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# MEDUSIVOROUS FISHES, A REVIEW

by

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Key words: Hydromedusae; Scyphozoa; Ctenophora; jellyfish; fishes; prey.
A preliminary review is presented of fish species having consumed pelagic Cnidaria (Scyphozoa and Hydrozoa) as well as Ctenophora. Quantitative data are scarce. Knowledge of morphological and physiological adaptations of fishes foraging on gelatinous plankton is almost non-existent. Many fish species consume medusae and some reasons to suspect that there are even more that do so, are discussed.
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## INTRODUCTION

In Indonesia, Japan, China and the Philippines some species of medusae are highly praised (Kishinouye, 1899; Ates, 1987). However, in the western world medusae have since long been despised for human consumption. Possibly for psychological reasons, the refusal of jellyfish as a food source in Europe went sofar that it was regarded most unlikely that they could serve other animals as such. So, Günther (1882), speculating in respect of *Schedophilus medusophagus*, stated: "The idea expressed by the specific name of our fish, viz. that it follows Medusae in order to feed on them could not be correct as the fish could draw but little nourishment from those animals . . .".

Jellyfishes as predators of fish and fish larvae have received much attention. Their impact on fish stocks is considerable (Möller, 1984). Their role as prey for other organisms, however, is neglected. Gudger (1934) reviewed fish eating jellyfishes and remarked: „Jellyfishes do eat fishes, and in turn some of the fishes eat medusae . . .". From the literature it does not appear that Gudger (1934) ever reviewed jellyfish-eating fishes, and later Mansueti (1955:2) stated in respect of jellyfish: ". . . as far as is known, the adults do not serve as food for other species . . .". Mansueti (1963:68) reviewed three

species of fish feeding upon jellyfishes calling them spectacular examples. A review by Von Salvini-Plawen (1972) demonstrated that Cnidaria are a vast source of food for marine invertebrates; the nematocysts contained by this type of prey are apparently no barrier for many predators and parasites contrary to a widely held belief. Von Salvini-Plawen (1972:387) also made allusion to a few fishes eating jellyfish and Siphonophora. Oviatt & Kremer (1977) mentioned four fish species consuming "such unlikely food sources as ctenophores, jellyfish . . .". Black & Low (1983) put forward that a jellyfish diet of fishes, in their case a ctenophore diet of two salmonids, may be more important than hitherto realized. Runge et al. (1987) confirmed *Scomber scombrus* to consume medusae, if available in the laboratory, and also stressed that such a diet may be important to this fish. Scattered in the literature many more incidental references, often somewhat obscured, are to be found of fishes preying upon pelagic Cnidaria and Ctenophora (cf. table 1 and 2).

Table 1. Review of medusivorous fishes as found in the literature, systematically arranged according to Nelson (1984).

Identification of predator and prey organisms has not been checked. Some authors did not, or could nog distinguish between certain prey items (/ = and/or; * = aquarium observation; ** see discussion; # = more references are available).

| predator | prey | locality | source |
|---|---|---|---|
| Callorhynchidae | | | |
| *Callorhynchus milii* (Bory de St. Vincent) | Scyphozoa | New Zealand | Graham, 1939 |
| Squalidae | | | |
| *Etmopterus spinax (L.)* | medusae | north Atlantic | Mauchline & Gordon, 1983a |
| *Centroscyllium fabricii* (Reinhardt) | medusae | north Atlantic | Bigelow & Schroeder, 1953 |
| *Centroscymnus coelolepis* Bocage & Capella | medusae *(Atolla)* | north Atlantic | Mauchline & Gordon, 1983a |
| *Somniosus microcephalus* (Schneider) | medusae | Gulf of Maine | Bigelow & Schroeder, 1953 |
| *Squalus acanthias* L. | *Pleurobrachia* | north Atlantic | Mortensen, 1912 |
| | Ctenophora | Danish waters | Blegvad, 1916 |
| | Ctenophora | Gulf of Maine | Bigelow & Schroeder, 1953 |
| | *Beroe* | North Sea | Holden, 1966 |
| | jellyfish | North Sea | Rae, 1967 |
| Elopidae | | | |
| *Megalops atlanticus* Cuvier & Valenciennes | Ctenophora | Florida waters | Randall, 1967 |
| Clupeidae | | | |
| *Sardinops melanostictus* | jellyfish-larva | Japanese waters | Yasuda, 1960 |

| | | | |
|---|---|---|---|
| (Temminck & Schlegel) | | | |
| *Opisthonema oglinum* (LeSueur) | Siphonophora | Caribbean | Randall, 1967 |
| Argentinidae | | | |
| *Argentina silus* (Ascanius) | Salpidae/Ctenophora | north Atlantic | Mauchline & Gordon, 1983b |
| Bathylagidae | | | |
| *Bathylagus euryops* Goode & Bean | Salpidae/Ctenophora | north Atlantic | Mauchline & Gordon, 1983b |
| Alepocephalidae | | | |
| *Alepocephalus bairdii* Goode & Bean | Ctenophora & medusae | central & east Atlantic | Golovan & Pakhorukov, 1975 |
| | *Periphylla hyacinthina* Streenstrup | north Atlantic | Du Buit, 1978 |
| | *Atolla* | north Atlantic | Wheeler, 1978 |
| | medusae | north Atlantic | Mauchline & Gordon, 1983b |
| | medusae | north Atlantic | Glukhov et al., 1983 |
| Salmonidae | | | |
| *Salmo salar* L. | Ctenophora | North Sea | Krumbach, 1928 |
| *Oncorhynchus keta* (Walbaum) | Ctenophora | Japanese waters | Suyehiro, 1942 |
| | Ctenophora | Br. Columbian waters | Black & Low, 1983 |
| *Oncorhynchus tshawytscha* (Walbaum) | Ctenophora | Br. Columbian waters | Black & Low, 1983 |
| Sternoptychidae | | | |
| *Argyropelecus aculeatus* Valenciennes | Siphonophora | eastern north Atlantic | Merrett & Roe, 1974 |
| Myctophidae | | | |
| *Ceratoscopelus warmingi* (Lütken) | Siphonophora | central Pacific | Clarke, 1980 |
| Gadidae | | | |
| *Gadus morrhua* L. | *Pleurobrachia* | Danish waters | Poulsen, 1931 |
| | *Beroe & Bolina* | Greenland waters | Jensen & Hansen, 1931 |
| | *Pleurobrachia, Beroe & Bolina, Mertensia* | Greenland waters | Hansen, 1949 |
| | *Pleurobrachia* | Gulf of Maine | Bigelow & Schroeder, 1953 |
| | *Beroe* | Barentsz Sea | Kamshilov, 1960 |
| *Melanogrammus aeglefinus* (L.) | *Beroe* | Barentsz Sea | Kamshilov, 1960 |
| *Merlangius merlangus* L. | *Cyanea* | North Sea | Scheuring, 1915* |
| | *Cyanea* | North Sea | Dahl, 1961* |
| *Pollachius virens* (L.) | Ctenophora | Gulf of Maine | Bigelow & Schroeder, 1953 |
| | *Pleurobrachia* | north Atlantic | Lie, 1961 |
| | medusae | North Sea | Robb & Hislop, 1980 |

| | | | |
|---|---|---|---|
| Macrouridae | | | |
| *Coryphaenoides rupestris* Gunnerus | Ctenophora/Salpidae | north Atlantic | Mauchline & Gordon, 1984 |
| | medusae | north Atlantic | Du Buit, 1978 |
| Scorpaenidae | | | |
| *Sebastes flavidus* (Ayres) | Siphonophora/ Ctenophora/Cnidaria | northeastern Pacific | Brodeur & Pearcy, 1984 |
| Hexagrammidae | | | |
| *Hexagrammos superciliosus* (Pallas) | jellyfish | north Pacific | Grossman, 1986 |
| Cyclopteridae | | | |
| *Aptocyclus ventricosus* (Pallas) | medusae/ Ctenophores | Bering Sea | Yoshida & Yamaguchi, 1985 |
| *Cyclopterus lumpus* L. | Scyphozoa/ Ctenophora | north Atlantic | see Ates, 1987# |
| *Paraliparis calidus* Cohen | Cnidaria/Ctenophora/ Salpidae | north Atlantic | Wenner, 1979 |
| *Paraliparis copei* Goode & Bean | Cnidaria/Ctenophora/ Salpidae | north Atlantic | Wenner, 1979 |
| Carangidae | | | |
| *Trachurus trachurus* (L.) | *Cyanea* | North Sea | Malm, 1852 |
| | *Cyanea* | North Sea | Scheuring, 1915 |
| *Caranx fusus* Geoffroy de St. Hilaire | Siphonophora | Caribbean | Randall, 1967 |
| Coryphaenidae | | | |
| *Coryphaena hippurus* L. | medusae | Mediterranean | Bannister, 1976 |
| Emmelichthyidae | | | |
| *Inermia vittata* Poey | Siphonophora | Caribbean | Randall, 1967 |
| Lutjanidae | | | |
| *Ocyurus chrysurus* (Bloch) | Siphonophora, Ctenophora | Caribbean | Randall, 1967 |
| Sparidae | | | |
| *Chrysophrys auratus* L. | scyphomedusae/hydromedusae | New Zealand waters | Godfriaux, 1969 |
| *Pagrosomus major* (= *Pagrus major* (Temminck & Schlegel) | certain jellyfishes | Japanese waters | Suyehiro, 1942 |
| Sciaenidae | | | |
| *Sciaenops ocellata* (L.) | Ctenophora | Gulf of Mexico | Bass & Avault, 1975 |
| Pomacentridae | | | |
| *Chromis cyanea* Poey | Siphonophora | Caribbean | Randall, 1967 |
| *Chromis multilineata* (Guichenot) | Siphonophora | Caribbean | Randall, 1967 |
| *Chromis vanderbilti* (Fowler) | Siphonophora | Hawaiian waters | Hobson, 1974 |
| *Chromis verater* | Siphonophora | Hawaiian waters | Hobson, 1974 |

| | | | |
|---|---|---|---|
| (Fowler) | | | |
| *Pomacentrus fuscus* (Cuvier & Valenciennes) | Scyphozoans | Caribbean | Randall, 1967 |
| Labridae | | | |
| *Clepticus parrae* (Bloch & Schneider) | Siphonophora | Caribbean | Randall, 1967 |
| Pholididae | | | |
| *Pholis gunnellus* (L.) | *Pleurobrachia* | North Sea | Greve, 1972* |
| Anarhichadidae | | | |
| *Anarhichas latifrons* Steenstrup | Quallen | north Atlantic | Künne, 1950** |
| Nototheniidae | | | |
| *Notothenia larseni* Lönnberg | Coelenterata/ Ctenophora | Antarctica | Daniels, 1982 |
| *Notothenia neglecta* Nybelin | Coelenterata/ Ctenophora | Antarctica | Daniels, 1982 |
| Opisthognathidae | | | |
| *Opisthognathus aurifrons* Jordan & Thompson | Siphonophora | Caribbean | Randall, 1967 |
| Acanthuridae | | | |
| *Acanthurus thompsoni* (Fowler) | Siphonophora | Hawaiian waters | Hobson, 1974 |
| *Naso hexacanthus* (Bleeker) | Siphonophora | Hawaiian waters | Hobson, 1974 |
| Scombridae | | | |
| *Scomber japonicus* Houttuyn | jellyfish-larva | Japanese waters | Yasuda, 1960 |
| | *Velella* | northwestern Pacific | Hart, 1974 |
| *Scomber scombrus* L. | Quallen | Baltic | Möbius & Heincke, 1883 |
| | jellyfish | western north Atlantic | Baird, 1889 |
| | *Pleurobrachia* | Irish Sea | Scott, 1920, 1924 |
| | Medusen und Ctenophora | North Sea | Künne, 1950 |
| | *Aglantha digitale* (O.F. Müller) | Canadian waters | Runge et al, 1987* |
| Luvaridae | | | |
| *Luvarus imperialis* Rafinesque | Scyphozoa & Ctenophora | eastern north Atlantic | Gotshall & Fitch, 1968 |
| Centrolophidae | | | |
| *Centrolophus niger* (Gmelin) | *Rhizostoma* | Mediterranean | Lo Bianco, 1909* |
| | Siphonophora | central Atlantic | Collett, 1896 |
| | jellyfishes | north Atlantic | Wheeler, 1978 |
| *Hyperoglyphe perciformis* (Mitchill) | Ctenophora | Gulf of Maine | Bigelow & Schroeder, 1953 |

| | | | |
|---|---|---|---|
| *Icichthys lockingtoni* Jordan & Gilbert | Siphonophora | north Pacific | Haedrich, 1966 |
| *Psenopsis anomala* (Temminck & Schlegel) | jellyfish | Japanese waters | Suyehiro, 1942 |
| *Schedophilus medusophagus* Cocco | medusae | north Atlantic | Haedrich, 1967 |
| | *Atolla* | north Atlantic | Wheeler, 1978 |
| *Schedophilus pemarco* Poll | jellyfish | north Atlantic | Haedrich & Cervigon, 1969 |
| Nomeidae | | | |
| *Nomeus gronovii* (Gmelin) | *Physalia* | Japanese waters | Kato, 1933 |
| | *Physalia* | Florida waters | Jenkins, 1983* |
| Stromateidae | | | |
| *Pampus argenteus* (Euphrasen) | medusae | Japanese waters | Suyehiro, 1942 |
| | Salpidae and hydromedusae | Arabian Sea | Rege & Bal, 1963 |
| | medusae | East China Sea | Higashikawa et al., 1981 |
| *Pampus chinensis* (Euphrasen) | Ctenophora and medusae | Bay of Bengal | Pati, 1980 |
| *Peprilus burti* Fowler | *Cyanea* | Gulf of Mexico | Phillips et al., 1969 |
| | jellyfish | Gulf of Mexico | Horn, 1970 |
| *Peprilus paru* (L.) | *Chrysaora* | north Atlantic | Dunnington & Mansueti, 1955 |
| | sea nettle | north Atlantic | Cargo & Schultz, 1966 |
| | *Chrysaora* | north Atlantic | Mansueti, 1963* |
| | jellyfish | western Atlantic | Horn, 1970 |
| *Peprilus triacanthus* (Peck) | Ctenophora | north Atlantic | Bigelow & Schroeder, 1953 |
| | *Chrysaora* | north Atlantic | Mansueti, 1963 |
| | jellyfish | north Atlantic | Horn, 1970 |
| | *Mnemiopsis* | north Atlantic | Oviatt & Kremer, 1977 |
| *Stromateus fiatola* L. | *Cotylorhiza* | Mediterranean | Lo Bianco, 1909* |
| Pleuronectidae | | | |
| *Pleuronectus platessa* L. | *Pleurobrachia* | North Sea | Greve, 1972* |
| Balistidae | | | |
| *Alutera schoepfi* (Walbaum) | *Chrysaora* | north Atlantic | Cargo & Schultz, 1966 |
| *Alutera scripta* (Osbeck) | *Physalia* | Arabian Sea | Chappgar, 1977* |
| *Canthidermis sufflamen* (Mitchill) | Siphonophora | Caribbean | Randall, 1967 |
| *Melichthys niger* Bloch | Siphonophora | Caribbean | Randall, 1967 |
| *Xanthichthys ringens* (L.) = *X. mento* Jordan & Gilbert | Siphonophora | Hawaiian waters | Hobson, 1974 |
| Ostraciidae | | | |
| *Acanthostracion quadricornis* L. | Scyphozoa | Caribbean | Randall, 1967 |

| | | | |
|---|---|---|---|
| Molidae | | | |
| *Mola mola* (L.) | medusae | north Atlantic | Binney, 1842 |
| | jellyfishes | Japanese waters | Suyehiro, 1942 |
| | jellyfish, Ctenophora | Gulf of Maine | Bigelow & Schroeder, 1953 |
| | jellyfish | northeastern Pacific | Hart, 1974 |
| | jellyfishes, comb-jellies | north Atlantic | Wheeler, 1978# |
| *Ranzania laevis* (Pennant) | medusae and combjellies | north Atlantic | Wheeler, 1978 |

Table 2. Fish species listed in table 1, reported to have their stomach(s) filled solely or for a considerable part with the remains of medusae [two references, however (indicated by asterisk), may relate to salps].

| species | source |
|---|---|
| *Alepocephalus bairdii* | Golovan & Pakhorukov (1975) |
| *Aptocyclus ventricosus* | Yoshida & Yamaguchi (1985) |
| *Cyclopterus lumpus* | Ates (1987) |
| *Icichthys lockingtoni* | Haedrich (1966) |
| *Mola mola* | Bigelow & Schroeder (1953), Wheeler (1978) |
| *Pampus argenteus* | Suyehiro (1942) |
| *Paraliparis copei* | Wenner (1979)* |
| *Paraliparis calidis* | Wenner (1979)* |
| *Peprilus paru* | Cargo & Schultz (1966) |
| *Peprilus triacanthus* | Horn (1970), Oviatt & Kremer (1977) |
| *Peprilus burti* | Phillips et al (1969) |
| *Psenopsis anomala* | Suyehiro (1942) |
| *Ranzania laevis* | Wheeler (1978) |
| *Schedophilus pemarco* | Haedrich & Cervigon (1969) |
| *Schedophilus medusophagus* | Wheeler (1978) |

## DISCUSSION

Larson (1986) suggested a high water content of gelatinous zooplankton to be an adaptation, a.o. to prevent these organisms from being consumed; a high water content would make "poor food for predators and parasites". However, many parasites of medusae are known (Thiel, 1976, Brandon & Cutress, 1985, Harbison et al., 1977 and Harbison et al., 1978 and others). In addition, the present paper reviews many fish species recorded to have consumed medusae, suggesting that medusae are a useful source of food instead.

Though the data are not overwhelming, it seems that the fishes listed in table 2 consume Cnidaria and Ctenophora indiscriminately. It is hard to

deduce from the information contained in tabel 1 if the non-specialized fishes distinguish between Cnidaria and Ctenophora.

Quantities of medusae found in the stomachs of non-specialized fishes sometimes are so small according to the records (often less than 1% of stomach contents), that including these fishes in table 1 may seem useless, but in point of fact it is quite likely that the amount of pelagic Cnidaria and Ctenophora consumed by various fish species is more significant than suggested:

a. Jellyfish prey presumably soon disintegrates after being consumed. Therefore, jellyfish remains may easily be overlooked in fish stomachs. Thus, only a small number of authors recognized the whitish mass in the stomachs of *Cyclopterus lumpus* as such (Ates, 1987). Most of the methods to analyze fish stomach contents as reviewed by Hyslop (1980) do not seem to be suitable to establish the presence or absence of jellyfish remains. For this purpose, microscopical research will invariably be necessary. Only the microscope could clear up the origin of the unidentified jelly/mucous in the stomachs of *Xenodermichthys copei* (Gill) (Alepocephalidae) as quoted by Mauchline & Gordon (1983b). On the other hand, there is the example of *Tetragonurus cuvieri* Risso, for more than 150 years believed to be a jellyfish-eating specialist (Risso, 1826), but which, as a result of microscopical investigations (Janssen & Harbison, 1981) turned out be a salp-eating specialist.

A method for stomach contents analysis in order to reveal the presence of remains of Cnidaria is described for sea turtles by Den Hartog (1980).

b. It seems from table 1 as if no special adaptations are involved for a fish to become a jellyfish predator. Considering the presumed fragility of their skins and sometimes the presumed unsuitability of their mouths, it is hard to imagine members of fish families such as Elopidae, Clupeidae, Argentinidae, Salmonidae, Sternoptychidae, Gadidae, Macrouridae, Carangidae, Sparidae, Pomacentridae, Opisthognathidae, and Scombridae to be predators of medusae if the records in table 1 would not prove that they are. It is clear from table 1 that jellyfish predation by fishes is a common phenomenon. In view of jellyfish abundance it seems reasonable to assume that in the future more planktonivorous fish species will be found to consume medusae if available.

c. Fisheries research started and is still mainly centered around the Atlantic. Most references concern fish species from the Atlantic and the references are disproportionately distributed among commercially important fish species. So it seems obvious that more jellyfish consuming fish species are to be discovered as soon as fisheries research develops elsewhere and in groups of non-commercial fish.

d. Many fishes belonging to the suborder Stromateoidei (families Amarsipidae, Ariommatidae, Centrolophidae, Nomeidae and Stromateidae) show

similarities in dentition (Janssen & Harbison, 1981: 925, Bühler, 1930: 88 and others), stomach morphology (Bühler, 1930: 94 etc.) and ecology (Haedrich, 1967) and at least some of them share a similar feeding behaviour (Haedrich in Horn, 1977). The stomachs of some species of the Stromateoidei invariably contain "chunks of whitish or transparent, amorphous tissue" (Horn, 1970). In view of the foregoing it seems likely that more, perhaps most, fishes of this suborder are medusivorous specialists.

Incidentally, it is noted that many species of Stromateoidei maintain a symbiotic relationship with a jellyfish host (Mansueti, 1963). Most of the records of the symbiosis between members of the Stromateoidei and medusae do not include the identification of the host (Mansueti, 1963). The information available on some of them (for instance *Schedophilus medusophagus* together with *Phacellophora camtschatika* Brandt according to Bone & Brook, 1973) suggests that these relationships may be with a limited number of hosts or strictly specific. In consequence, it is tempting to speculate that the variations in dentition, gullet morphology etc., within the suborder Stromateoidei may be related to specialisation on certain jellyfish prey. As *Cyclopterus lumpus, Aptocyclus ventricosus* and (possibly) members of the genus *Paraliparis* are jellyfish predators to a large extent, it may be worth-while to investigate whether other members of the Cyclopteridae are jellyfish predators as well. More specialist medusivorous fishes may be found among other slow moving oceanic fishes like Alepocephalidae, Molidae and Balistidae (in respect of the latter, see Anon., 1985).

e. Another reason to assume that there are more fish species consuming medusae is the circumstance that certain species of jellyfish are used in Japan as bait to catch *Monacanthus* (Balistidae) and *Pagrus* (Sparidae) (Kishinouye, 1899). Similar information is quoted by Townsend (1929) according to Randall (1967) for *Chaetodipterus faber* (Broussonet) (Ephippididae) who states that fishermen in Trinidad catch this fish with pieces of *Physalia* as bait.

## FURTHER NOTES

*Anarhichas denticulatus* as a jellyfish predator. — Künne (1950:75) asserts that the flesh of the jelly-cat, *Anarhichas denticulatus* Krøyer (= *A. latifrons* Steenstrup) becomes whitish and of low quality when it eats many jellyfishes. A stomach content analysis, however, does not seem to have been carried out. Therefore, the statement of Künne (1950) may be questioned. According to Wheeler (1978) the flesh of this species is weak and watery without exception, although its normal diet consists of hard-shelled benthic invertebrates like crustaceans, sea-urchins and brittle-stars.

Amphipod remains in fish stomachs. — Hyperiid amphipods in fish stomachs may originate from consumed jellyfishes, but not necessarily so. Many authors (a.o. Haedrich & Cervigon, 1969: 3; Glukhov et al., 1983; Mauchline & Gordon, 1983b: 69; Brodeur & Pearcy, 1984: 276, 277; and Ates, 1987) report the combined presence of remains of hyperiid amphipods and jellyfish in fish stomachs. However, some species of hyperiid amphipods regularly found with medusae, are also capable to lead a life separate from these hosts [see Von Westernhagen & Rosenthal, 1976, concerning *Hyperoche medusarum* (Krøyer) and note that it is unknown what happens to the countless numbers of *Hyperia* symbiotic with medusae such as *Aurelia* when the latter disappear from the plankton after a bloom]. This implies that the presence of hyperiid amphipod remains in fish stomachs should not be interpreted as an indication for the consumption of jellyfish, unless the presence of the latter is obvious. Thus, a high percentage of hyperiid remains, coinciding with significant amounts of unidentifiable matter in fish stomachs, as reported by Peterson et al. (1982:848) for salmon in the north Pacific, may result from the consumption of medusae. Although Peterson et al. do not consider this possibility, the studies by Black & Low (1983) strongly suggest so.

## CONCLUSION

Many fish species have apparently adapted to live on medusae and it is obvious that there are many more that do so than those contained in table 1. It remains to be seen if jellyfish stocks are controlled by fishes as calculated to be possible by Oviatt & Kremer (1977) and by Runge et al. (1987) for certain pairs of predator/prey species.

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