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Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes)*)

Matthias F. W. Stehmann
Institute for Sea Fisheries (ISH), Federal Research Centre for Fisheries, Hamburg, Germany

Abstract

A principal scale for identifying maturity stages of cartilaginous fishes is proposed for the first time. It applies to oviparous sharks, skates and holocephalans and mainly aplacental viviparous sharks and distinguishes a different number of maturity stages for females and males. The background information and observations were gathered predominantly during *in situ* observations in the northern NE Atlantic of shelf species, as well as deep-water mainly squaloid sharks and chimaeras. Although used in field work for more than 10 years mainly by partners of two EC projects and improved in practise, unavoidably this scale cannot equally be applied to all chondrichthyan species, particularly not to tropical/subtropical shelf placental live-bearers. However, it offers for the first time a standard for defining maturity stages for a majority of cartilaginous fishes, as it is common usage since a long time for exploited marine bony fish species.

Kurzfassung

Vorschlag einer Skala der Reifegrade für eierlegende und lebendgebärende Knorpelfische (Pisces, Chondrichthyes).

Erstmalig wird ein grundsätzliches Schema vorgestellt zur Festlegung der Reifegrade bei Knorpelfischen. Die Skala ist anwendbar für eierlegende Haie, Rochen und Chimären sowie hauptsächlich für aplazental lebendgebärende Haie. Reifegrade werden in unterschiedlicher Zahl für Weibchen und Männchen erfaßt. Praktische Felduntersuchungen und -beobachtungen im nördlichen NO-Atlantik an Arten des Schelfs wie auch im Tiefwasser, vor allem an Dornhaiartigen und Chimären, lieferten die Grundlage der Reifegradskala. Zwar wurde die Skala mehr als 10 Jahre in der Feldarbeit erprobt und auch verbessert, besonders seitens der Partner zweier EU-Projekte, aber sie kann dennoch nicht in gleicher Weise auf alle Knorpelfischarten angewandt werden. Das gilt besonders für plazental lebendgebärende Arten subtropisch/tropischer Schelfmeere. Trotzdem bietet die Skala erstmals einen Standard an zur Festlegung der Reifegrade für eine Mehrheit der Knorpelfischarten, wie es seit langem allgemeine Praxis für genutzte Meeresarten der Knochenfische ist.

Résumé

Proposition d'une échelle de stages de maturité des poissons cartilagineux ovipares et vivipares (Pisces, Chondrichthyes)

Pour la première fois on présente une échelle pour identifier les stages de maturité des poissons cartilagineux. Elle s'applique aux requins, raies et chimères ovipares ainsi qu'aux requins vivipares aplacen-

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*) Dedicated with gratitude and affection to the memory of my mentor and guide into professional ichthyology, the late Dr. Gerhard Krefft, on the occasion of his 90th birthday on 30 March 2002. Without his committed guidance, my interest in and devotion to particularly chondrichthyan fishes would never have grown to the present extent.

Arch. Fish. Mar. Res. 50(1), 2002, 23–48 0944-1921/2002/50/1-23/15.00$/0

taires, et montre un nombre différent des stages de maturité pour les femelles et les mâles. L'information de fond sur les espèces du plateau continental de l'Atlantique du nord et les requins d'eaux profondes, surtout sur les requins squaloides et les chimères, a été rassemblée *in situ*. Bien que cette échelle ait été utilisée et améliorée pendant plus de 10 ans sur le terrain par des partenaires de deux projets d'UE elle ne peut pas être appliquée en même temps à toutes les espèces chondrostéennes. Notamment pas aux espèces vivipares placentaires du plateau continental tropique et sous-tropique. Toutefois, elle offre, pour la première fois, un standard pour définir les stages de maturité de la majorité des poissons cartilagineux, comme il est d'usage depuis long temps pour les espèces exploitées de poissons osseux .

Resumen

Propuesta de una escala de estadios de madurez para peces cartilaginosos ovíparos y vivíparos (Pisces, Chondrichthyes)

Es propuesta, por primera, vez una escala para identificar estadios de madurez sexual de peces cartilaginosos. Se aplica a tiburones, rayas y holocéfalos ovíparos y también a tiburones y rayas vivíparos aplacentados, distinguiendo un número diferente de estadios de madurez para machos y hembras. La información procede, en su mayoría, de la observación *in situ* de especies de plataforma en el norte del Atlántico NE, así como también de especies de aguas profundas como tiburones del suborden Squaloidei y quimeras. A pesar de haber sido usada en el campo por mas de 10 años, principalmente por colegas de dos proyectos EC y mejorada en la práctica, esta escala inevitablemente no puede ser aplicada a todas las especies de condríctios, particularmente a las tropicales/subtropicales placentadas vivíparas. Sin embargo, ofrece por vez primera un estándar para definir estadios de madurez en gran parte de los peces cartilaginosos, como las escalas que comúnmente se han usado desde hace mucho tiempo para especies explotadas de peces óseos marinos.

Resumo

Proposta de uma escala de estádios de maturação para peixes cartilaginosos ovíparos e vivíparos (Pisces, Chondrichthyes)

É proposta pela primeira vez uma escala para identificar estádios de maturação sexual para peixes cartilaginosos. Aplica-se a tubarões, raias e holocéfalos ovíparos e a tubarões e raias aplacentados vivíparos, distinguindo um número diferente de estádios de maturação para machos e fêmeas. A informação principal e as observações foram reunidas predominantemente durante a observação *in situ* de espécies de plataforma no norte do Atlântico NE, assim como espécies de águas profundas, principalmente tubarões da suborden Squaloidei e quimeras. Apesar de ter sido usada no campo por mais de 10 anos, principalmente por colegas de dois projetos EC, e melhorada na prática, esta escala inevitavelmente não pode ser aplicada a todas as espécies de Chondrichthyes, particularmente às tropicais/subtropicais placentadas vivíparas. Porém, oferece pela primeira vez um padrão para definir estádios de maturação para uma grande parte dos peixes cartilaginosos, como as que comumente tem sido usadas há muito tempo para espécies exploradas de peixes ósseos marinhos.

Introduction

Maturity stages scales for exploited marine bony fish species are in common usage for several decades already, as introduced early last century in national European fishery research and principally later by the ICES in variously modified form. Likewise have regional fishery conventions and national fishery research institutes all over the world established such maturity scales following the ICES standard, or in a modified form adapted to certain species of concern. Only occasional debates are remaining, whether to further simplify such scales, rather than to subdivide them into more detailed maturity stages. General tendency, however, is toward more simplified scales.

Nothing comparable has so far been established to define maturity stages also for cartilaginous fishes. This was partly due to the historically rather limited interest of commercial fisheries in these fishes, and thus fishery research saw no actual need to also register sex and maturity stages of chondrichthyan fishes. Further is the urogenital system of sharks, rays and skates and holocephalans quite different from that in bony fishes, and also possess cartilaginous fishes a number of biological peculiarities, as compared with most bony fishes, so that lacking experience with and knowledge of chondrichthyan fishes have hindered for a long time their being considered and treated by fishery research and management as was established standard for so many bony fish species.

After a long period with limited interest in fishing commercially for mainly sharks, except in southeast Asian countries for their traditions of food and medical application and for a few shark species *(e.g.* spiny dogfish, *Squalus acanthias*) and rajoid skates for human consumption in some European countries, the situation has drastically changed during the past about 25 years. Already during WW II, a few species of sharks were intensively fished for and processed mainly for extracting oil from their over proportionally large livers with high content of squalene oil. Known examples are, *e.g.* a fishery off the U.S. west coast for the tope or soup-fin shark (*Galeorhinus galeus*) to produce from their liver oil vitamin A preparations for supplying the U.S. troops; likewise fished Japan intensively for deep-water mainly squaloid sharks for producing a top quality, finely refined natural lubricating oil for high speed aircraft and other engines of such kind.

The former U.S. example documents quite well the biological peculiarities of chondrichthyan fishes making them manifold more vulnerable by targeted fishery exploitation and having led all too often in following years to over-fishing of stocks within only a few years. Prior to WW II, the annual catch of U.S. west coast tope or soup-fin shark (constituting three fourths of the following total demersal shark landings) was in the magnitude of 270 t (prior to 1937) and increased rapidly from 1937 with intensified target fishery to 4185 t in 1939. Already in 1941 catches dropped considerably to only 2172 t and further to 287 t in 1944, when finally this target fishery was closed, along with the beginning synthetic production of vitamins (T. Walker 1999).

The major biological peculiarities of cartilaginous fishes, in contrast to the vast majority of bony fishes, are: a) very slow growth of these in average large fishes, b) very late first sexual maturity only after several, and up to about 15 years in many cold water species, c) extremely low reproductive rate from just one or two to mostly only 20 to 30 large young annually per female in aplacental and placental live-bearers, with maximum numbers of up to 80–135 young only in a very few shark species (*e.g.* tiger shark, Compagno 1984) and blue shark (Pratt and Castro 1990); reproductive rates for oviparous egg-layers among sharks, skates and for all chimaeras are in the average magnitude of about 40–140 capsules per year (for skates: P. A. Walker 1999; Walker and van Steenbergen 1999), d) relatively long to extremely long embryonic development from at least a few months to up to two years or even longer (skates in extreme cold water Arctic and Antarctic habitats) until littering or hatching from egg capsules (*e. g.* Clark 1922, for skates; Pratt and Castro 1990, for sharks).

That cartilaginous fishes do not pass a larval stage, often accounting for another considerable loss of recruits in bony fishes, and as individuals become in average very old (*e. g.* spiny dogfish to at least 60 years; Springer and Gold 1989) does not compensate for their very low reproductive rate, because most species do not reproduce annually. Taking these biological peculiarities into account, one will not be surprised that not only stocks of sharks, rays and skates are easily over-fished within very short time, but that these stocks also need manifold longer time for recovery than those of bony fishes. So has the North Eastern Pacific tope or soupfin shark population until to date not recovered to its pre-WW II size (T. Walker 1999), and a recent example of over-fishing the Western North Atlantic stock of spiny dogfish (*Squalus acanthias*) has led by the U.S. National Marine Fisheries Service (NMFS) to closing per 1 May 2000 any target fishery for this species during the next 10 years (AES 2000).

The rapidly increasing interest in cartilaginous fishes during the past about 25 years has developed for various reasons. The depletion, despite fishery management regulations, of traditional bony fish stocks due to over-fishing in many areas of the world oceans upgraded the still largely unregulated mainly elasmobranch fishes (sharks, rays and skates) to become an interesting, profitable resource and alternative for commercial fisheries. Market demand developed increasingly for a wide scope of products from the flesh for human consumption and pet food, over the skeletal cartilage for various products or as basis for those, the liver oil for manifold applications, to finally exploding demand for shark fins to supply the Asian markets mainly for the traditional soup. As a consequence, the world catch of chondrichthyan fishes nearly doubled from 271 813 t in 1950 to 508 130 t in 1970 and went up rapidly to 822 189 t in 1999 (FAO world fishery statistics, 2001), with a considerable proportion of catches not being registered at all (*e. g.*, no catch records at all by the PR of China prior to 1999, when only 380 t from all oceans were reported, *i. e.* hardly more than only 'China Hongkong' with 300 t). Geographically, the major fishing areas for elasmobranchs are southeast Asian, North and South American waters, and depletion of mixed species stocks, as well as even individual species occurred soon in various places. The Gulf of Mexico shark population, *e. g.*, became rapidly and critically decimated by the mid-eighties, so that action had to be taken. The American Elasmobranch Society (AES), founded in 1983, formed the spearhead for gathering precise scientific data and for campaigning, and its effort finally led in 1993 to the implementation of the U.S. NMFS' Shark Management Plan restricting commercial and leisure fishing for sharks along the U.S. east coast and in the Gulf of Mexico U.S. waters. Nonetheless, the quota set for three categories of sharks and individual species in these waters had to be reduced further during following years again and again, and several species even had to be protected totally. A few other countries also took action, like *e.g.* South Africa, Australia, New Zealand, in protecting certain species and/or monitoring and regulating their national fisheries for sharks and operations per license by foreign fishing vessel in their waters.

Despite such more or less strict, effective and wide-ranging measures here and there, the negative trend went on with further depletion of shark stocks to a degree, that international concern by the FAO, the IUCN and NGOs grew and called for immediate and partly drastic actions to prevent from ongoing endangerment to eventual extinction of species and certain populations. So were also first time in 2000 proposals submitted to CITES to list White Shark, Basking Shark and Whale Shark on Appendices I and II.

In this context, serious deficits in general knowledge of these "different" kind of fishes became obvious soon. On this background, the FAO initiated in 1998 and issued in early 1999 the "International Plan of Action - Sharks" (IAOP, "sharks" standing for all cartilaginous fishes, including batoids and holocephalans) claiming the voluntary establishing of national shark action plans by the member countries and regular reporting to the FAO by those countries following the claim. On the European level, based on initiative taken by the ICES Study Group "Elasmobranch Fishes", a multinational EC-CFP Study was proposed and granted on "Development of Elasmobranch Assessment" (DELASS, CT 99/055) to elaborate from 2000 to 2002 the methodological basis for having sharks and skates incorporated in regular stock monitoring and also assessment under ICES regime. The results of this EU Study are supposed to provide the scientific basis for future management recommendations by ICES to the EC also for elasmobranch fishes, which so far underlie largely no fishery regulations.

Profound knowledge of reproductive biology and requirements is among the most important information needed for adequately managing fish stocks, and this holds true in particular for cartilaginous fishes with their various biological peculiarities. Having available an agreed standard for assessing sexual maturity stages is essential for properly monitoring, assessing and managing elasmobranch stocks, be it for analysing the given stock structure, for knowing of the size at first sexual maturity of males and females, or for assessing the reproductive potential of individual species' stocks of egg-layers and life-bearers.

It is thus the purpose of the here presented proposal of a maturity stages scale to provide the tool for standardised data sampling. Another maturity scale published by Walker and Witte (1999) was only applied to rajoid skates but may be useful in field work also for other oviparous chondrichthyan species. However, this cited scale distinguishes somewhat simplified only the three stages "immature, adolescent, mature" for females and males, respectively, and does not take into account separate ovarian and uterine stages for the females (see 'Remark' below); further are the three stages for males externally relating mistakenly clasper length to pectoral fins, instead of correctly pelvic fins.

Material and methods

The author's data and experiences were gathered mainly during surveys on board FRV "Walther Herwig" from 1974 to 1986 in the Rockall Trough area and vicinity and Bay of Biscay in the course of a special exploration programme for deep-water resources by the Federal Research Centre for Fisheries Hamburg. Commercial bottom trawls of 140- and 200-foot size, however with a 20 mm mesh size inset in the codend, were systematically fished from the slope edge to a maximum of about 2200 m depth and mostly yielded considerable quantities of squaloid and scyliorhinid deep-water sharks and chimaeroids of various species, but rajoid skates appeared in much smaller numbers generally. All cartilaginous species were registered with weight, number of specimens, their individual length (TL, or BL *sensu* Hardy and Stehmann 1990, for chimaeroids), sex and maturity stage, at least by external recognition for the males, as far as time and catch size did allow. Maturity stages images of such deep-water taxa were mainly taken by the author.

On this basis, the first approach to a standard scheme of maturity stages was developed in the course of the M. Sc. thesis by Hennemann (1985) co-supervised by the author. A little modified version was introduced by Stehmann (1987) for discussion internationally. Another again improved version was later used by partners of the FAIR CT 95/655 EC research project (1995-1998) on deep-water fishery resources, when the German data originating largely from the pre-commercial period were assembled and analysed, including the information about maturity stages (Stehmann 1999).

Further was this maturity stages scale also used by partners of the current EC-CFP Study DELASS and modified again a little, based on field experience gathered by various partners. Additional image material was provided by DELASS partners (IEO and MNHN) and a collaborator of the British Antarctic Survey for oviparous catsharks and skates.

The present paper focuses on demonstrating by *in situ* photographic images the various maturity stages to provide realistic illustrated information for field work, rather than use schematic, more or less generalised drawings. It is thus for purpose, that the extent of illustrations exceeds that of text and tables, although not all stages of females and males could be documented completely and equally in quality. If not labelled with other image author names, photographs were taken by the author, and image copyrights remaining with the author, respectively.

Recommendation

To overcome the largely still existing deficit of reliable data for chondrichthyan fishes and for proper description of, as well as for assessing their stocks, the following minimum requirements for data collecting should be considered, whether on board research or commercial vessels, at landings places and markets and in laboratories ashore:

a) distinguish processed specimens by **sex** – as all male cartilaginous fishes from smallest size on possess paired, rod- or stick-like external copulation organs (claspers) along the inner margins of their pelvic fins, males and females can externally be easily recognized.

b) note at least roughly **sexual maturity stage of males** – again this is easily done by external characteristics. If the claspers are still thin, flexible and short, i.e. not yet exceeding the posterior pelvic fin tips = **immature**; if claspers already extended and broader, with their length more or less exceeding the posterior pelvic fin tips, but with their skeleton still being flexible = **adolescent**, at which stage skate (Rajidae) males would also show first traces on upper wing tips of developing so-called alar thorns; if claspers massive, extending beyond posterior tips of pelvic fins (very distinctly so in rajid skates) and being stiff due to their calcified skeleton, including cartilaginous components in their spread-able tips, = **mature**, at which stage rajid skate males will show a large patch of sharp alar thorns longitudinally across each upper wing tip.

c) take **size/length measurements** of specimens – sharks will usually be measured total length (TL) from snout tip to tip of caudal fin; rajid skates should also be measured TL from snout tip to end of tail, and additionally their greatest width across disc (DW) from one wing tip to the other should be taken; other batoids may be measured TL (sawfishes, guitarfishes, electric rays) or DW (stingrays, eagle rays, devil rays and Mantas); holocephalans (chimaeras), because of their soft snouts and often incomplete whip-like tail ends, should be measured body length (BL) horizontally between level of upper gill slit corner and origin of dorsal caudal fin fold (Hardy and Stehmann 1990).

d) take total catch **weight** per species, plus number of specimens at least; ideally, individual weights should be taken, along with individual sex and length as above.

e) if possible, also define individual maturity stage according to scale introduced here, for which purpose females must be cut open.

Remark

Unlike maturity scales for bony fishes, the here introduced scale for cartilaginous fishes distinguishes for females between three ovarian and three uterine stages. Although these six stages are numbered continuously, this distinction is due to also a reproductive peculiarity of cartilaginous fishes. Ovarian follicles develop within the ovary through the three stages specified in the scale. When finally passing through the Fallopian tubes – and further through the shell glands in oviparous species – into the uteri when being fertilised internally, although mating with a male may have happened a considerable period of time prior to fertilization, the embryonic development continues within either the deposited egg capsules independently (egg-layers) or within the female's uteri with indirect or direct nourishment by the mother (life-bearers).

In oviparous species, the encapsulation of a fertilised ovum and its passage down the uterus until extrusion may in average not take very long, whereas after deposition of the egg capsules on the sea floor the embryonic development until hatching may take a very long time of several months and up to two years under extreme cold water conditions. When normally a pair of egg capsules has been extruded, the next pair of ripe ovarian follicles will pass through the shell glands for encapsulation.

In aplacental and placental viviparous species, the ovarian stages are similar to those in oviparous species, except for their ripening all to the same stage and size mainly in the aplacental species, so that their ovaries can take on huge size (see plate 10, figure 4). The entire number of large, ripe ovarian follicles passes within a short period of time through the Fallopian tubes into the uteri, which then may appear as huge and stuffed with ova as before the ovaries (see plate 11, figures 3 and 4). After fertilization, the embryonic development within the uteri can last a very long time of up to more than a year especially in cold water habitat of aplacental viviparous species, during which period the embryo subsists on the yolk of its individual follicle, until all embryos are full term and littered at the same time (see plate 12, figures 1–3; plate 13, figures 1–3). The latter holds true also for placental viviparous species, or those nourishing embryos by uterine "milk", but usually the number of littered young is lower (often just one or two) in the latter group of species than in the aplacental viviparous ones.

The distinction in the maturity scales between ovarian and uterine stages for females does thus not mean, no activity would happen in the ovaries, while egg capsules are being formed or embryos developing in the uteri. However, ovarian activities are in a way reduced or even on quasi "stand by", as long as follicles are being encapsulated, and especially in aplacental viviparous species the embryos develop a long time within the uteri.

This entire reproductive process in females of cartilaginous fishes has no equivalent in bony fishes, even not in live-bearing species, in which a comparable uterine phase of embryonic development does not exist but embryos hatch from their internally fertilised eggs and grow within the ovaries, until all at the same time are littered through the oviducts.

Scales of maturity stages for sharks, rays and skates, and chimaeras

The maturity scale is here divided into three parts:

Part I: MATURITY SCALE *ELASMO 1* (oviparous sharks, rays and skates, and chimaeras)
Part II: MATURITY SCALE *ELASMO 2* (aplacental and placental viviparous sharks)
Part III: An additional graph displaying Part II maturity stages A - D/G (text figure 1)

MATURITY SCALE *ELASMO 1*

MALES

A or 1 = **immature, juvenile** (plate 3, figs 1-2; plate 6, fig. 2; plate 8, fig. 1)
Claspers undeveloped as small, flexible sticks being much shorter than extreme tips of posterior pelvic fin lobes. Gonads (testes) small, sperm ducts straight and thread-like.

B or 2 = **maturing, adolescent, subadult** (plate 3, fig. 3; plate 8, fig. 2)
Claspers becoming extended, approaching tips of posterior pelvic lobes, as long as or a bit longer than posterior pelvic lobes, their terminal region (glans) becoming structured, but skeleton still soft and flexible. Gonads enlarged, sperm ducts eventually beginning to meander (coil).

C or 3 = **mature, adult** (plate 4, fig. 1; plate 6, fig. 3; plate 7, fig. 2; plate 8, fig. 3)
Claspers full length, as long as or longer than posterior pelvic lobes, their external and internal glans structures fully formed, skeleton hardened so that claspers stiff and glans' free cartilaginous components sharp. Gonads greatly enlarged, sperm ducts meandering over almost their entire length and tightly filled with sperm.

D or 4 = **active, copulating** (plate 4, figs 2 + 3; plate 8, fig. 4)
Glans clasper often dilated, its structures reddish and swollen. Sperm flowing on pressure from cloaca and/or present in clasper groove or glans. Sperm ducts largely as stage C/3 but may be less tightly filled, whereas seminal vesicle may be well filled. For oviparous sharks and chimaeras, this stage does not necessarily mean that the glans is spread open, but fleshy pads are obviously enlarged and sperm is present in clasper grooves.

FEMALES – ovarian stages

A or 1 = **immature, juvenile** (plate 1, fig. 1; plate 5, fig. 1; plate 9, fig. 1)
Ovaries small, their internal structure gelatinous or granulated. No oocytes differentiated or all uniformly small, granular. Oviducts (uteri) narrow, thread-like.

B or 2 = **maturing, adolescent** (plate 1, fig. 2; plate 5, fig. 2; plate 9, fig. 2)
Ovaries somewhat enlarged, walls more transparent. Oocytes becoming differentiated to various small sizes. Uteri largely as stage A/1 but may become widened posteriorly.

C or 3 = **mature, adult** (plate 1, fig. 3; plate 7, fig. 1)
Ovaries large and tight. Oocytes enlarged, with some being very large. Uteri enlarged and widening over nearly their entire length.

FEMALES - uterine stages

D or 4 = **active** (plate 2, fig. 1)
A distinctly large yolk-egg present in one or both Fallopian tubes. No egg capsule yet visible in shell gland, or beginning formation of egg capsule at most.

E or 5 = **advanced** (plate 2, fig. 2; plate 6, fig. 1; plate 9, fig. 3)
Large yolk-eggs in Fallopian tubes, or already passing through into egg capsules. Egg capsules about fully formed in one or both oviducts but still soft at upper end and located very close to Fallopian tubes.

F or 6 = **extruding** (plate 2, fig. 3; plate 7, fig. 3; plate 9, fig. 4)
Completed, hardened egg capsules in one or both oviducts, more or less separated from Fallopian tubes. Skate capsule surface mostly covered with dense silky fibres. Either no enlarged oocytes in Fallopian tubes, or one or two in position. If oviducts empty but still much enlarged and wide, capsules have probably just been extruded - this corresponds with either stage D/4 or E/5.

MATURITY SCALE *ELASMO 2*

See schematic illustration text figure 1.

MALES

A or 1 = **immature, juvenile**
Claspers undeveloped as small, flexible sticks being shorter than extreme tips of posterior pelvic fin lobes. Gonads (testes) small, whitish, sperm ducts straight and thread-like.

B or 2 = **maturing, adolescent, subadult** (plate 14, fig. 3; plate 15, fig. 3)
Claspers becoming extended, longer than tips of posterior pelvic fin lobes, their tips (glans) becoming structured, but their skeleton still soft and flexible. Gonads enlarged, sperm ducts beginning to meander.

C or 3 = **mature, adult** (plate 14, fig. 4; plate 15, figs 1 + 2)
Claspers fully formed and stiff, eventually present cartilaginous hooks, claws or spines of glans free and sharp. Gonads enlarged, well rounded, filled with flowing sperm and often reddish in colour. Sperm ducts tightly coiled and well filled with sperm.

D or 4 = **active**
Glans clasper often dilated and swollen, with free cartilaginous spines mostly erect; sperm flowing from cloaca under pressure on seminal vesicle and/or present in clasper groove.

FEMALES - ovarian stages

A or 1 = **immature, juvenile** (plate 10, fig. 1)
Ovaries small, their internal structure gelatinous or granulated. No oocytes differentiated or all uniformly small, granular. Oviducts (uteri) narrow, thread-like.

B or 2 = **maturing, adolescent** (plate 10, figs 2 + 3)
Ovaries somewhat enlarged, walls more transparent. Oocytes becoming differentiated to various small sizes. Uteri largely as stage A/1 but may become widened posteriorly. Ovaries at first maturity will not show *corpora lutea*, or a very few only,

whereas ovaries of resting females prior to repeated reproduction will show *corpora lutea* in greater number.

C or 3 = **mature, adult** (plate 10, fig. 4; plate 11, figs 1 + 2)
Ovaries large, well rounded. Oocytes obviously enlarged, all to about the same size, can easily be counted and measured.

FEMALES - uterine stages

D or 4 = **developing** (plate 11, fig. 3)
Uteri well filled and rounded with seemingly unsegmented yolk content ("candle")

E or 5 = **differentiating** (plate 11, figs 3 + 4; plate 12, figs 1-3)
Uteri well filled and rounded with segmented content of large yolk balls, can easily be counted and measured. Embryos variously small, atop their huge yolk balls, larger ones with external gills filaments and unpigmented (still "candle").
(Stages D and E, or 4 and 5, have for convenience been rather artificially separated and might be seen also as substages of one and the same stage D/E, or 4/5)

F or 6 = **expecting** (plate 13, figs 1-3)
Embryos more or less fully formed, pigmented, external gill filaments lost, yolk sacs obviously reduced. Can be counted, measured and sexed easily.

G or 7 = **post-natal, spent** (plate 14, figs 1 + 2)
Ovaries at resting stage, similar to stages A/1 or B/2. Uteri empty but still widened considerably over their full length in contrast to stages A/1 or B/2.

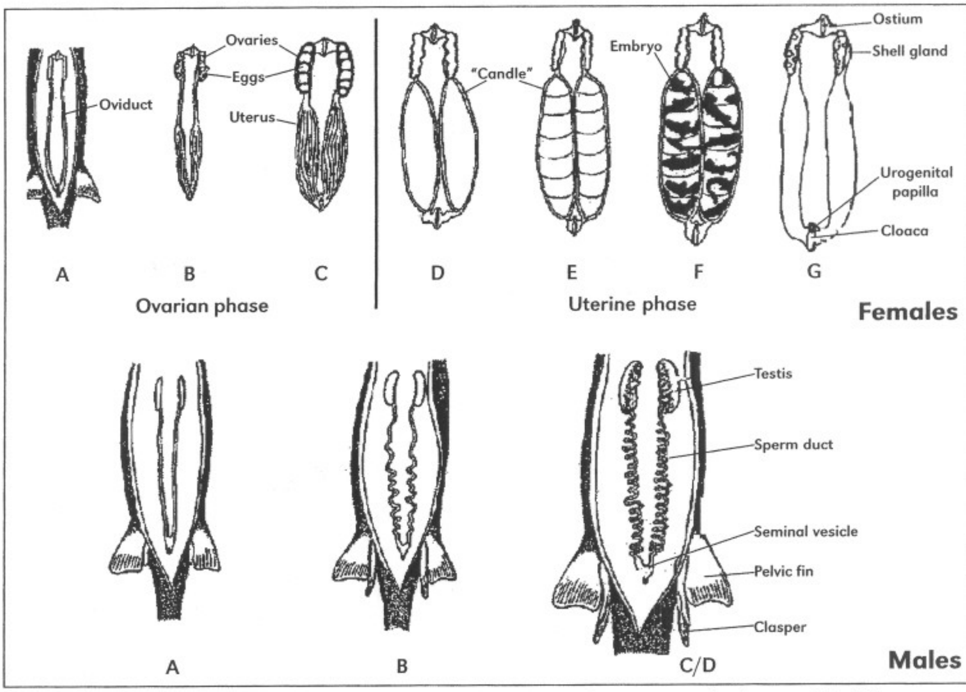

Figure 1. Schematically illustrated maturity stages for aplacental viviparous sharks, modified from example in unpublished M. Sc. thesis by Hennemann (1985).

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Acknowledgements

Thanks to R. M. Hennemann for inspiring discussions during the period of his M.Sc. thesis preparation. I am grateful to Dr. I. Olaco and M. Sc. Cristina Cabello (IEO, Santander), M. Sc. Béatrice Pleven and Dr. Marine Girard (MNHN, Concarneau), and to M.Sc. Michael Endicott (BAS, UK) for having provided maturity stages images reproduced in the colour plates. Lic. M. Cristina Oddone and M.Sc. Gonzalo Velasco (FURG, Brazil) have kindly assisted with preparing the abstracts in Spanish and Portuguese, respectively. Thanks also to various colleagues of the FAIR CT 95/655 and DELASS CT 99/055 EC projects, who helped to improve previous versions of the maturity scales, and to Dr. C. M. Vooren (FURG, Brazil) for helpful comments on a first draft. Colour printing of the plates was supported by the EC DELASS project.

Author's address: Dr. Matthias F. W. Stehmann, Bundesforschungsanstalt für Fischerei, Institut für Seefischerei, Palmaille 9, D – 22767 Hamburg, Germany. E-mail: M.Stehmann@ichthys-fisch.info

Communicated by G. Hubold; received: 28th February 2002, accepted: 10 July 2002; print proof received from author: 21th August 2002.

Plate 1

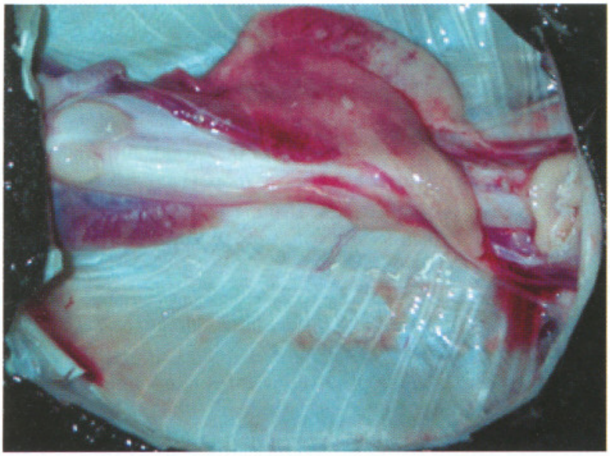


Figure 1:
Amblyraja sp.
Female: stage A/1.

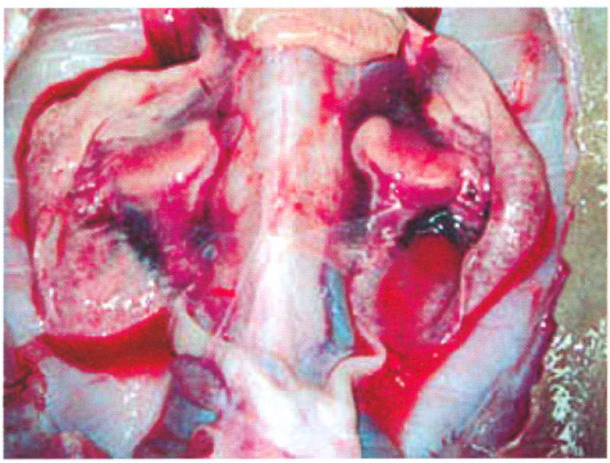


Figure 2:
Amblyraja sp.
Female: stage B/2.

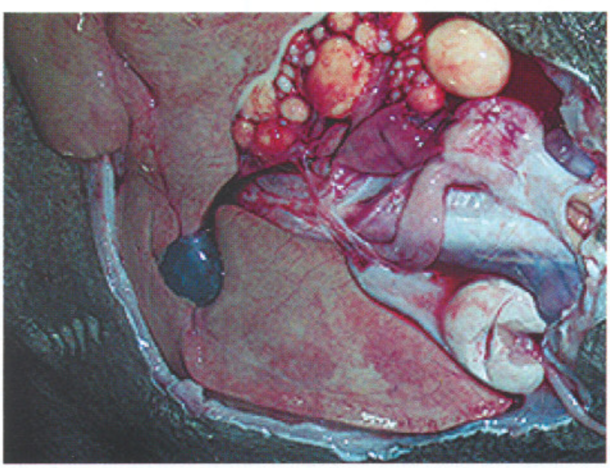


Figure 3:
Amblyraja sp.
Female: stage C/3.

Plate 2

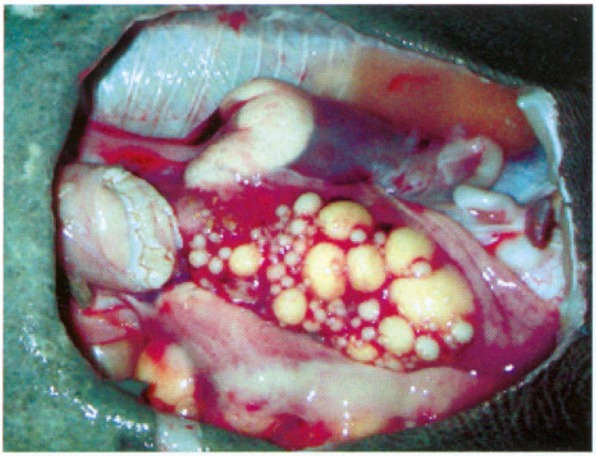


Figure 1:
Amblyraja sp.
Female: stage D/4.

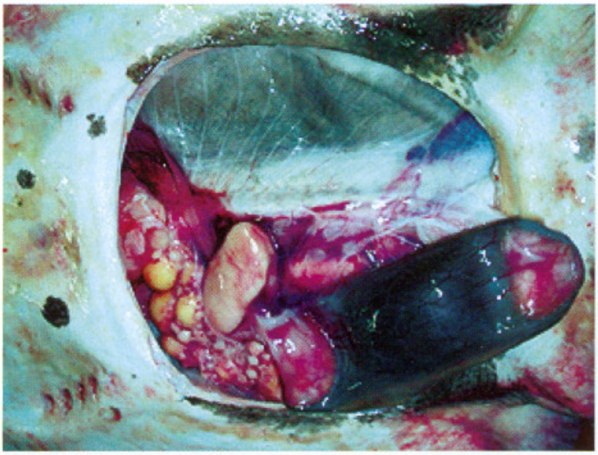


Figure 2:
Amblyraja sp.
Female: stage E/5.

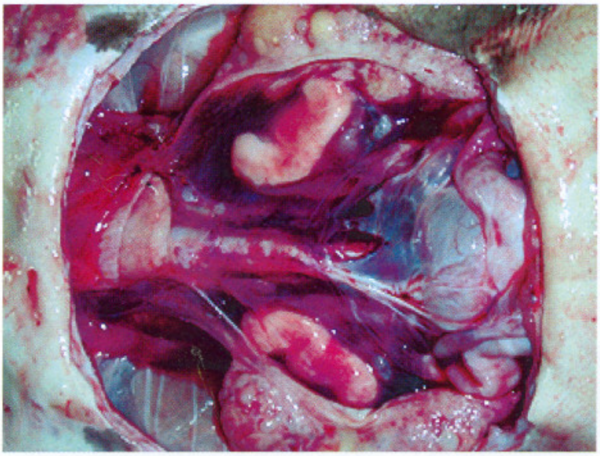


Figure 3:
Amblyraja sp.
Female: stage F/6.

Plate 3

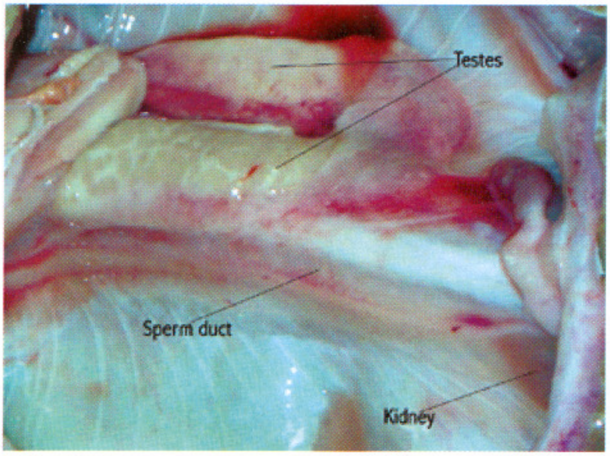


Figure 1:
Amblyraja sp.
Male: stage A/1.

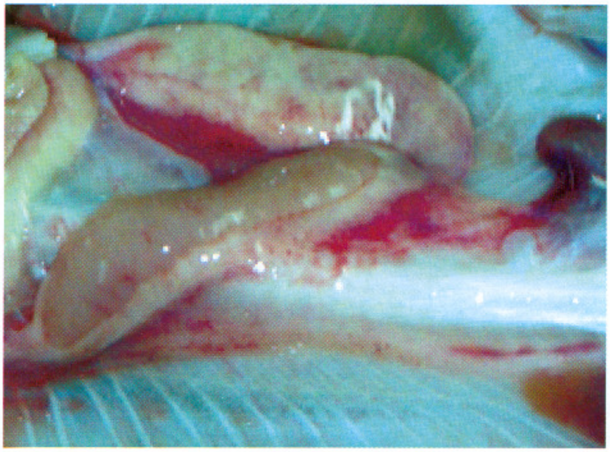


Figure 2:
Amblyraja sp.
Male: stage A/1.

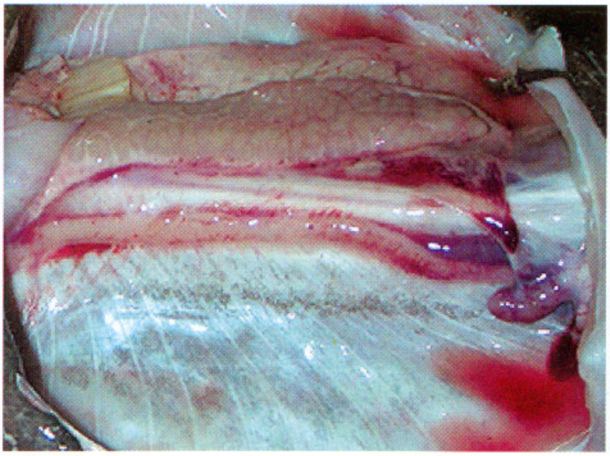


Figure 3:
Amblyraja sp.
Male: stage B/2.

Plate 4

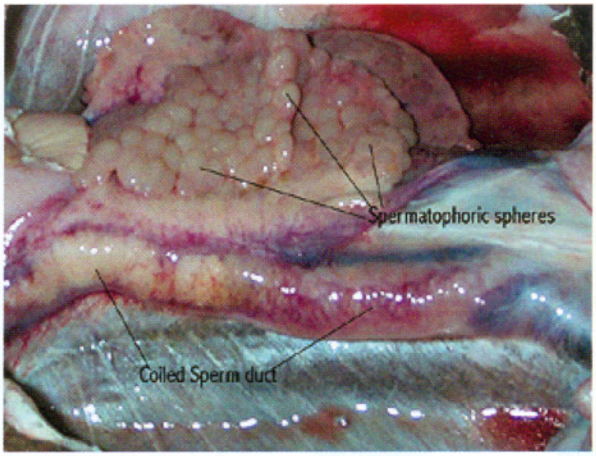


Figure 1:
Amblyraja sp.
Male: stage C/3.

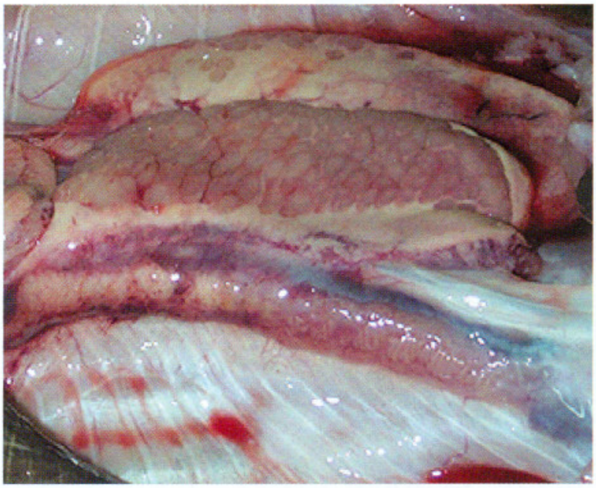


Figure 2:
Amblyraja sp.
Male: stage D/4.

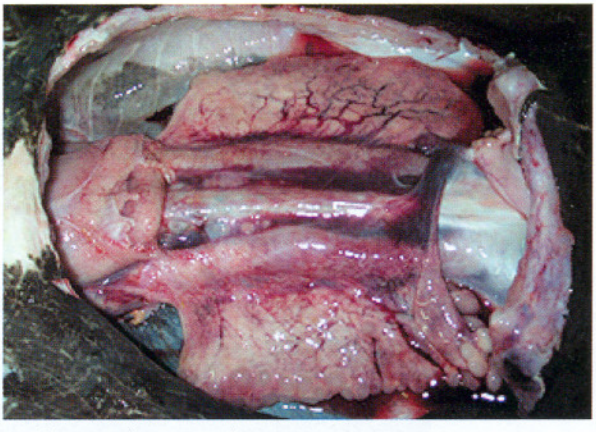
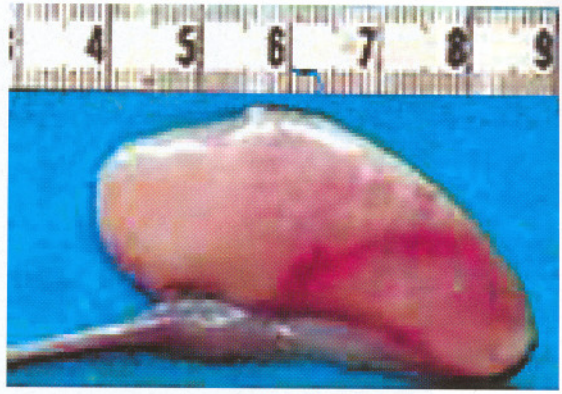


Figure 3:
Amblyraja sp.
Male: stage D/4.

Plate 5



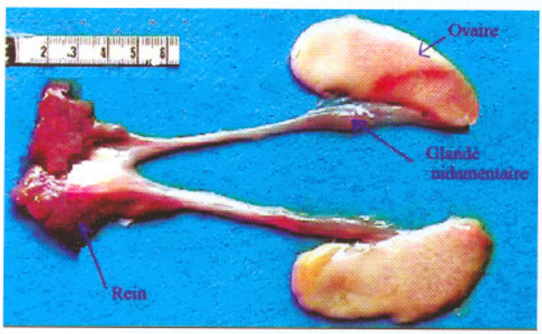


Figure 1: *Leucoraja naevus*, gonades.
Left: 55.6 cm TL. Female: stage A/1.
Right: right ovary stage A/1 in close up.

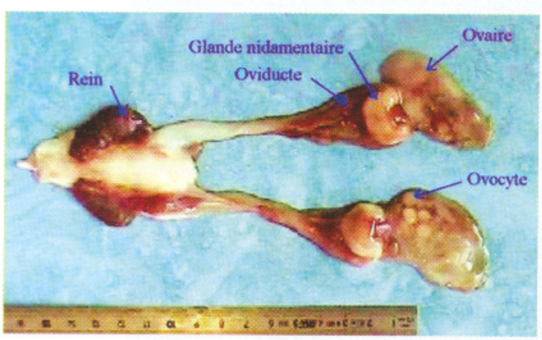


Figure 2: *Leucoraja naevus*, gonades.
Left: 59.6 cm TL. Female: stage B/2.
Right: left ovary stage B/2 in close up.

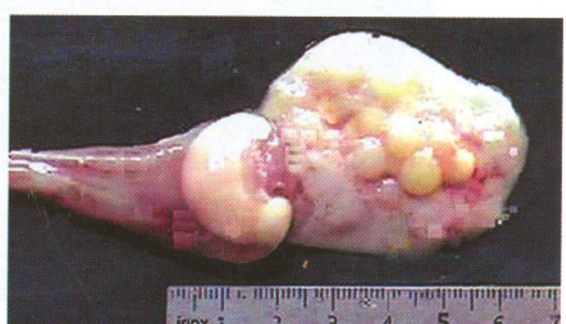


Plate 6

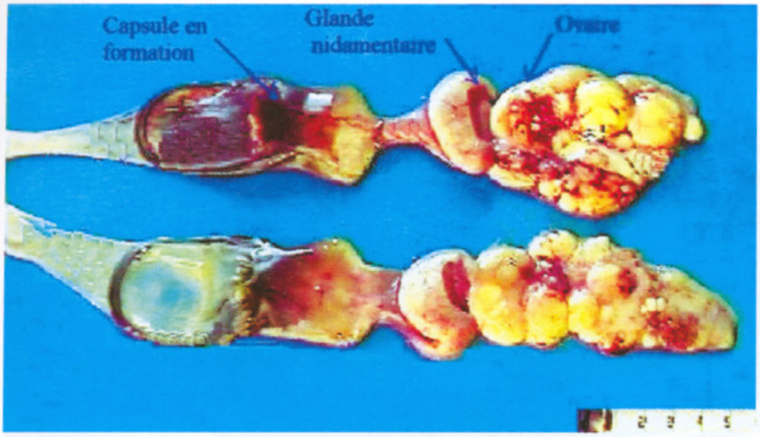


Figure 1:
Leucoraja naevus,
gonades, 71 cm TL
Female: stage E/5.

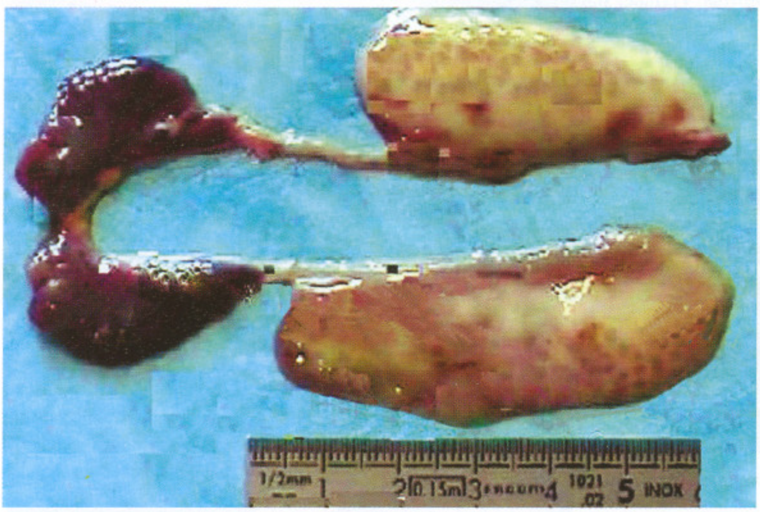


Figure 2:
Leucoraja naevus,
gonades,
Male: stage A/1.

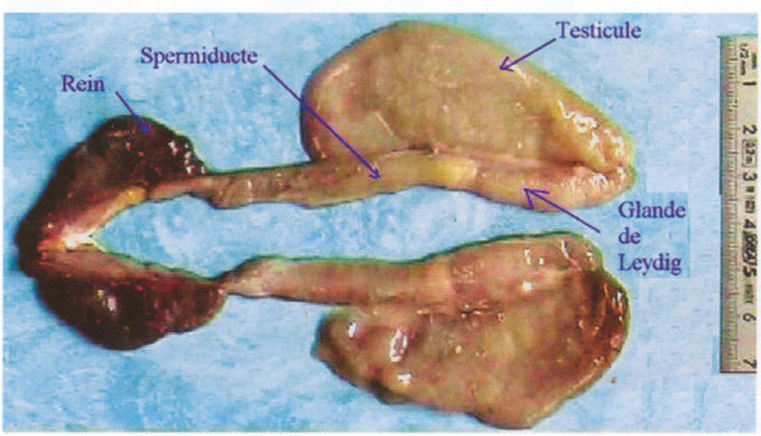


Figure 3:
Leucoraja naevus,
gonades,
Male: stage C/3.

Plate 7

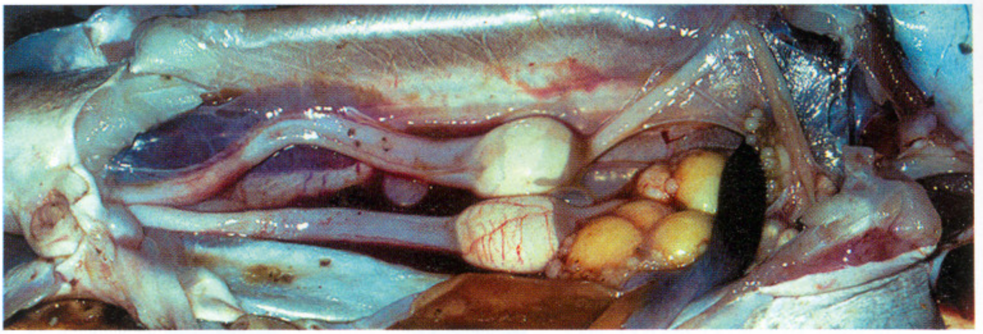


Figure 1: *Chimaera monstrosa*. Female: stage C/3.

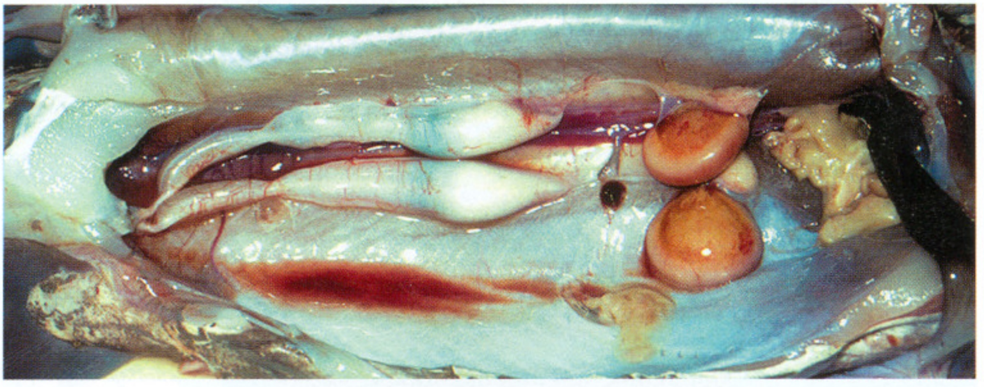


Figure 2: *Chimaera monstrosa*. Male: stage C/3.

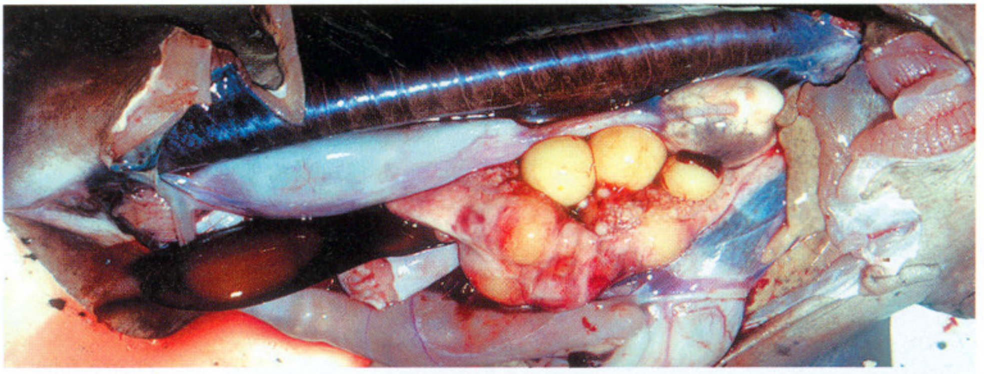


Figure 3: *Galeus melastomus*. Female: stage F/6.

Plate 8

Figure 1: *Scyliorhinus canicula*
Male: stage A/1

Figure 2: *Scyliorhinus canicula*
Male: stage B/2.

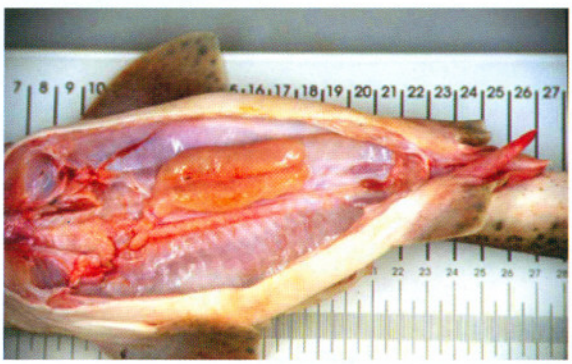


Figure 3: *Scyliorhinus canicula*
Male: stage C/3.

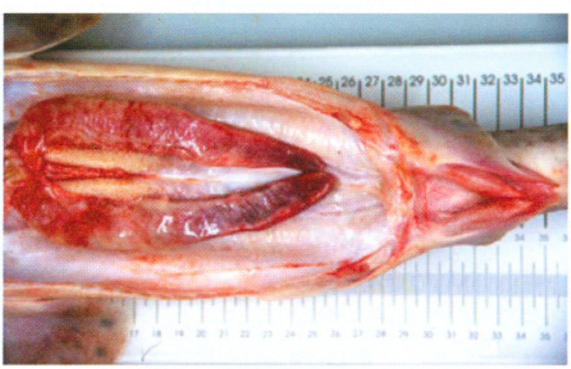


Figure 4: *Scyliorhinus canicula*
Male: stage D/4.

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Plate 9

Figure 1: *Scyliorhinus canicula*
Female: stage A/1

Figure 2: *Scyliorhinus canicula*
Female: stage B/2.

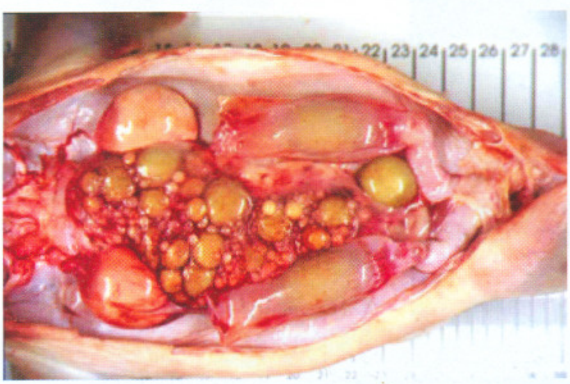

Figure 3: *Scyliorhinus canicula*
Female: stage E/5.

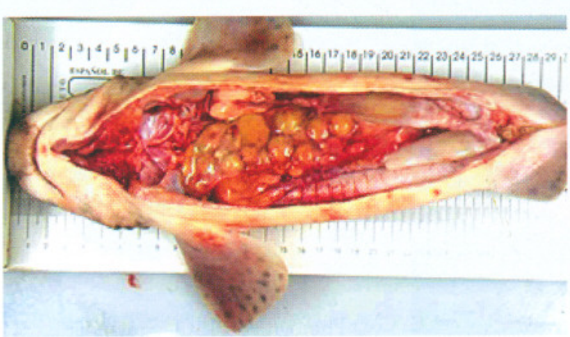

Figure 4: *Scyliorhinus canicula*
Female: stage F/6.

Plate 10

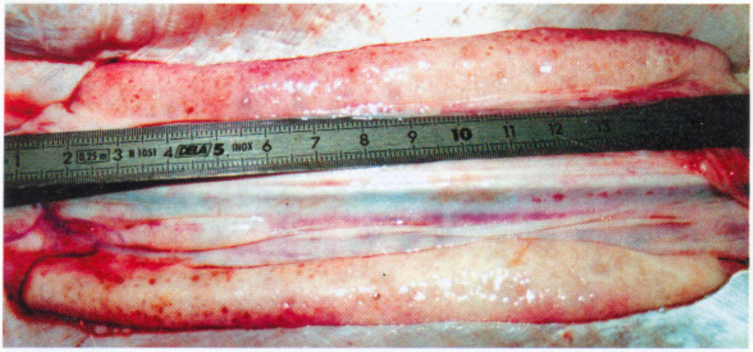

Figure 1:
Centrophorus squamosus
Female: stage A /1.

Figure 2:
Centroscymnus coelolepis
Female: stage B/2.

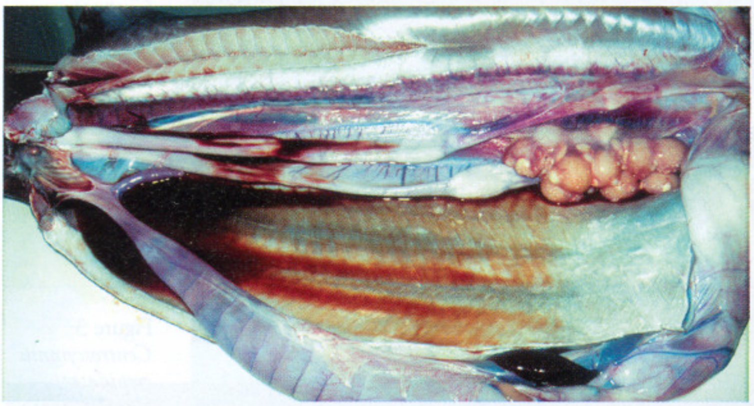

Figure 3:
Centrophorus squamosus
Female: stage B/2.

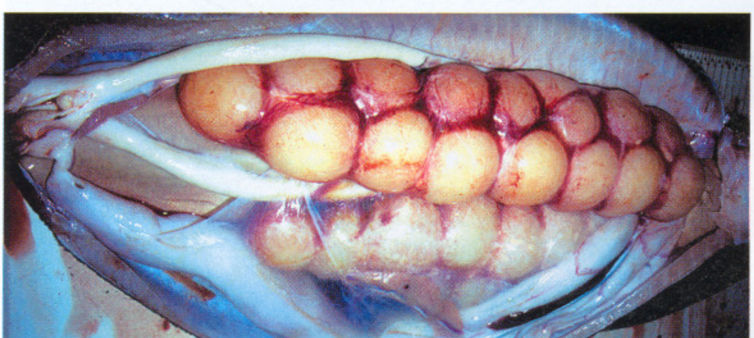

Figure 4:
Centroscymnus coelolepis
Female: stage C/3.

Plate 11

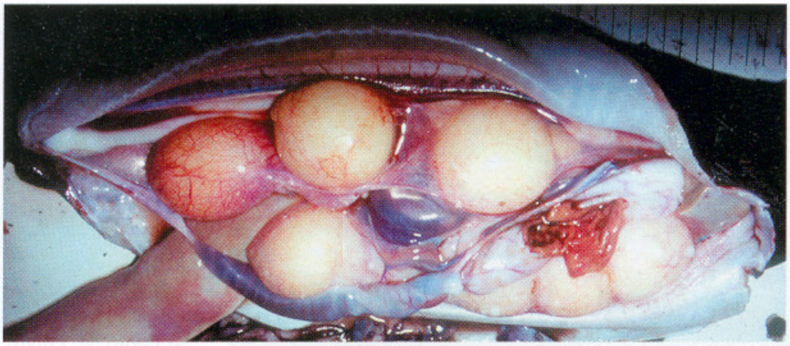

Figure 1:
Centroscymnus crepidater
Female: stage C/3.

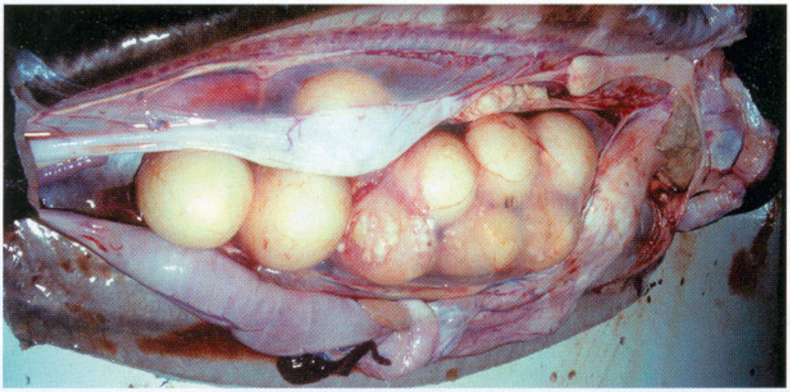

Figure 2:
Centrophorus squamosus
Female: stage C/3.

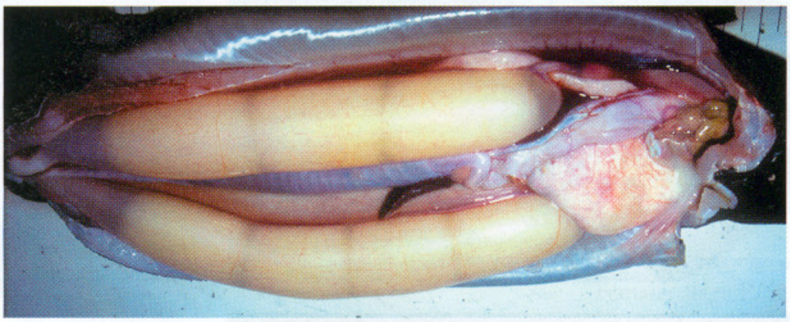

Figure 3:
Centroscymnus crepidater
Female: stage D/4 – E/5.

Figure 4:
Centroscymnus coelolepis
Female: stage E/5.
© Photo:
M. Girard

Plate 12

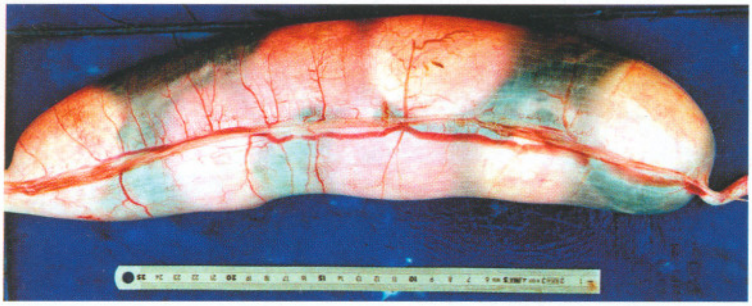

Figure 1:
Centroscymnus coelolepis
Female: stage E/5, uterus.
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Figure 2:
Centroscyllium fabricii
Female: stage E/5.
Early embryos, close up.

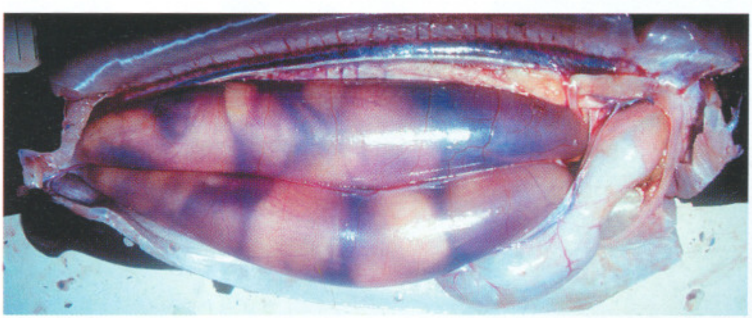

Figure 3:
Centroscyllium fabricii
Female: stage E/5.

Plate 13

Figure 1:
Centroscymnus crepidater
Female: stage F/6

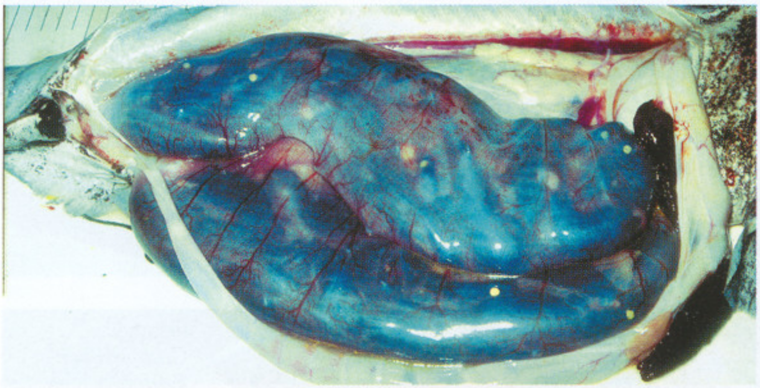

Figure 2:
Centroscyllium fabricii
Female: stage F/6.

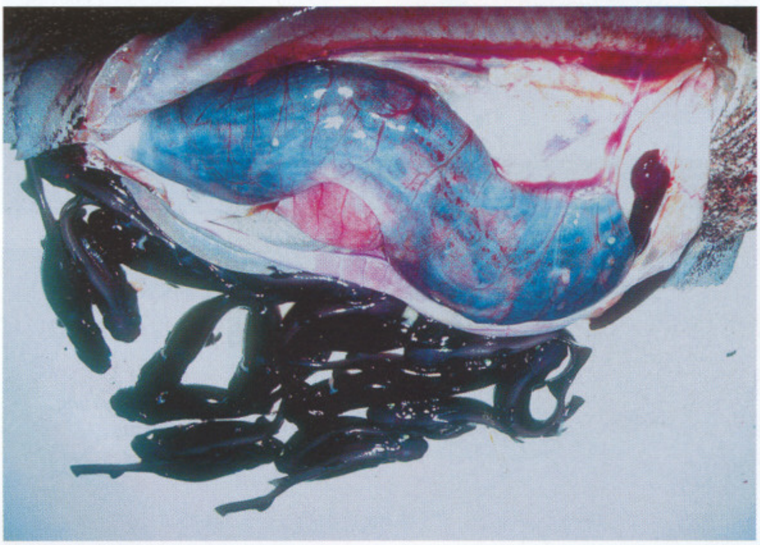

Figure 3:
Centroscyllium fabricii
Female: stage F/6.

Plate 14

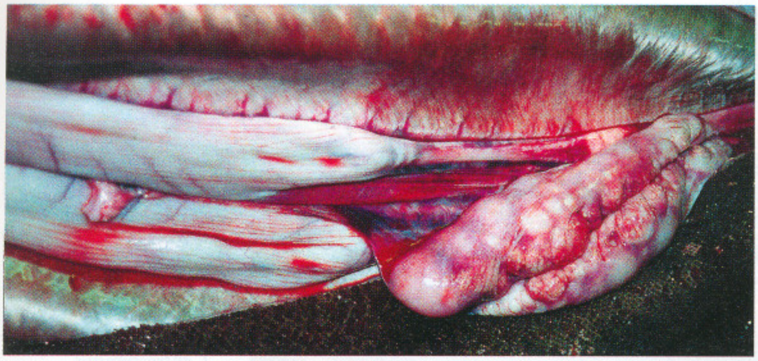

Figure 1:
Centrophorus squamosus
Female: stage G/7
© Photo M. Girard

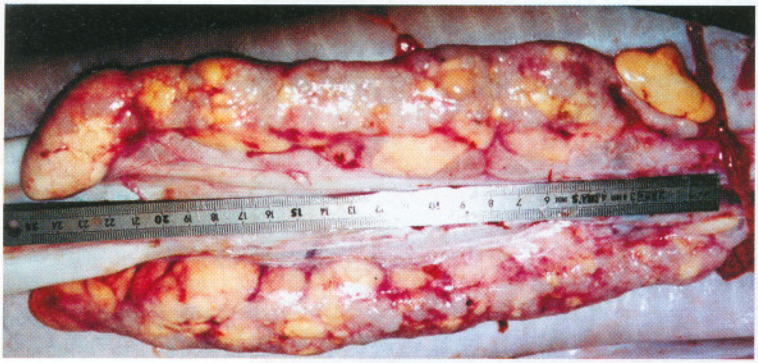

Figure 2:
Centrophorus squamosus
Female: stage G/7, ovaries.
© Photo M. Girard

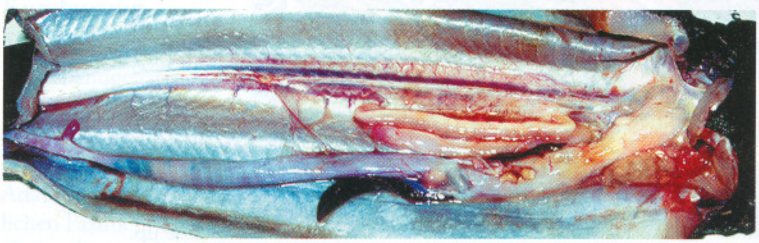

Figure 3:
Centroscymnus crepidater
Male: stage B/2.

Figure 4:
Centrophorus squamosus
Male: clasper stage C/3.
© Photo M. Girard

Plate 15

Figure 1:
Centroscymnus coelolepis
Male: stage C/3.

Figure 2:
Centroscymnus coelolepis
Male: stage C/3, close up.

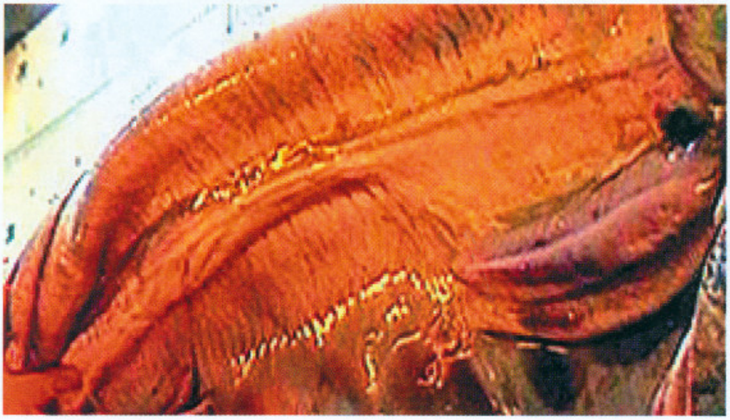

Figure 3:
Pseudotriakis microdon
Male: stage B/2