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November 1, 2007
SIO 277
Challenger Project

The History of Grenadier Life History:
Growth, Reproduction, and Early Life History of the Family Macrouridae from the Challenger Expedition to Present Day

The family Macrouridae, which is commonly known as the grenadiers or the rattails, contains a total of 386 fish species (Froese and Pauly, 2007) that share a characteristic elongated body with long dorsal and anal fins supported by numerous fin rays. Grenadiers are typically bathydemersal and are found along the continental slope and abyssal plain in all oceans. Most grenadiers are nomadic foragers that can act as both predators and scavengers that will can consume benthic prey (e.g., crabs, ascidians, polychaetes, echinoderms, foraminifera, and even sponge spicules) and mid-water, pelagic organisms (e.g., euphausiids, prawns and myctophids) (Marshall, 1964; Gage and Tyler, 1991). Compared to other families of deepwater fish, the Macrouridae are extremely abundant, making up almost 100% of the fish biomass in the northeast Pacific Ocean at depths below 2,000 m (Stein and Pearcy, 1982). Due to the large volume covered by the deep sea, the total biomass of just two macrourid species (i.e., *Coryphaenoides armatus* and *C. yaquinae*) is globally estimated to be 150 million tonnes, which is larger than the total annual, commercial catch of all marine fishes combined (Gage and Tyler, 1991). Despite their high numerical abundance and cosmopolitan distribution, little is known about the biology of the grenadiers compared to shallow-water species of fish. This is especially true of grenadier early life history traits, reproduction patterns, and population age structure.

Prior to the publication of Volume LVII of the H.M.S. Challenger Reports, few species in the family Macrouridae were known and specimens from this group were poorly represented in taxonomic collections. The Challenger expedition collected over 140 specimens of macrourid fish, belonging to 30 species (Günther, 1887). While 140 specimens may not sound like many by today's standards, these specimens provided some of the first evidence that macrourids were widely distributed and quite abundant at depth in all oceans. Based on the new data provided by the Challenger expedition, the taxonomic classification of genera in the family Macrouridae was re-ordered, resulting in the recognition of 46 species belonging to 4 genera (Günther, 1887).

Part of the reason why it was necessary to reorganize the genera in this family was that juvenile and adult life stages of fish belonging to the same species had previously been classified as separate species. The collection of 12 species of juvenile macrourids during the Challenger expedition revealed to taxonomists the changes in macrourid morphology that occur as juvenile fish reach maturity, thus allowing them to better determine whether juvenile and adult specimens belong to the same or different species. While many morphological traits that differed between juveniles and adults were species specific, Günther (1887) proposed that the number of spines on the scales of several macrourid species increased during the transition from the juvenile to adult life stages. Also, the barbs on several species' dorsal spines tended to further apart and less numerous in juvenile specimens. The only other piece of information on grenadier life history presented in the Challenger report is that the species *Trachyrhynchus longirostris* likely spawns during the month of July and produces "millet-sized" eggs (Günther, 1887). Despite of the progress made during the Challenger expedition, researchers remained unable to collect any specimens of larval macrourid fish. Günther (1887) commented that the absence of grenadier larvae appeared strange given the abundance and diversity of juvenile and adult macrourids that were collected during the expedition.

For several decades following the Challenger expedition, references to macrourid fish in the scientific literature were mainly limited to descriptions of new species and reports documenting the distribution of this family across different geographic regions. Increased surveying of the deep-sea fishes of the North Pacific during this time period, resulted in the discovery of several new species from areas offshore of Japan and the Hawaiian Islands (Gilbert and Hubbs, 1916; Gilbert and Hubbs, 1917; Katayama, 1942; Matsubara, 1943). During his tenure as a professor at Scripps Institution of Oceanography, Carl Hubbs was particularly involved in describing the distribution of Pacific macrourids. As was the case with the Challenger Report, information included in these early publications on macrourid life history characteristics was mainly limited to what could be divined from incidental collections of juvenile specimens. In fact, up until the early 1980s, there were only two descriptions of pre-juvenile, macrourid species from the entire North Pacific (Stein, 1980). Likewise, information on macrourid eggs was extremely scarce, although Marshall (1964) did contain a brief description of the eggs of the benthypelagic fish *Cynomacrurus piriei*.

One of first papers to focus solely on characterizing the larval and juvenile phases of macrourid fish was Stein (1980). This paper contained the first key for identifying larval specimens from the genus *Coryphaenoides* collected off of the eastern North Pacific. Characteristics that Stein (1980) found useful for identifying larval species of macrourids include premaxillatory and dentatory teeth, the number of rays on their dorsal and pelvic fins, the number gas glands and retia, and pigmentation. Once larval grenadiers could be identified more consistently to species, Stein's research group at Oregon State University, as well other research teams, began to paste together more information on macrourid larval ecology.

The eggs of most grenadier species are easily identifiable by raised hexagonal sculpturing on their surface (Collette and Kein-MacPhee, 2002). These eggs have a large oil globule, which makes them buoyant. After being spawned and fertilized at depth, the buoyant, macrourid eggs float upwards into the area above the seasonal thermocline (Gage and Tyler, 1991). Once the eggs hatch, larval grenadiers are retained in pelagic habitats where they consume copepods as their primary prey (Merrett, 1978). Metamorphosis between the larval and juvenile stages occurs once an individual reaches approximately 10-15 mm HL (head length) (Stein, 1980). The rapid metamorphosis phase is characterized by loss of the peduncle on the pectoral fin, changes in the angle of the mouth, the development of a distinct snout, and a reduction in the relative size of the stomach. Juvenile grenadiers generally become benthic at ages between 1-2 years and lengths between approximately 10-20 mm HL (Stein and Pearcy, 1982; Swan and Gordon, 2001). While it is still unknown what macrourids eat during their juvenile stages, they likely experience difficulties finding food in the deep sea environment due to their limited mobility and small mouth size, which prevents them from taking advantage of large food falls. It has been proposed that different macrourid species settle to the bottom at distinct sizes in order to reduce interspecific competition for food resources (Stein and Pearcy, 1982).

As many macrourid species grow in size, their distribution continuously shifts into deeper waters. Stein (1980) documented this pattern in great detail, revealing that post-larvae of *Coryphaenoides acrolepis* are typically collected at depths of approximately 500 m; juveniles are found at depths of 650-800 m, and; fishes longer than 13 mm HL tend to reside below 800 m. Similar types of ontogenetic migrations have been observed amongst other grenadier species, including *Coryphaenoides carapinus, Coryphaenoides guentheri, Coryphaenoides armatus, Coryphaenoides rupestris, Coryphaenoides armatus, Coelorhynchus coelorhynchus, Hymenocephalus italicus, Trachyrincus murrayi* and *Nezumia schlerorhynchus* (Haedrich and Polloni, 1977; Stein and Pearcy, 1982; Gage and Tyler, 1991; D'Onghia *et al.*, 2000; Swan and Gordon, 2001). It has been hypothesized that these migratory patterns are related to an increase in foraging efficiency that allows growing macrourids to progressively find scarcer food sources at deeper depths (Polloni *et al.*, 1979). Nevertheless, several exceptions to this pattern have been detected, where there is either no relationship between fish size and depth or where the largest sized fish occur at intermediate depths (Stein and Pearcy, 1982; Swan and Gordon, 2001).

The age at which grenadiers reach sexual maturity is known for only a few species, but females seem to typically become mature later than males. For example, female roundnose grenadiers (*Coryphaenoides rupestris*) mature at age 10, while males mature at age 8 (Bergstad, 1990). Similarly, the average age of the onset of maturity for *Macrourus whitsoni*, a species native to the Ross Sea, takes place at 10.6 years and 13.6 years for males and females, respectively (Marriott *et al.*, 2006). Fecundity of macrourids has been found to be correlated with body size in at least two species (Stein and Pearcy, 1982; Coggan *et al.*, 1998). When comparing grenadier species, it is notable that the number of eggs produced by different species varies by several orders of magnitude. This is demonstrated by the contrast in fecundity between the common Atlantic grenadier (*Nezumia aequalis*), which have been known to produce as few as 2,109 eggs per individual, and the abyssal grenadier (*Coryphaenoides armatus*), which can spawn up to 2.7 million eggs (Stein and Pearcy, 1982; Coggan *et al.*, 1998). When examining ripe females, eggs of multiple size classes have been detected within a single individual, indicating that some grenadier species may spawn multiple times during a given year (Coggan *et al.*, 1998; Collette and Klein-MacPhee, 2002). While most macrourids spawn seasonally, the exact season when spawning takes place varies greatly from species-to-species with no recognizable pattern (Gage and Tyler, 1991).

Since 80% of the flesh of grenadiers consists of water with relatively little lipids or proteins, humans generally consider grenadiers to be fairly "unpalatable" (Koslow, 2007). Nevertheless, this fact hasn't prevented the development of commercial fisheries for grenadiers. The Russians initiated a fishery for the roundnose grenadier (*Coryphaenoides rupestris*) in the late 1960s. This species was first targeted by fishermen in the Northwest Atlantic, but as its stock size rapidly decreased, the fishery began to refocus its effort on catching roundnose grenadiers in the Northeast Atlantic (Swan and Gordon, 2001; Koslow, 2007). Catch of *C. rupestris* peaked at 83,800 tonnes per year between 1976 and 1978, but then declined throughout the 1980s and 1990s (Gage and Tyler, 1991; Koslow, 2007). In Canadian waters, a recent stock assessment indicates that the abundance of roundnose grenadier has been reduced by 99.6%, which would make this fish critically endangered according to IUCN standards (Koslow, 2007). In addition to the roundnose grenadier fishery, there are smaller fisheries that target roughhead grenadier in European waters (*Macrourus berglax*), big-eye grenadier (*Macrourus holotrachys*) and ridge scaled rattail (*M. carinatus*) on the Patagonian Shelf, and Pacific grenadier (*Coryphaenoides acrolepis*) off California (Swan and Gordon, 2001; Collette and Klein-MacPhee, 2002). At least, five other grenadier species are caught as by-catch in commercial fisheries (Coggan *et* al., 1998; Collette and Klein-MacPhee, 2002; Marriott *et al*., 2003). Since many deep-sea fish are slow-growing and long-lived, concerns have proliferated regarding whether it is possible to manage a grenadier fishery in a sustainable manner. In turn, these concerns have prompted the initiation of several studies that have attempted to estimate and validate the age of grenadiers.

Swan and Gordon (2001) provide a comprehensive overview of papers that have estimated and/or validated the age of macrourid fishes. The most common method used to determine the age of a fish is to count the number of annual growth rings found on the fish's scales and otolith. The history of examining macrourid scales dates back to Murray and Hjort (1912), who were the first researchers to note that ring structures appear on the scales of the macrourid fishes *Coryphaenoides armatus* and *Bathygadus melanobranchus*. However, almost immediately problems were noted in scientists' ability to accurately interpret these ring structures in order to estimate fish age. Gilbert and Hubbs (1920) commented that the rings on macrourid scales tended to become less distinct with depth, while Farran (1924) observed that the number of rings on different scales from the same fish was somewhat variability. Later, it was discovered that the otoliths (i.e., ear bones) of grenadiers have rings that seem similar to the annual growth bands found on the otoliths of shallow water fishes. Nevertheless, the interpretation of grenadier otolith rings turned out to be just as complicated as interpreting the bands on grenadier scales. For many grenadier species, only 30-50% of the otoliths collected were "readable" (Koch, 1976; Middleton and Musick, 1986). These problems didn't prevent a couple of early researchers from using scales and otoliths to estimate the age of grenadiers. For example, Kulikova (1957) used scales to examine the age of 4 macrourid species, while Motais (1960) determined that the ages of several specimens of rough snout grenadier (*Trachyrincus scabrus*) were between 3-7 years. While these studies were followed by a proliferation of investigations that examined the otoliths and scales of macourid fishes (Table 1), the value of many age estimates may be dubious, because the assumption that each ring on a scale or otolith represents a year's worth of growth has not been validated for most grenadier species.

A number of techniques exist to validate the ages of grenadiers, but each of them has distinct drawbacks. Mark-recapture techniques are often used to validate the age of shallow water fish, but this approach cannot be applied to deep water fish, as almost all bathybenthic fauna die immediately when they are first captured. The analysis of length-frequency histograms can be used to track growth rates and at times may be useful for determining and/or validating fish ages. However, more often the absolute age of a fish cannot be determined by a length-frequency histogram alone (Gage and Tyler, 1991). Also, the year classes seen in length-frequency histograms tend to become less distinct over time due to changes in growth and mortality rates. This means that this technique cannot be used to easily determine the age of long-lived species. Andrews *et al.* (1999) applied a radiometric dating technique using the isotopes of ^{210}Pb and ^{226}Ra to successfully resolve a controversy regarding the age of *Coryphaenoides acrolepis*. Despite the success of this particular application of radiometric dating, this technique is unable to precisely determine the exact age of fish specimens, but remains helpful for confirming approximate ages (Swan and Gordon, 2001). A final method that has been used to validate the age of macrourid fishes is to examine the growing edge of otoliths from fish caught during seasonal surveys. Macrourid otoliths contain repeated opaque and translucent zones that are believed to form over the course of one year (Swan and Gordon, 2001). Through surveys conducted on a monthly or seasonal basis, the timing when these opaque and translucent zones begin to form on the outer edge of otoliths can be confirmed. Swan and Gordon (2001) used this method to validate the ages of 10 macrourid species.

While most grenadier age estimates have not been validated, the results of ageing studies have made some contributions to developing a greater understanding of macrourid life history. Based on Table 1, the maximum age of grenadier species ranges between 8 and 73 years. Different studies examining the ages of *Coryphaenoides rupestris* and *C. acrolepis* have generated dramatically different results. At this time, it is not entirely possible to determine whether such discrepancies are due to differences in the techniques used to analyze otoliths or variations in longevity throughout the range of these species (Swan and Gordon, 2001). By combining estimates of macrourid age and length-frequency data, two research groups have fitted von Bertalanffy growth models for *Macrourus whitsoni* and *Nezumia aequalis* (Coggan *et al.*, 1998; Marriot *et al.*, 2006). Estimates of model parameters indicate that *Macrourus whitsoni* is a particularly slow-growing species (i.e., $k = 0.065$ year^{-1} for males; $k = 0.055$ year^{-1} for females). Based on studies of macrourid growth, two predominant patterns have come to light. First, in almost all species, female grenadiers grow at a faster rate and tend to be larger than their male counterparts (Stein and Pearcy, 1982; Bergstad, 1990; Coggan *et al.*, 1998; Swan and Gordon, 2001; Collette and Klein-MacPhee, 2002). Second, Swan and Gordon's (2001) review of macrourid growth patterns revealed that most species exhibit faster growth rates during the late summer and autumn. The seasonal timing of these quicker rates of growth coincides with the annual period when deep-sea benthic habitats receive an increased influx of organic particles.

In conclusion, scientific knowledge of macrourid life history characteristics has increased greatly since the time of the Challenger expedition. However, in order to effectively manage fisheries for macrourid species, greater knowledge of life history traits is still needed. Advances in age validation techniques hopefully should soon confirm age estimates from many macrourid species. A better understanding of natural mortality rates during different life stages would likely enhance macrourid stock assessments. Also, additional information on spawning sites, migration patterns, and larval connectivity could help determine the stock structure of fished macrourid species. Even when armed with detailed life history information, fisheries managers may still fail to sustainably manage fisheries for grenadiers due this family's longevity and slow growth rates.

Literature Cited:

Andrews, A.H., G.M. Cailliet, and K.H. Coale. 1999. Age and growth of the Pacific grenadier (*Coryphaenoides*) with age estimate validation using an improved raidometric ageing technique. *Canadian Journal of Fisheries and Aquatic Sciences* 56(8): 1339-1350.

Bergstad, O.A. 1990. Distribution, population structure, growth and reproduction of the roundnose grenadier *Coryphaenoides rupestris* (Pisces: Macrouridae) in the deep waters of the Skagerrak. *Marine Biology* 107: 25-39.

Coggan, R.A., J.D.M. Gordon and N.R. Merrett. 1998.Reproduction, age and growth in the grenadier *Nezumia aequalis* (Gunther, 1878) (Pisces: Macrouridae), a by-catch species of deep-water fisheries to the west of the British Isles. Talk presented at the Council Meeting of the International Council for the Exploration of the Sea, Cascais, Portugal, Sept. 16-19, 1998.

Collette, B.B. and G. Klein-MacPhee. 2002. Bigelow and Schroeder's Fishes of the Gulf of Maine, 3rd Edition. Smithsonian Institution Press, Washington, D.C. 748 p.

Cronin, M., I.M. Davies, A. Newton, J.M. Pirie, G. Topping and S. Swan. 1998. Trace metal concentrations in deep sea fish from the North Atlantic. *Mar. Environ. Res.* 45(3): 225-238.

D'Onghia, G., M. Basanisi and A. Tursi. 2000. Population structure, age and growth of macrourid fish from the upper slope of the Eastern-Central Mediterranean. *Journal of Fish Biology* 56: 1217-1238.

Farran, G.P. 1924. Seventh Report on the Fishes of the Irish Atlantic Slope. Proceedings *of the Royal Irish Academy* 36B: 91-148.

Froese, R. and D. Pauly (eds.). 2007. FishBase. www.fishbase.org. Accessed on October 25, 2007.

Gage, J.D. and P.A. Tyler. 1991. Deep-sea Biology. A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, Cambridge, UK. 504 p.

Gilbert, C.H. and C.L. Hubbs. 1916. Report on the Japanese Macrourid fishes collected by the United States fisheries steamer "Albatross" in 1906, with a synopsis of the genera. *Proceedings of the United States National Museum* 51(2149): 135-214.

Gilbert, C.H. and C.L. Hubbs. 1917. Description of *Hymenocephalus tenuis*, a new Macrouroid fish from the Hawaiian Islands. *Proceedings of the United States National Museum* 54: 173-175.

Gilbert, C.H. and C.L. Hubbs. 1920. The macrourid fishes of the Philippine Islands and the East Indies. *US National Museum Bulletin Part 7* 100(1): 369-588.

Günther, A. 1887. Report on deep-sea fishes. Report of the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873-1876, Vol. 22. 353+43 p.

Haedrich, R.L. and P.T. Polloni. 1977. A contribution to the life history of a small rattailfish, *Coryphaenoides carapinus*. *Bulletin of the Southern California Academy of Science* 75(2): 203-211.

Katayama, M. 1942. A new macrouroid fish from the Japan Sea. *Zoological Magazine* 54(8): 332-334.

Koch, H. 1976. A contribution on the methods of age determination in roundnose grenadier (*Coryphaenoides rupestris* Gunn). *ICNAF Res. Doc.* 76/VI/28 3 p.

Koslow, T. 2007. The Silent Deep: the Discovery, Ecology, and Conservation of the Deep Sea. University of Chicago Press, Chicago, IL. 270 p.

Kulikova, E.B. 1957. Growth and age of deepwater fishes. *Trudy. Inst. Okean. Aka. Nauk* 20: 347-355.

Lombarte, A. and B. Morales-Nin. 1989. Crecimiento de *Nezumia aequalis* y *Coelorhynchus fasciatus* (Pisces: Macuridae) en aguas de Namibia. *Coll. Sci. Pap. Int. Commun. SE Atl. Fish.* 16: 191-198.

Marriott, P., P.L. Horn and P. McMillan. 2003. Species identification and age estimation for the ridge-scales macrourid (*Macrourus whitsoni*) from the Ross Sea. *CCAMLR Science* 10: 37-51.

Marriott, P.M., M.J. Manning and P.L. Horn. 2006. Age estimation and maturity of the ridge-scaled macrourid (*Macrourus whitsoni*) from the Ross Sea. *CCAMLR Science* 13: 291-303.

Marshall, N.B. 1964. Bathypelagic macrourid fishes. *Copeia* 1: 86-93.

Matsubara, K. 1943. On a new Macrouroid fish, *Coelorhynchus kanetomoi*, obtained from Misaki. *Bulletin of the Biogeographic Society of Japan* 13(14): 95-98.

Matsui, T., S. Kato and S.E. Smith. 1990. Biology and potential use of Pacific grenadier, *Coryphaenoides acrolepis*, off Calfiornia. *Mar. Fish. Rev.* 52: 1-17.

Merrett, N.R. 1978. ON the identity and pelagic occurrence of larval and juvenile stages of rattail fishes (Family Macrouridae) from 60° N, 20° W and 53° N, 20° W. *Deep-Sea Research* 25: 147-160.

Middleton, R.W. and J.A. Musick. 1986. The abundance and distribution of the family Macrouridae (Pisces: Gadiofrmes) in the Norfolk Canyon area. *Fishery Bulletin* 84: 35-62.

Motais, R. 1960. Quelques observations sur la biologie d'un poisson abyssal *Trachyrinchus trachyrinchus* Risso et sur les condition de vie en mer profunde. *Bull. Inst. Oceangr. Monaco* 1165: 1-79.

Mulcahy, S.A., J.S. Killingley, C.F. Phleger and W.H. Berger. 1979. Isotopic composition of otoliths from a benthopelagic fish *Coryphaenoides acrolepis*, Macrouridae: Gadiformes. *Oceanologia Acta* 2: 423-427.

Murray, J. and J. Hjort. 1912. The Depths of the Ocean. Macmillan, London, UK. 821 p.

Polloni, P., R. Haedrich, G. Rowe and C.H. Clifford. 1979. The size-depth relationship in deep ocean animals. *Internationale Revue der gesamten Hydrobiologie* 64: 39-46.

Rannou, M. 1976. Age et croissance d'un poisson bathyal: *Nezumia schlerorhynchus* (Macrouridae, Gadiforme) de la mer d'Alboran. *Cah. Biol. Mar.* 17: 413-421.

Relini Orsi, L. and M. Wurtz. 1979. Biologia di *Nezumia aequalis* (Osteichthyes, Macruridae) sui fondi da batiali liguri. *Quaderni della Cilvica Stazione Idrobiologica di Milano* 7: 71-77.

SavvAtimskiy, P.I. 1971. Determination of the age of grenadiers (order Macruriformes). *Journal of Ichthyology* 11: 397-403.

Stein, D.L. 1980. Description and occurrence of macrourid larvae and juveniles in the northeast Pacific Ocean off Oregon, U.SA. *Deep-Sea Research* 27A: 889-900.

Stein, D.L. and W.G. Pearcy. 1982. Aspects of reproduction, early life history, and biology of macrourid fishes off Oregon, U.S.A. *Deep-Sea Research* 29(11A):-1313-1329.

Swan, S.C. and J.D.M. Gordon. 2001. A review of age estimation in macrourid fishes with new data on age validation of juveniles. *Fisheries Research* 51: 177-195.

Table 1. Estimates of the maximum ages of macrourid species via the examination of otolith and scale growth rings. Please note that the age estimates of most species have not been validated to confirm their accuracy.

Species	Max. Age of Specimens Examined (Years)	Reference
Albatrossia pectoralis	8	Kulikova (1957)
Albatrossia pectoralis	17	Novikov (1970)
Caelorinchus fasciatus	14	Lombarte and Morales-Nin (1989)
Coelorhynchus coelorhynchus	8	D'Onghia et al. (2000)
Coryphaenoides acrolepis	25	Mulcahy et al. (1979)
Coryphaenoides acrolepis	62	Matsui et al. (1990)
Coryphaenoides acrolepis	73	Andrews et al. (1990)
Coryphaenoides armatus	15	Cronin et al. (1989)
Coryphaenoides labiatus	16+	Cronin et al. (1989)
Coryphaenoides mediterraneus	21	Cronin et al. (1989)
Coryphaenoides rupestris	35	Cronin et al. (1989)
Coryphaenoides rupestris	27	Savvatimskiy (1971)
Coryphaenoides rupestris	72	Bergstad (1990)
Hymenocephalus italicus	9	D'Onghia et al. (2000)
Macrourus berglax	34	Cronin et al. (1989)
Nezumia aequalis	10	Coggan et al. (1998)
Nezumia aequalis	9	Lombarte and Morales-Nin (1989)
Nezumia bairdii	11	Middleton and Musick (1986)
Nezumia schlerorhynchus	23	Rannou (1976)
Nezumia schlerorhynchus	9	D'Onghia et al. (2000)
Trachyrincus scabrus	6	Relini Orsi and Wurtz (1979)