



## THE POTENTIAL OF FISHES FOR THE CONTROL OF GELATINOUS ZOOPLANKTON

by G.R. Harbison, Woods Hole Oceanographic Institution, Woods Hole, MA 02543 U.S.A.

### Abstract

A large variety of gelatinous zooplankton are preyed upon by marine fishes. In most cases gelatinous zooplankton are incidental components of the diet. There are, however, a number of species that prey heavily on gelatinous organisms, and appear to have evolved special adaptations for the consumption of gelatinous prey. These species are presently being investigated with the goal of introducing one or more of them into the Black Sea, to try to control populations of the introduced ctenophore, *Mnemiopsis leidyi*. The criteria for selection are: the fish should preferentially feed on gelatinous zooplankton at all stages of its life history; it should be able to survive and reproduce in the specialized environmental conditions found in the Black Sea; it should be amenable to laboratory culture; and it should be a commercially valuable food fish. On the eastern coast of North America, the butterflyfish, *Peprilus triacanthus*, has been reported to control populations of *M. leidyi*. This fish is a member of the perciform suborder Stromateiodei, most members of which appear to preferentially feed on gelatinous zooplankton. At present, this fish appears to be a good candidate for introduction, although it is not clear that it will be able to reproduce in the low salinity of the Black Sea. If a commercially useful fish that preys on *M. leidyi* can be successfully introduced, an improvement in the present situation will be achieved, even if the fish does not control ctenophore populations to the extent that the pelagic fishery can recover, since a new fishery will be developed.

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As a generalization, it is reasonable to expect that gelatinous zooplankton will generally have a negative impact on fisheries. For example, Fraser (1962) discussing the role of gelatinous zooplankton in the North Atlantic, concluded that "ctenophores ... and salps both occur in swarms and the general evidence suggests that both may severely reduce the zooplankton standing crop, with its concurrent effect on the food cycle." Since, as a rule, gelatinous zooplankton are not directly consumed by human beings, this shunting of zooplankton production into gelatinous organisms results in a decrease in the biomass of commercially valuable species.

There is probably nowhere that this effect has been clearer than in the Black and Azov Seas, where the introduced ctenophore, *Mnemiopsis leidyi*, has had a profound and devastating impact on stocks of the tyul'ka, *Clupeonella cultriventris*, and the anchovy, *Engraulis encrasicolus* (Studenikina *et al*, 1991; Harbison and Volovik, in press). In the Azov Sea, in particular, the impact of the massive blooms of the ctenophore has resulted in the virtual elimination of the formerly bountiful catches of these species. The impact of *M. leidyi* has been particularly deleterious on these particular fishes, since the ctenophore not only outcompetes them for food, but also preys heavily on their eggs and larvae (Govoni and Olney, 1991).

However, not all species of fish are affected by massive blooms of gelatinous predators in such a negative way -- some species actually exploit gelatinous organisms by using them as shelter or as a source for food. Perhaps the best-known examples of fishes using gelatinous organisms for shelter are found among gadids and carangids (Mansueti, 1963). It is possible that these juvenile fishes could actually benefit from massive blooms of predatory medusae, since an abundance of potential shelter



would be available. No one has attempted to study the role of shelter in the survival of juvenile gadids and carangids, so such a benefit must be regarded as speculative at this stage.

Predation by fishes on gelatinous zooplankton has been reviewed recently by Kashkina (1986), Ates (1988), Arai (1988). A wide variety of fishes consume gelatinous zooplankton to some extent, and it may be concluded that practically any planktivorous fish also consumes gelatinous zooplankton. However, for most species, the consumption of gelatinous zooplankton is probably relatively minor. There nevertheless remain several groups of fishes that consume gelatinous zooplankton heavily, and, in fact, some of them appear to depend on gelatinous zooplankton as their primary source of nutrition.

I would like to discuss one of these groups, the Stromateoidei (a suborder of the Order Perciformes), with regard to its potential to exploit and control massive blooms of predatory gelatinous zooplankton such as have occurred in the Black and Azov Seas. I stress at this point that this discussion is purely illustrative, since there are other groups of fishes that show a similar dependence on gelatinous zooplankton as a food source. The stromateoids are merely the group for which we have the best evidence at present. Their obvious feeding preferences for gelatinous zooplankton were obscured until recently by the failure of earlier investigators to identify gelatinous remains in fish stomachs. As evidence for the validity of this statement, see reviews of the older literature by Bühler (1930) and Haedrich (1967). Even today, the importance of gelatinous zooplankton to the nutrition of any fish remains difficult to determine since gelatinous material is expected to remain in recognizable condition for a far shorter period than such indigestible matter like crustacean exoskeletons, fish otoliths and squid beaks.

Fishes are listed in Table 1 according to the classification of Eschmeyer (1990), with a few modifications based on recent revisions. Apparent discrepancies between generic and trivial names given by the authors cited in the tables are based on my attempt to use the most up-to-date synonymies that I could, in order to avoid artificially inflating the list with junior synonyms.

In table 1, the names of fishes that prey heavily on gelatinous zooplankton are capitalized. Using literature reports to determine the importance of gelatinous zooplankton in the diets of fishes is somewhat subjective, since gut content studies are so diverse in the ways in which data are reported. Basically, if gelatinous zooplankton constitute over 15% of the total diet volume, weight or number, or if they occur in more than 20% of the stomachs examined, I have considered them as important components of the diet. Likewise, if an author states that particular gelatinous organisms are the main prey, or that the stomachs are filled with gelatinous material, the name of the fish is also capitalized. In most cases, I have not reported studies in which gelatinous zooplankton were not reported.

The suborder Stromateoidei contains 17 genera distributed into 5 families (Horn, 1984; Agafonova and Piotrovskiy, 1990). Species in 16 of these genera are known either to associate with or feed upon gelatinous zooplankton, or both. The only exception is the genus *Parapsenes* in the Nomeidae, which has been recently resurrected by Agafonova and Piotrovskiy (1990).

In the Centrolophidae, all genera, with the exception of the monotypic *Tubbia*, have members that have been reported to feed heavily on gelatinous organisms. The Centrolophidae contains about 25 species (Haedrich, 1967, McDowell, 1982), 10 of which have been shown to consume large

quantities of gelatinous organisms. There is some evidence of feeding specificity at the generic level. Species of *Hyperoglyphe* and *Seriotelella* seem to prefer prey that lack nematocysts, such as salps, pyrosomes and ctenophores, while species of *Centrolophus* and *Psenopsis* seem to feed primarily on cnidarians. *Ichthyos lockingtoni* appears to feed on both medusae and salps, and species of *Schedophilus* appear similarly catholic in their diets.

Among the Nomeidae, *Cubiceps caeruleus* and *C. pauciradiatus* seem to prefer salps, while the close relationship between *Nomeus gronovii* and *Physalia physalis* is well-known. Evidence for feeding by species of *Psenes* on gelatinous zooplankton is restricted to a single report, but there are numerous reports on association with various gelatinous organisms.

Two families, the Amarsipidae and Tetragonuridae, probably are specifically associated with and feed on salps. Janssen and Harbison (1981) found that all three species of *Tetragonurus* fed heavily on salps and pyrosomes, concluding that earlier reports that members of this family fed on eel fish were probably erroneous. Therefore, members of these families probably do not feed on gelatinous predators.

I have found no reports that ariommatids feed on gelatinous zooplankton, but there is one report of an association with a medusa. Haedrich (1967) suggests that they may feed on organisms in muddy bottoms, since the pharyngeal sacs are often filled with mud, and thus it is unlikely, based on present information, that members of this family feed on gelatinous predators.

All three genera in the Stromateidae have members that have been reported to feed on gelatinous zooplankton; these probably represent about half of the known species. Although the evidence is not overwhelming for the genus *Stromateus*, there are numerous reports of gelatinivory in the other two genera, *Pampus* and *Peprilus*. The reluctance of ichthyologists to accept that these fishes eat gelatinous zooplankton is clearly demonstrated by the report of Pati (1980b) for *Pampus argenteus*. He found that copepods accounted for 10% of the identifiable gut contents, while ctenophores and medusae only accounted for 4%. However, he was unable to identify the vast majority of the material in the gut contents (79%). He concluded that *P. argenteus* therefore preferred copepods. Even if one grants that the unidentifiable material was not gelatinous zooplankton, this hardly constitutes evidence that it was the remains of copepods. At any rate, any fish that preys on medusae and ctenophores must have numerous copepods in its gut contents, since they are often the major prey of these gelatinous animals. When one considers that gelatinous zooplankton are much more rapidly degraded in the guts of fishes than are crustaceans, it is hardly surprising that abundant crustacean remains would be found. Likewise, although Pati (1980a) reports that medusae and ctenophores were present in the stomach contents of *Pampus chinensis*, along with 76% unidentifiable material, he also concludes that this species prefers copepods as well, since they represent 11% of the diet. When one examines papers on the feeding preference of other fishes that specialize on gelatinous organisms, such a high percentage of unidentifiable material is commonly found. For example, similarly high percentages of unidentifiable material have been reported from the stomachs of many bathylagids (Gorelova and Kobylansky, 1985) and *Cyclopterus lumpus* (Ates, 1987; Bowman, personal communication).

Bühler (1930) concluded that the morphological peculiarities of the construction of the alimentary canal of stromateoids reflected adaptations for the consumption of gelatinous organisms. At the time he wrote, most gut content studies conflicted with this conclusion, and he was able to find reports on only three species that corroborated his hypothesis (Lo Bianco, 1909 on *Stromateus fiatola* and *Centrolophus niger* and Brehm, 1922 on *Schedophilus medusophagus*). Subsequent studies have amply confirmed the validity of his speculations, and have thereby demonstrated the power of Bühler's (1930) morphological methods.

Stromateoids have distinctive (with the exception of the Amarsipidae) paired sacks in the pharynx. These pharyngeal sacks are diverse in morphology, but are usually equipped with denticulate papillae. Based on the arrangement of the papillae and the musculature in their walls, the pharyngeal sacks appear to be used for triturating food. The fine spines on the papillae are unusually delicate, so that they can only be used for the shredding of delicate gelatinous organisms such as medusae, ctenophores and salps. In many stromateoids, the stomach is exceptionally large, and the intestine is often extremely long (ranging from 4 times body length in *Stromateus fiatola* to 0.75 times body length in *Nomeus gronovii*). Bühler (1930) suggested that the large stomach and pharyngeal sacks probably worked in concert, with the movement of the large gelatinous prey organisms back and forth between stomach and pharyngeal sacks until they were shredded and reduced in volume.

In the stromateoids, there appear to be three adaptations to deal with gelatinous bulky material - the specialized pharyngeal sacks, the large stomach, and the long intestine. These adaptations are reminiscent of the adaptations of herbivores, which also have gastric mills, large stomachs, and long intestines (Horn, 1989). Indeed, gelatinivory may have evolved from herbivory, or vice versa.

As Haedrich pointed out, the "stromateoid look" is characteristic. Haedrich (1967) described it as "a fat-nosed, wide-eyed, stuffed-up look, smug and at the same time apprehensive. Some stromateoids might even be accused of a certain prissiness." This look is also characteristic of a number of other fishes, many of which have been shown to eat gelatinous zooplankton. In fact, once this general look has been recognized, it is easy to thumb through the pages of a general book on fishes, spot known or potential "jelly-eaters." Non-stromateoid fishes which have the look of jelly-eaters include members of the Cyclopteridae, Caristiidae, Ephippidae, Luvaridae, Oreostomatidae, Monocentridae, Carangidae, and Molidae. It is tempting to speculate that the "look" is somehow related morphologically to the preference of members of all these groups for eating jellies. Certainly, the deep bodies of many species in these families reflect a greatly enlarged alimentary canal, suitable for packing in large quantities of gelatinous material. In most, the dentition on the jaws are reduced or lacking, and the jaw is underslung, perhaps as the optimal configuration for slicing off pieces of their gelatinous prey.

Of course, other factors are important in determining whether or not a fish can survive in a particular habitat besides dietary preference. Tolerance to environmental conditions is also important, and it is noteworthy that none of the Mediterranean stromateoids have penetrated into the Black Sea. However, species from other regions, such as the east coast of the Americas, may be better able to tolerate the low salinities and cold temperatures found in the Black and Azov Seas. However, the massive occurrence of large blooms of gelatinous predators is a relatively recent occurrence in the

Black Sea, and previously there may not have been sufficient quantities of gelatinous organisms to permit the survival of the Mediterranean species. Since, however, the butterfish, *Peprilus triacanthus*, occurs in regions that are environmentally very similar to the Black and Azov Seas, this seems a reasonable candidate to consider for introduction. It should be noted that stromateoids are highly prized as food fish, and are the subject of commercial fisheries in many regions of the world.

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Table 1. Feeding by stromateoid fishes on gelatinous zooplankton

Species	Prey	Location	Reference
Amarsipidae			
<i>Amarsipus carlsbergi</i> Haedrich	Jellyfish-like tissues, chaetognaths Young associate with <i>Cyclosalpa affinis</i> Young associate with <i>Cyclosalpa affinis</i>	Indo-Pacific Seychelles Coral Sea	Haedrich, 1969 Janssen & Harbison, 1981 Harbison, personal observations
Centrolophidae			
<i>CENTROLOPHUS NIGER</i> (Gmelin)	Eats <i>Rhizostoma</i> in laboratory Young associate with medusae Feed heavily on medusae Scyphozoa 81%, Siphonophora 1%, Ctenophora 2%, hyperiids 15% weight Medusae and ctenophores	Mediterranean  North Atlantic Southwest Africa	Lo Bianco, 1909 Haedrich, 1967 Wheeler, 1978 Macpherson, 1983
<i>HYPEROGLYPHE ANTARCTICA</i> (Carmichael)	<i>Pyrosoma atlanticum</i> major prey	Namibia	Macpherson & Roel, 1987
<i>Hyperoglyphe japonica</i> (Döderlein)	<i>Pyrosoma atlanticum</i> major prey	Tasmania	Cowper, 1960
<i>Hyperoglyphe perciformis</i> (Mitchill)	Gelatinous zooplankton	S.E. Australia	Winstanley, 1978
<i>ICICHTHYS LOCKINGTONI</i> Jordan & Gilbert	Salps, algae Salps, Ctenophora <i>Pelagia</i> sp. Young associate with medusae Siphonophores <i>Salpa</i> sp. 36%, unidentified 34% weight Gelatinous zooplankton	Hawaii Northwest Atlantic Northwest Atlantic California California North Pacific Northeast Pacific California	Seki, personal communication Linton, 1901 Bigelow & Schroeder, 1953 Fitch, 1949 Mansueti, 1963 Haedrich, 1966 Brodeur <i>et al.</i> , 1987 Robison, personal communication Suyehiro, 1942 Haedrich, 1967 Shojima, 1961 Graham, 1939
<i>PSENOPSIS ANOMALA</i> (Temminck & Schlegel)	Jellyfish & gelatinous remains Young associate with medusae	Japan	Gavrilov & Markina, 1979
<i>Psenopsis</i> sp.	<i>Aurelia</i> , <i>Stomolophus nomurai</i>	New Zealand	Shuntov, 1979
<i>SERIOLELLA BRAMA</i> (Günther)	Salps <i>Iasis zonaria</i> 38%, <i>Pyrosoma atlanticum</i> 24%, coelenterates 2%	S.E. New Zealand	Gavrilov & Markina, 1979
<i>SERIOLELLA CAERULEA</i> Guichenot	Salps 21%, pyrosomes 47%, coelenterates 21% frequency 58% <i>Iasis zonaria</i> , 40% <i>Pyrosoma atlanticum</i> 0.5% coelenterates	New Zealand New Zealand	Shuntov, 1979 Gavrilov & Markina, 1979
<i>SERIOLELLA PUNCTATA</i> (Forster)	Salps, pyrosomes principal food, coelenterates common 59% <i>Iasis zonaria</i> , 39% <i>Pyrosoma atlanticum</i> 0.3% coelenterates	New Zealand New Zealand	Shuntov, 1979 Gavrilov & Markina, 1979
<i>Seriolella violacea</i> Guichenot	Salps 12%, pyrosomes 70% frequency Young associate with medusae	S.E. New Zealand Peru	Shuntov, 1979 Mansueti, 1963
<i>Schedophilus griseolineatus</i> (Norman)	Eat gelatinous organisms	Atlantic	Menni & López, 1979
<i>Schedophilus maculatus</i> Günther	Young associate with <i>Physalia</i>	Atlantic	Mansueti, 1963
<i>SCHEDOPHILUS MEDUSOPHAGUS</i> Cocco	Young associate with and eat medusae Medusae Bathypelagic medusae, especially <i>Atolla</i> Eats medusae exclusively	North Atlantic North Atlantic North Atlantic Southwest Africa	Mansueti, 1963 Haedrich, 1967 Wheeler, 1975, 1978 Macpherson, 1983
<i>SCHEDOPHILUS OVALIS</i> (Cuvier & Valenciennes)	Associate with medusae Pyrosomes always found in guts 8 <i>Cymbulia peroni</i> in 1 stomach	Australia Madeira	Mansueti, 1963 Maul, 1964
<i>SCHEDOPHILUS PEMARCO</i> (Poll)	Jellyfish, amphipods, euphausiids, fish	Mediterranean	Orsi Relini <i>et al.</i> , 1990
<i>Tubbia tasmanica</i> Whitley	Associate with medusae	North Atlantic Australia	Haedrich & Cervigón, 1969 Mansueti, 1963

Table 1 (Continued)

Species	Prey	Location	Reference
Nomeidae			
<i>CUBICEPS CAERULEUS</i> Regan	Salps primary food	Southwest Pacific North Atlantic Atlantic E. Central Atlantic	Agafonova, 1992
<i>Cubiceps capensis</i> (Smith)	"Possibly remains of coelenterates"		Pequeño, 1976
<i>Cubiceps gracilis</i> (Lowe)	Young associate with <i>Cyclosalpa polae</i>		Janssen & Harbison, 1981
<i>CUBICEPS PAUCIRADIATUS</i> Günther	Young associate with medusae		Mansueti, 1963
	Salps, siphonophores, crustaceans, fish	South Africa Japan Worldwide Florida Northwest Pacific Western Pacific Japan Seychelles Northwest Pacific Worldwide S. China Sea	Salekhov, 1989
	Adults eat mainly salps, siphonophores, heteropods, squids, fish, polychaetes		Agafonova, 1992
<i>Cubiceps squamiceps</i> (Lloyd)	Young associate with medusae		Mansueti, 1963
<i>Nomeus gronovii</i> (Gmelin)	<i>Physalia</i>		Kato, 1933
	Associate with <i>Physalia</i> , medusae, chondrophores	Northwest Pacific Japan Seychelles Northwest Pacific Worldwide S. China Sea	Mansueti, 1963
	Eats tentacles of <i>Physalia</i> in the lab		Jenkins, 1983
<i>Psenes arafurensis</i> Günther	Young associate with medusae, chondrophores		Mansueti, 1963
<i>Psenes cyanophrys</i> Cuvier & Valenciennes	Young associate with medusae, chondrophores		Mansueti, 1963
	Young feed on <i>Physalia physalis</i>	Japan Seychelles Northwest Pacific Worldwide S. China Sea	Masuda <i>et al.</i> , 1975
	Young associate with <i>Pegea confoederata</i>		Janssen & Harbison, 1981
<i>Psenes maculatus</i> Lütken	Young associate with medusae		Mansueti, 1963
<i>Psenes pellucidus</i> Lütken	Young associate with medusae		Mansueti, 1963
<i>Psenes whiteleggi</i> Waite	Young associate with medusae		Mansueti, 1963
Ariommatidae			
<i>Ariomma indica</i> (Day)	Young associate with ctenophores	South Africa	Fowler, 1934
Tetragonuridae			
<i>TETRAGONURUS ATLANTICUS</i> Lowe	Associate with and eat salps	North Atlantic Mediterranean California North Atlantic North Atlantic	Janssen & Harbison, 1981
<i>TETRAGONURUS CUVIERI</i> Risso	Salps		Emery 1882
	Pyrosomes, cnidaria, ctenophores		Fitch 1949, 1952
	Associate with and eat salps		Janssen & Harbison, 1981
<i>TETRAGONURUS PACIFICUS</i> Abe	Associate with and eat salps		Janssen & Harbison, 1981
Stromateidae			
<i>PAMPUS ARGENTEUS</i> (Euphrasen)	Medusae major prey	Japan Bombay Arabian Sea Bay of Bengal Bay of Bengal	Suyehiro, 1942
	Medusae, ctenophores		Chopra, 1960
	Salps, hydromedusae main prey		Rege & Bal, 1963
	<i>Salpa</i> 0.8%		Srinivasa Rao, 1964
	Ctenophores & medusae 4%, unidentifiable	East China Sea Bay of Bengal Gulf of Mexico Gulf of Mexico Northwest Atlantic North Atlantic Northwest Atlantic Northwest Atlantic Northwest Atlantic	Pati, 1980b
	78-81% volume		
<i>Pampus chinensis</i> (Euphrasen)	Medusae over 90% total weight		Higashikawa <i>et al.</i> , 1981
<i>PEPRILUS BURTII</i> Fowler	Ctenophora & medusae 2%, unidentifiable 76% weight		Pati, 1980a
	Feeds voraciously on <i>Cyanea capillata</i> , <i>Nemopsis bachei</i> , and <i>Mnemiopsis mccradyi</i>	Gulf of Mexico Northwest Atlantic North Atlantic Northwest Atlantic Northwest Atlantic Northwest Atlantic	Phillips <i>et al.</i> , 1969
	Jellyfish		Horn, 1970
<i>PEPRILUS PARU</i> (Linnaeus)	Associate with and eat medusae, ctenophores		Dunnington & Mansueti, 1955
	Associate with and eat medusae, siphonophores		Mansueti, 1963
	Feed heavily on <i>Chrysaora quinquecirrha</i>	Northwest Atlantic Northwest Atlantic Northwest Atlantic	Cargo & Schultz, 1966
	Jellyfish present in gut contents		Horn, 1970
	White translucent material, often containing nematocysts		Sminkey, 1986



Table 1 (Concluded)

Species	Prey	Location	Reference
<i>PEPRILUS TRIACANTHUS</i> (Peck)	Ctenophora	Northwest Atlantic	Hildebrand & Schroeder, 1928
	Ctenophora	Northwest Atlantic	Bigelow & Schroeder, 1953
	Associate with and eat medusae, siphonophores	Northwest Atlantic	Mansueti, 1963
	Stomachs full of jellyfish	Northwest Atlantic	Horn, 1970
	Thaliacea 41% weight	Northwest Atlantic	Maurer & Bowman, 1975
	<i>Mnemiopsis leidyi</i>	Northwest Atlantic	Oviatt & Kremer, 1977
	Thaliacea 12 % weight	Northwest Atlantic	Bowman & Michaels, 1984
	68% unidentified material, no nematocysts	Northwest Atlantic	Sminkey, 1986
	Urochordata 29%, <i>Clione</i> 17%, Cnidaria 1%, Ctenophora 0.1%, Unidentified 46%	Northwest Atlantic	Bowman, personal communication
	Eats <i>Cotylorhiza</i> , other medusae and salps in aquarium	Mediterranean	Lo Bianco, 1909
<i>Stromateus fiatola</i> Linnaeus	Associate with and eat medusae	Mediterranean	Mansueti, 1963