne, 1964), *Blennius pholis* and *Centronotus gunnellus* (Qasim, 1955, 1959) and *Mylio macrocephalus* (Kasahara *et al.,* 1960; Hirano, 1969). Barnacles have a short spawning season, however, and this limits their usefulness as larval fish food (Blaxter, 1962, 1968a). Blaxter (1965, 1968b) found that herring larvae required more light to feed on *Balanus* nauplii than on *Artemia* nauplii, presumably because the former are smaller and more transparent.

Since nauplii of calanoid copepods are frequently the dominant organisms in the guts of larval fishes caught at sea (e.g., Lebour, 1920), they would appear to be a natural choice as a food for use in laboratory fish-rearing. But copepod nauplii have never been cultured on a large scale for the purpose of feeding larval fishes, probably because of the technical difficulties of producing sufficient numbers. Kotthaus (1939) harvested nauplii which hatched from eggs carried by adult copepods collected in plankton tows, but he worked on a rather small scale. Kasahara *et al.* (1960) listed copepod nauplii as one of the foods they used but did not say how the nauplii were obtained.

Morris (1956) stated that nauplii of the spray-pool harpacticoid *Tigriopus* sp. are thigmotactic and hence not available to larval fishes, and most recorded attempts to use them as food have met with no success (Budd, 1940; Orcutt, 1950; Bishai, 1961; Blaxter, 1962). Nevertheless, Fahey (1964) mentioned, without further elaboration, that he reared *Bairdiella chrysura, Alosa pseudoharengus,* and *Mugil caphalus* using mass-cultured first and second naupliar stages of *T. californicus* as food. Certain other crustaceans such as young mysids (Kasahara *et al.,* 1960) and adult *Tigriopus* (Morris, 1956; Blaxter, 1965, 1968a) have been used to feed older larvae.

Mollusc larvae. The larvae of certain molluscs are attractive food sources because of their availability and small size (most under 0.2 mm, many under 0.1 mm—see Loosanoff and Davis, 1963; Hirano and Oshima, 1963) and have been used successfully several times, especially to feed very young larvae. Most such experiments have employed the larvae of bivalve molluscs, which generally hatch as trochophores and later develop into veligers. Kurata (1956) found mussel larvae an excellent food for early larvae of the flatfish *Liopsetta obscura,* and Okamoto (1969) gave mussel and oyster trochophores to early red sea bream, *Pagrus major,* larvae. Morris (1956) describes a procedure for obtaining eggs from the California mussel, *Mytilus californianus.* Dannevig (1948) used oyster larvae successfully to feed smaller larvae of several fish species, and Hirano (1969) reared *Mylio macrocephalus* using oyster larvae as the first food. Gastropod larvae, which in most cases hatch as veligers, have been used much less frequently than bivalve larvae. Lasker et al. (1970) found that the veligers of three species of opisthobranch gastropods were too large to be taken by first-feeding anchovy larvae but that they increased the growth rate and survival of older larvae which had fed first on a dinoflagellate. May (unpublished data) reared the atherinid *Leuresthes tenuis* through metamorphosis using veligers of the gastropod *Bulla gouldiana* as the sole food, with a survival of 16.7 percent through metamorphosis.

Other living foods. Kasahara et al. (1960) fed the hypotrichous ciliate *Stylonichia* sp. to larval *Mylio macrocephalus* 3-3.5 mm in length. (It is interesting in this connection that Kotthaus (1939), Schach (1939), and Bishai (1961) considered hypotrichous ciliates as undesirable contaminants in rearing experiments with herring and even suggested that they may have attacked and killed larvae.) The use of the rotifer *Brachionus plicatilis* to rear larval fishes has been reported recently by Japanese workers (Hirano, 1969; Mito *et al.*, 1969; Okamoto, 1969) who offered it to first-feeding or very young larvae.

Kurata (1959) found that first-feeding *Clupea pallasii* larvae took trochophores of the sabellid polychaete *Chone teres* in preference to *Artemia* nauplii, which were larger; but he considered *C. teres* as an unsuitable food source, because its spawning season was very short and the trochophores settled quickly. Cunningham (1893–95b) fed *Nereis* eggs to larval plaice with very limited success.

Several workers have tried echinoderm larvae as larval fish foods. Morris (1956) reared the sciaenid *Geneonymus lineatus* beyond yolk-absorption by feeding first with eggs and larvae of the sand-dollar *Dendraster* and later switching to *Artemia* nauplii. In their successful rearing trials Rubinoff (1958), Fujita (1965) and Richards and Palko (1969) offered sea urchin eggs or larvae (along with other foods) to larval fishes but did not state whether this food was taken to a significant extent.

Bruun (1949) cited the common use of nematodes for feeding freshwater tropical aquarium fishes and suggested that they might be a suitable food for marine fish larvae. But Blaxter (1962) tried the nematode *Anguillicula* sp. as a food for herring larvae without success, and Korovina (1962), working in freshwater, reported that the hard skin and sharp extremeties of larval nematodes (*Panagrelus redivivus*) injured the digestive tract of *Coregonus* larvae and killed them. Riley (1966) found free-living nematodes in the detritus on the bottom of some of his tanks which were occasionally taken by plaice post-larvae.

Algae growing on the walls of rearing containers was eaten by advanced herring larvae (Kotthaus, 1939) and by 8-day-old gobies (Delmonte *et al.*, 1968), and "slime" on tank walls was browsed off by plaice larvae in sufficient quantity to color the gut brown in larvae which had a restricted supply of *Artemia* nauplii (Riley, 1966).

Fabre-Domergue and Biétrix (1905) found that sole larvae soon began to feed on other larval fishes, including especially sprat larvae but also larvae of their own species. Schumann (in Bardach, 1968) attributed a 50% reduction in the number of Pacific mackerel larvae, *Scomber japonicus*, during the first 9 days after hatching, to intraspecific predation; he also found that Pacific barracuda fry, *Sphyraena argentea,* are exclusively piscivorous at a length of 4.5 mm.

Series of food types. Some Japanese investigators have developed rather complicated feeding schedules in which progressively larger food types are offered to the growing fish larvae, there being periods of overlap to eliminate abrupt transitions from one food type to the next (Kasahara *et al.*, 1960; Hirano, 1969; Okamoto, 1969). For example, Okamoto (1969) fed *Pagrus major* the following succession of foods: oyster and mussel trochophores, *Brachionus plicatilis,* barnacle nauplii, *Artemia* nauplii, zooplankton, annelid larvae, shrimp meat, and finally fish meat—the administration of each new food type overlapping for several days that of the previous type.

Prepared aquaria. In some rearing attempts workers have allowed a flora and fauna to develop in the rearing containers prior to introduction of the fish eggs or larvae. These "prepared aquaria" usually contain attached algae, phytoplankton, zooplankton, and ciliates. Growth of the biota has been encouraged by adding fertilizers and vitamins (Delmonte *et al.,* 1968) and by placing the tanks in direct sunlight (Schach, 1939; Heuts, 1947; Bishai, 1961). Unfortunately, authors who describe such aquaria rarely specify exactly what organisms are in them, and it is impossible to tell from their accounts which items served as food for the fish larvae. After the fish larvae hatch, specific food items are usually added to prepared aquaria, such as egg yolk (Heuts, 1947) or *Artemia* nauplii (McHugh and Walker, 1948). The flora in prepared aquaria seems to maintain chemical equilibrium in the water by stabilizing pH and O_2 tension and taking up fish metabolites. This role of green plants was appreciated by some of the early investigators: Garstang (1900) placed one of his rearing containers in direct sunlight and added green algae (*Ectocarpus*) "as a means of aerating and purifying the water," and Fabre-Domergue and Biétrix (1902) used algae to assure *"d'une part l'oxygénation continue du mileu, d'autre part l'élimination d'une proportion de déchets nuisibles impossible à éviter."* Shelbourne (1964) incorporated *Enteromorpha* into closed systems of sea-water circulation for the specific purpose of stabilizing water chemistry.

Schach (1939) and Bishai (1961) siphoned food organisms into their rearing containers from tanks which were essentially prepared aquaria, containing phytoplankton and copepods and placed in sunlight. Kotthaus (1939) and Schach (1939) both had *Enteromorpha* growing in their rearing containers, and Kotthaus achieved success only in containers which received some direct sunlight during the day.

Nonliving foods. Food types in this category are attractive because of their great convenience, but they present the difficulty that uneaten food accumulates on the bottom of the rearing container and decays rapidly, fouling the water. Anthony (1910) considered artificial foods unsuitable due to the decay problem, and Fabre-Domergue and Biétrix (1905) believed that running water was necessary when artificial foods were used. By far the most widely used non-living food has been cooked chicken-egg yolk made into fine particles. Fabre-Domergue and Biétrix (1897) were apparently the first to try this food source, and Heuts (1947), Fishelson (1963), Fujita (1966), and Ivanchenko and Ivanchenko (1969) have used it successfully. Egg yolk has served primarily as a food for newly-hatched larvae, and larvae are soon given living food such as wild plankton (Ivanchenko and Ivanchenko, 1969) or *Artemia* nauplii (Fishelson, 1963; Fujita, 1966). Nikitinskaya (1958), Kurata

(1959), and Ivanchenko and Ivanchenko (1969) were able to keep *Cluepea pallasii* alive only for short periods on egg yolk alone. Heuts (1947) fed egg yolk to stickleback larvae in prepared aquaria, but it is not clear how long he continued to administer the yolk. Bückmann *et al.* (1953) and Fishelson (1963) observed that particles of egg yolk were consumed by larvae only when the particles were moving in water currents, such as are set up in aquaria by a stream of air bubbles. Korovina (1962) noted that egg yolk, especially in excess, tended to pollute the water during rearing trials in fresh-water with *Coregonus* larvae.

Delmonte *et al.* (1968) successfully fed newly-hatched goby larvae in prepared aquaria on commercial fish-fry foods, although they noted a tendency for the uneaten food to decay; Blaxter (1962) and Klima *et al.* (1962) had no success with such foods. Bits of meat (squid flesh, crab meat, chopped fish, etc.) are unsuitable for young larvae (Kurata, 1959; Bishai, 1961), but very advanced larvae commonly have eaten such items (e.g. Dannevig, 1948; Kasahara *et al.,* 1960; Blaxter, 1965, 1968; Hirano, 1969). Blaxter (1965), however, found that the feeding rate of herring larvae 22–40 mm in length was higher on live *Tigriopus* than on pieces of squid flesh, which indicates that even advanced larvae prefer live food.

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